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Structure and Usage of the Vocal Repertoire of *Callithrix jacchus*

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Abstract We recorded the vocal repertoire and behavior of individuals from 3 groups of wild common marmosets (*Callithrix jacchus*) via focal sampling and *ad libitum* sampling in a fragment of Atlantic Rain Forest in Pernambuco, northeast Brazil. Our aims were: 1) to provide a detailed quantitative description of the vocalizations and vocal repertoire of common marmosets in the wild, and to compare the repertoire with that described from conspecific captives; 2) to investigate if differences exist in vocal repertoire between wild individuals of different ages; and 3) to explore the behavioral contexts associated with specific vocalizations in free-living *Callithrix jacchus*. This is the first study describing common marmoset calls in the wild and it shows that their vocal repertoire comprises 13 different calls. Though wild and captive calls were similar, differences occurred in the form of the alarm calls given for different potential predators, the *tsê* call, and very brief whistle. In addition, the tsee call did not occur in wild individuals and wild infants did not utter the twitter call. The age of the subjects influenced the call types present in the vocal repertoire, e.g., the loud cry was specific to infants, whereas only adults gave alarm calls. The behavior of both the caller and the potential receivers seemed to affect the frequency of wild common marmoset calls. One could predict intricate vocalization-based communications for the system based on their relatively complex social organization and densely leafed arboreal habitat. Our study confirms the prediction.

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Introduction

Primates communicate via olfactory, visual, and auditory signals (Napier and Napier 1996). Vocal signals are a particularly important tool for communication in arboreal social primates, owing to the poor visibility in their habitats (Altmann 1967). Understanding the vocalizations of primates is an important step to understand better their behavior, sociality, and ecology.

According to Ghanzafar and Hauser (2001), differences in the structure of vocalizations may occur not only interspecifically but also intraspecifically, between sexes, within sexes, and between groups. Information about the age and sex of a vocalizing individual, and clear considerations of the behavioral and environmental context of the vocalization, are prerequisites to ascertain its function (Bradbury and Vehrencamp 1998; McLanahan and Green 1977). Within a repertoire of vocalizations, individual calls are often associated with specific behaviors. For example, vervets (*Cercopithecus aethiops*) produce different predator alarm calls depending on the type of predator, which result in predator-specific responses by the group (Cheney and Seyfarth 1990); cotton-top tamarins (*Saguinus oedipus*) emit short, high-pitched calls during foraging, which seem to be related to individual food preferences (Roush and Snowdon 1999); and infant *Cebuella pygmaea* make babbling calls that are an immature version of adult vocal signals. The babbling calls seem to be related to social interactions and the infants that use them more frequently are also the ones that are carried more often by older group members (Snowdon 2001).

Callitrichid species, in general, have a large and varied vocal repertoire (Cleveland and Snowdon 1982; McLanahan and Green 1977; Pook 1976, 1977). The use of vocalizations differs from species to species, in part reflecting the variations in their social organization and ecology (Pook 1977). Species with more complex social systems have the most diverse vocalizations (Bradbury and Vehrencamp 1998). Accordingly, common marmosets (*Callithrix jacchus*) have a wide repertoire of vocalizations (Epple 1968; Pook 1977; Winter 1977; Winter and Rothe 1979; all based on captive individuals) because they possess a relatively complex social system (Bezerra *et al.* 2007; Digby 1995; Smith 2006) and live in an arboreal habitat (Stevenson and Rylands 1988). The acoustic structure of the *phee* calls in captive common marmosets can even reveal information about sex of the caller and the behavioral and social context of the call (Jones *et al.* 1993; Norcross and Newman 1993; Norcross *et al.* 1999).

There has been no prior published study on the vocal repertoire of common marmosets in the wild. Carrying out such a study is important because captivity alters and limits the behavior of many mammals (McPhee 2003). Moreover, the changes appear to be specially pronounced in primates (Boere 2001), wherein the connection between the natural environment and the individuals' ethology is too complex to reproduce fully under captive conditions. It is possible then that captive conditions affect the vocalization of common marmosets.

Our main objectives were to provide a first detailed quantitative description of the vocalizations and vocal repertoire of common marmosets in the wild, and to compare the repertoire with that described from conspecific captives. Further, we investigated whether differences exist in vocal repertoire between wild individuals of different ages, and explored the behavioral contexts associated with specific vocalizations in wild-living *Callithrix jacchus*.

Methods

Study Site

We conducted the study in a 32-ha fragment of Atlantic rain forest in Camaragibe, Pernambuco, northeast Brazil (7°56′97″S, 35°1′23″W: Souto *et al.* 2007). We observed the subjects in the forest and in the gardens, which also provided food for the marmosets owing to the presence of fruit and gum trees.

Subjects

We studied 30 individuals in 3 social groups. Before we took observations, we classified the subjects into 3 broad age categories per Stevenson and Rylands (1988): adults (>15 mo: 17 individuals); juveniles (6–10 mo: 6 individuals) and infants (0–5 mo: 7 individuals). All subjects were free-living.

We identified the subjects without capture, by their natural features (size and color of the ear-tufts, scars, natural mutilations, and pelage coloration). In 2 twin infants, we cut a small portion of the tail fur once every 40 d to facilitate identification (Souto *et al.* 2007). Data collection in the study site has been in progress since 2001 and the individuals are well habituated to the presence of observers. We collected data daily during December 2004–April 2005 and July–September 2005.

Recording Vocal Repertoires

We used focal individual and *ad libitum* sampling techniques (Altmann 1974) to obtain recordings of the vocal repertoire. We made all recordings between 0500 and 1730 h (the daylight hours). To record behaviors and calls, we used a digital camcorder (Panasonic PV-GS400). Researchers have used camcorders to record vocalizations to study marine mammals (Dudzinnski 1998, 1999; Herzing 1996), but less so to study terrestrial ones (*cf.* Taglialatela *et al.* 2003: *Pan paniscus*). However, the advantage of using a video camera is the presence of simultaneous-linked audio and video records for subsequent behavioral analysis (Taglialatela *et al.* 2003). Accordingly, we recorded vocalizations via an AKG C1000S II hypercardioid microphone (linear frequency response range 50 Hz−20 kHz), which is well suited for camcorders (Shopmann 1999). We connected the microphone to the camcorder, which had a linear frequency response within the range of 50 Hz−20 kHz (at a 16-bit quantization and 48-kHz sampling rate: Biebel 2004). A sampling frequency of 48 kHz can result in a reliable frequency response of up to 22 kHz. We used a Hosa® cable to connect the microphone with the camcorder and earphones (Intersound, linear frequency response within the range of 20 Hz–20 kHz), the latter to monitor the sound while recording. The system is sufficient both to capture the behaviors of the subjects and the full bandwidth of the fundamental frequencies of their vocalizations.

We conducted the recordings at 2–5 m from the subjects. Once we acquired the vocalizations, we digitally transferred them, via Fire Wire Cable, from the video camera to a PC, through MediaStudio Pro 6.5 (Ulead System), set to capture DV 1 at 16 bits and at 48-kHz sampling rate. We saved each vocalization as an uncompressed WAV file and then analyzed it via SYRINX-PC sound-analysis software (J. Burt, Seattle, Washington; available upon request), from which we produced sonograms. In a sonogram a vocalization is graphically represented as frequency against time (Omedes Regas 1983; Owren and Linker 1995). We recorded >1000 vocalizations in total. After the removal of ones with excessive background noise, 754 remained for analysis. The physical characteristics used to describe the vocalizations are: the number of call units, call unit duration, duration of intercall unit interval, the highest frequency of the vocalization (maximum frequency of the call), the lowest frequency (minimum frequency of the call), the range of frequencies, the start and end frequencies, the duration from the start of the vocalization to the highest frequency, the duration from the time of the highest frequency to the end of the vocalization, the number of harmonics in the vocalization (≤22 kHz), and the interval between harmonics. We extracted these measures from the sonograms per Jones *et al.* (1993), Newton-Fisher *et al.* (1993), and Norcross *et al.* (1999).

Owing to background noise, e.g., wind, bird, and insect sounds, we were not able to generate sonograms for all call types of juveniles and infants. However, we included them in the description of the vocal repertoires of juveniles and infants. We used the existing vocal repertoires for captive common marmosets as a starting point for our description and afterwards we matched the vocalizations with the known ones. The sonograms of the different call types (Fig. 1), together with the physical characteristics (Table 1), and the brief description of each call type provide a detailed description of the vocal repertoire of wild common marmosets.

Recording the Frequency of Behaviors

Bezerra used focal sampling (Altmann 1974) to record the frequency of behaviors in the subjects. She conducted all observations between 0500 and 1730 h, with subjects at ≤5 m because from greater distances some of the vocalizations were not clearly audible. Bezerra dictated information on the observations —date, time, location, description of the behaviors and/or vocalizations, initial behavior and responses— onto a tape via a Sony-M-529V recorder during 5-min sessions of the focal individual, and recorded subjects within the vicinity of the focal individual (≤5 m). Bezerra conducted a total of 1105 observational sessions from December 2004 to April 2005, in 338 h 36 min of fieldwork. The dictations did not appear to disturb the subjects. We considered a vocalization as initial when it followed ≥10 s of vocal

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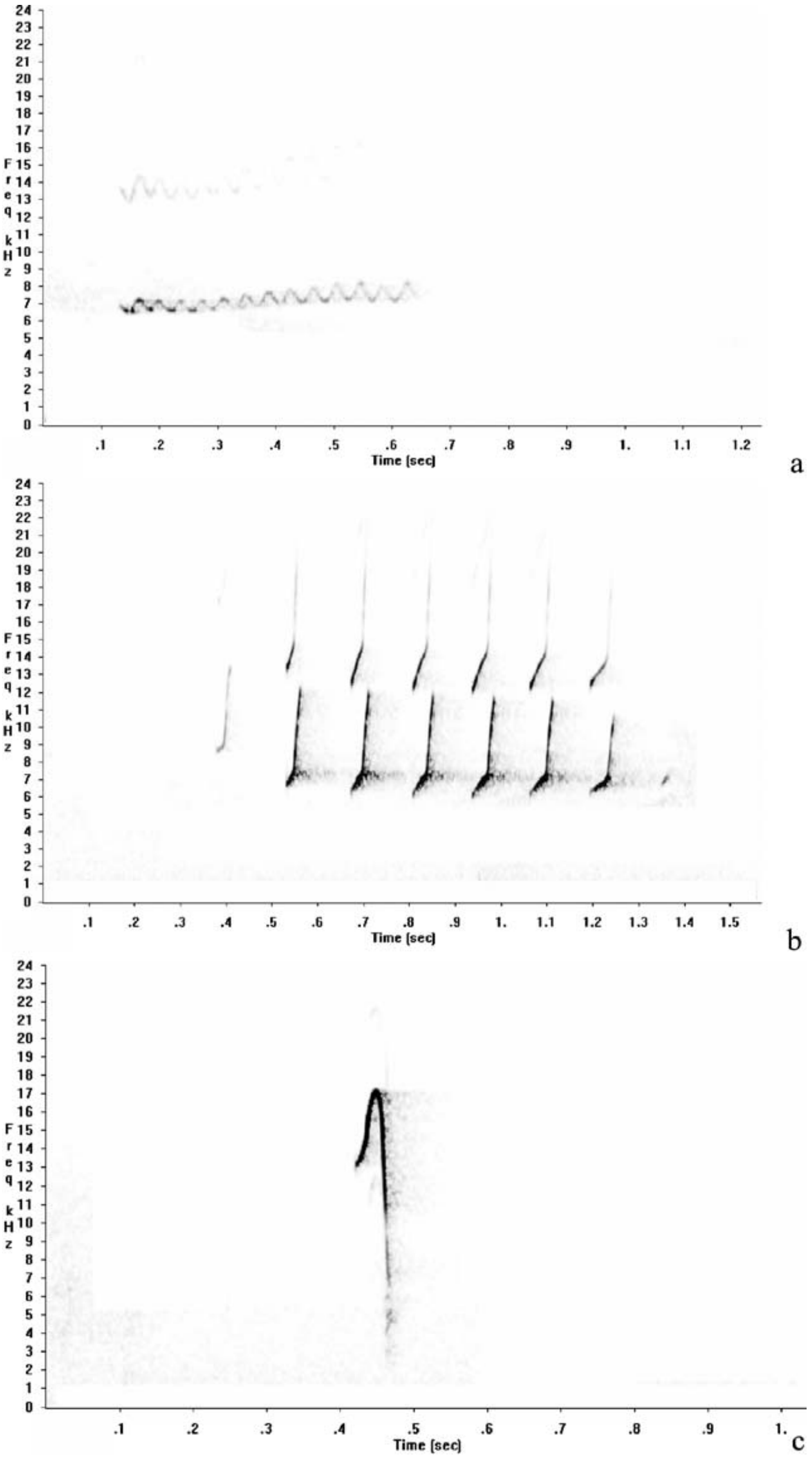
Fig. 1 Sonograms of wild common marmoset vocalizations. (**a**) Trill; (**b**) twitter; (**c**) *tsik*; (**d**) *tsê*; (**e**) *egg*; (**f**) chatter; (**g**) submissive squeal; (**h**) loud squeal; (**i**) moaning; (**j**) very brief whistle; (**k**) alarm 1; (**l**) alarm 2; (**m**) scream; (**n**) long *phee* call + brief phee call 1; (**o**) brief *phee* call 2; (**p**) brief *phee* call 3. ▶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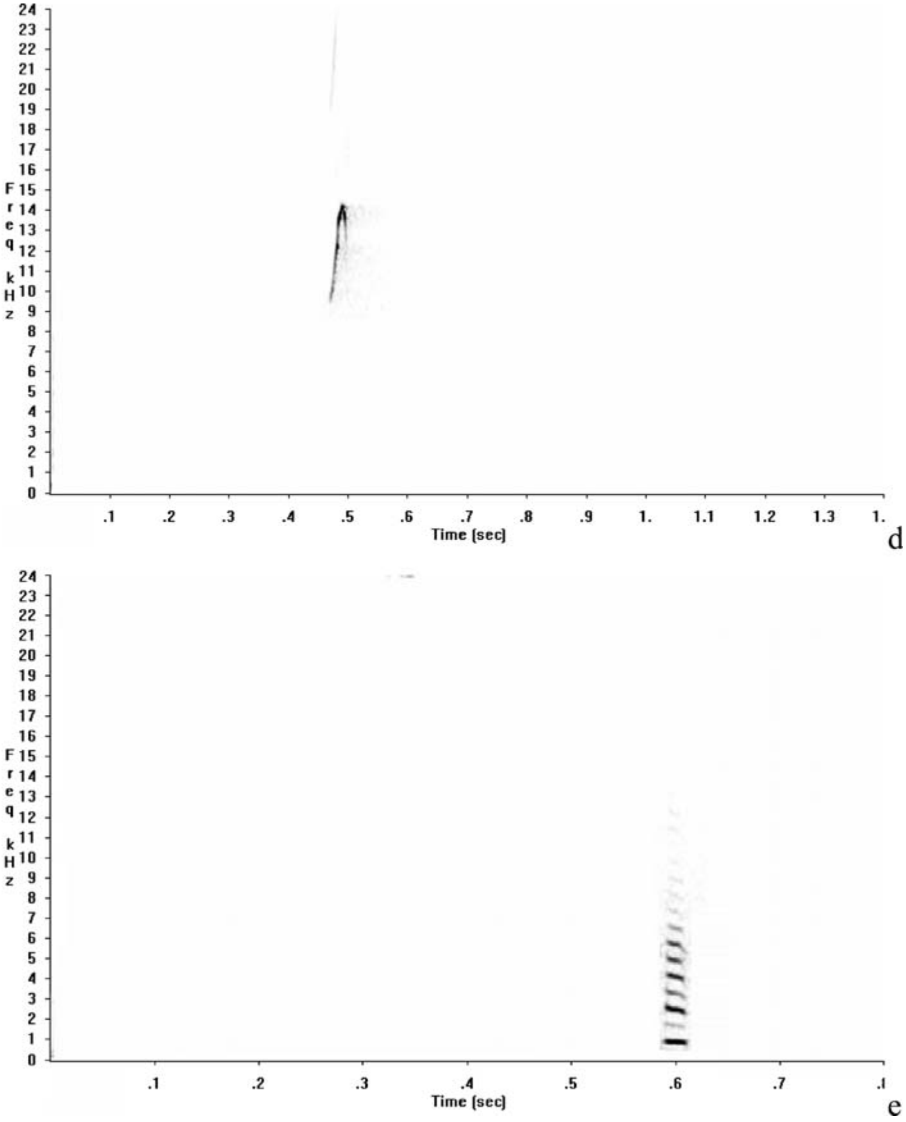
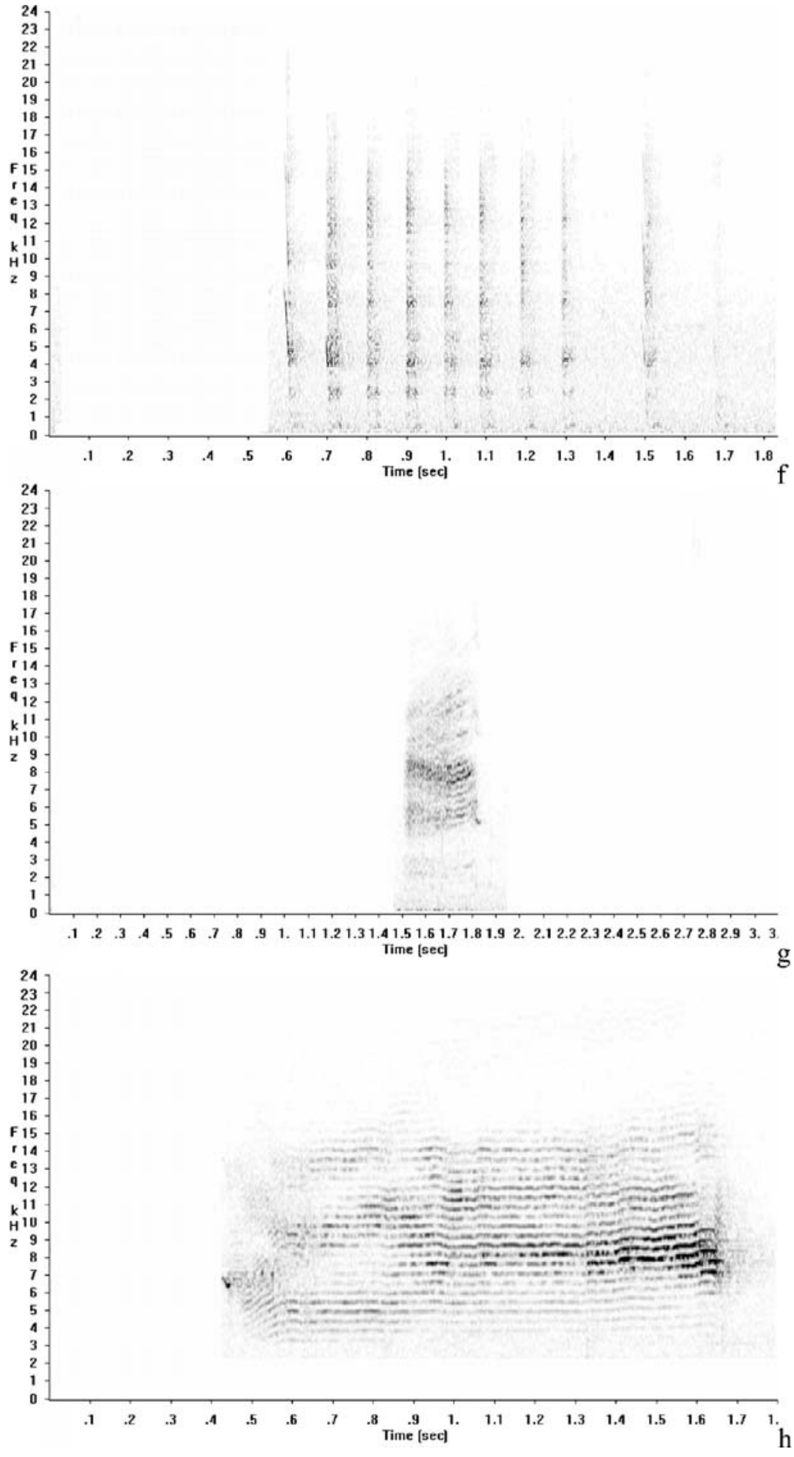


Fig. 1 (continued).

silence and as a response when it was performed ≤4 s of an initial vocalization. We considered a behavior as a response when the subject performed it ≤4 s of an initial vocalization (Soltis *et al.* 2002). In addition, we selected common behaviors to ascertain the behavioral contexts associated with certain vocalizations. The production and usage of long distance calls in neotropical primates can have both intragroup and intergroup functions (Oliveira and Ades 2004). Individuals use long-distance calls for mate attraction, defense and territorial behavior (Norcross and Newman 1993). Oliveira and Ades (2004) suggested that an understanding on long-distance calls can even contribute insights into the evolution of communicative



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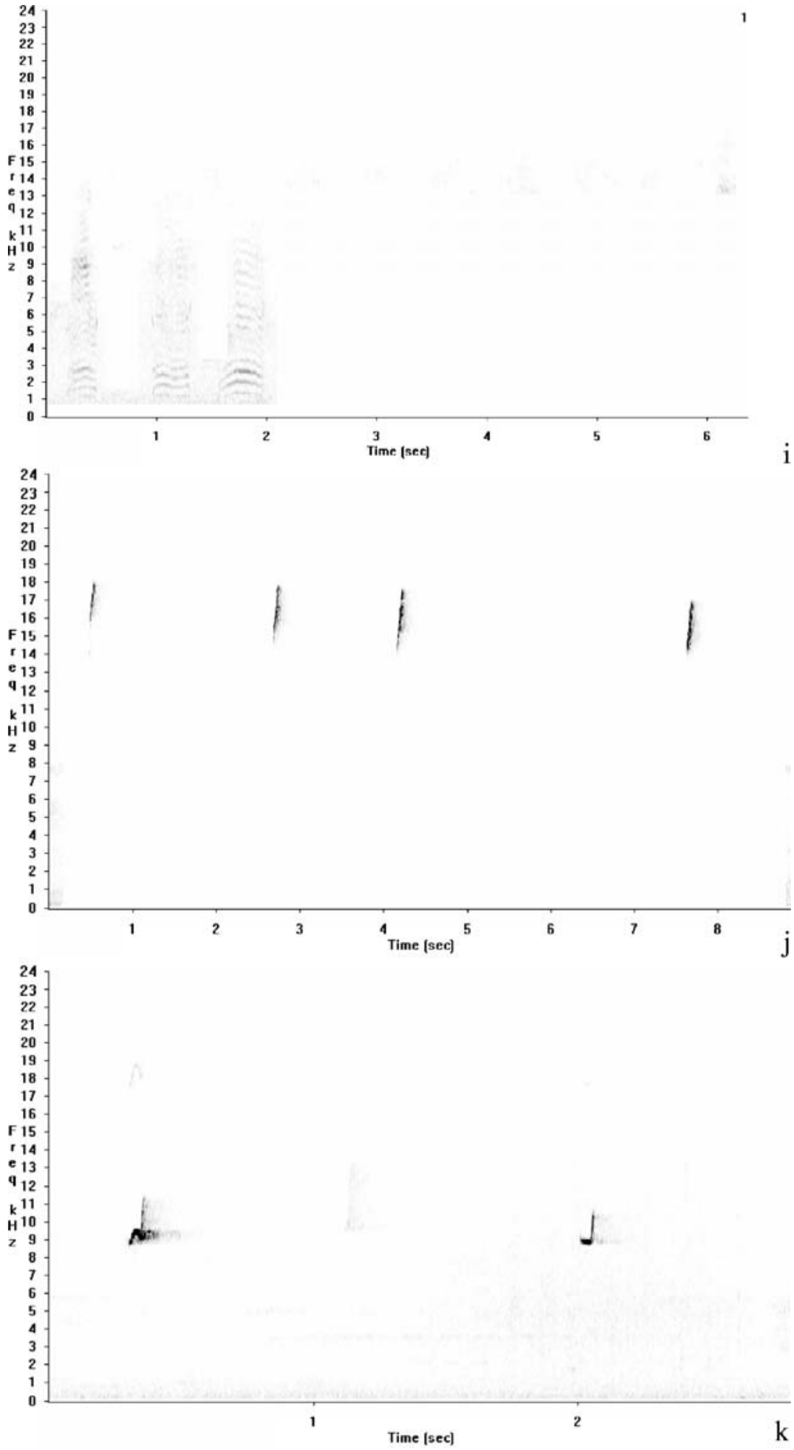

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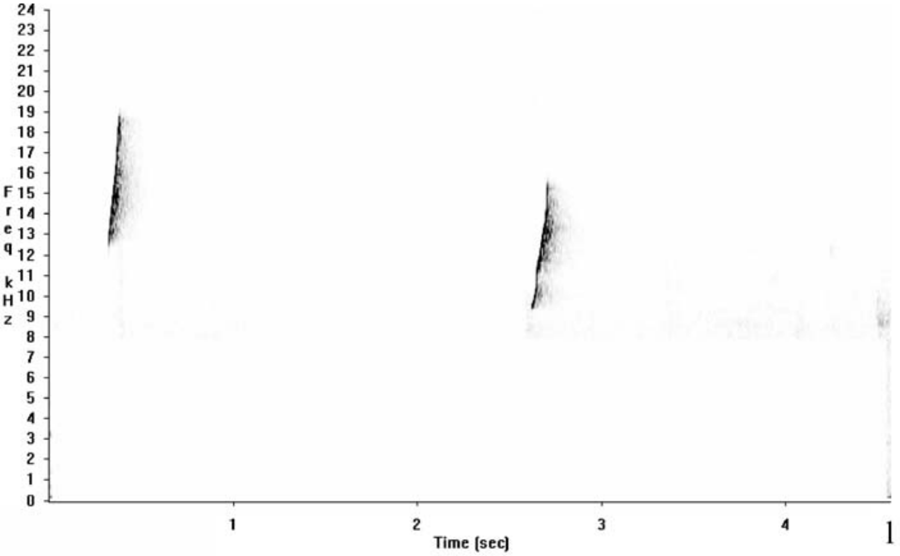

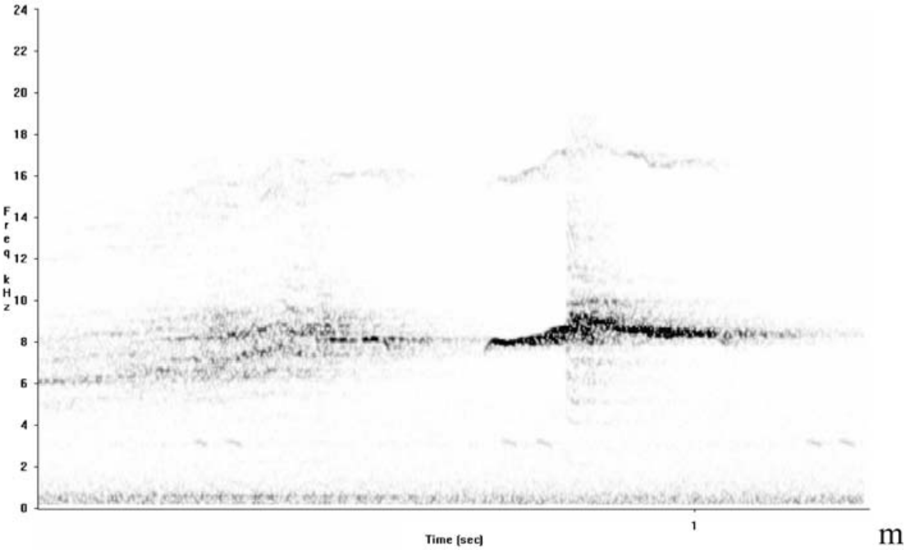

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signals, because they travel for long distances, losing minimum information and achieving a specific function. Thus, considering the importance of the long-distance calls, we selected the 3 that we most frequently heard in the wild, to verify the behavioral and vocal responses of common marmosets when hearing them. They are 1) twitter (Epple 1968; Winter 1977; Winter and Rothe 1979); 2) *phee* (Epple 1968; Winter 1977; we used a combination of long *phee* plus brief *phee* call 1); and 3) loud cry.

According to Maurus *et al*. (1988), the auditory recognition of call types depends on the physical ability of the receiving individual to distinguish the acoustical

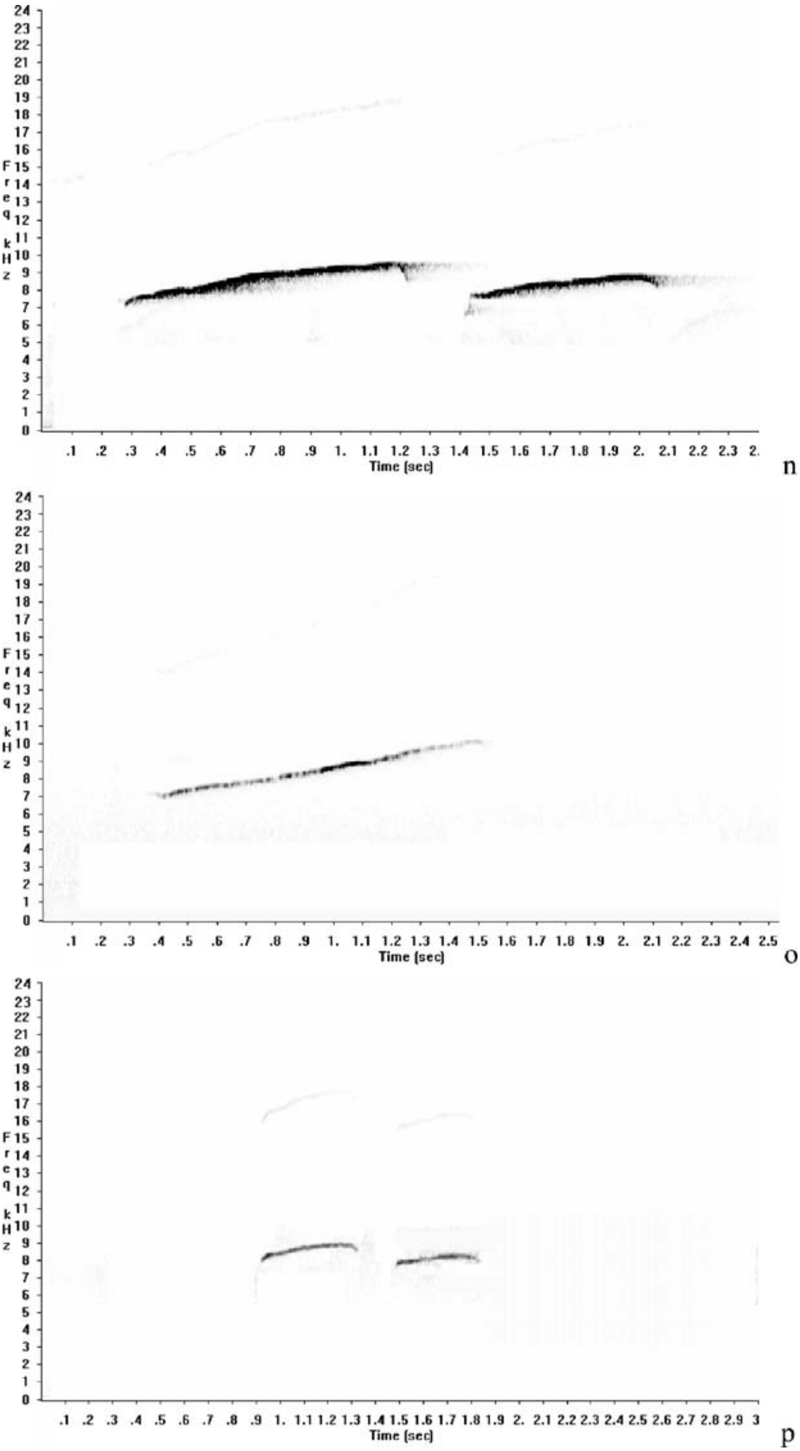

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Table 1 Calls in the vocal repertoire of adults, juveniles and infants

Calls	Adult	Juvenile	Infants
Trill	X	X	X
Twitter	X	X	
Tsik	X	X	X
Tsê	X	X	X
Egg	X	X	X
Chatter	X	X	X
Scream	X	X	X
Submissive squeal	X	X	X
Loud squeal			X
Moaning		X	X
Very brief whistle	X	X	
Alarm 1	X		
Alarm 2	X		
Long *phee* call	X	X	
Brief *phee* call 1	X	X	X
Brief *phee* call 2	X	X	X
Brief *phee* call 3	X	X	X

structures of the call and its capacity to categorize the perceived sounds. Results from 2 hospital examinations attested that Bezerra is able to hear the bandwidth of fundamental frequencies of the vocalizations emitted by common marmosets, i.e., from 250 Hz to 20 kHz (Winter 1977). In addition, Bezerra has been conducting behavioral observations of common marmosets in the study area since 2001 (Schiel and Huber 2006); therefore, her presence is accepted by the subjects and she is well practiced in distinguishing their vocalizations. However, we have to consider that calls may have subtle differences in ranges where human hearing is not sensitive, e.g., *coo* calls of Japanese monkeys (*Macaca fuscata*; Tanaka *et al.* 2006) or there may be subtle structural differences that one can reveal only via careful acoustic analyses.

Statistical Analyses

We used InStat for Windows v. 3.0 (GraphPad Software Inc., San Diego, CA) and Excel (Microsoft Corporation, Redmond, WA) for the statistical analyses. We present the physical characteristics of the vocalizations (Table 2) as means ± SEM. We compared 6 of the characteristics (the start and end frequencies, lower and higher frequencies, frequency range, and syllable duration) via Mann-Whitney U test; we adjusted α via a sequential Bonferroni correction (Lamprecht 1999; Rice 1989). If all results of a given family of tests are $p \leq 0.05$ then we consider them significant without the need for correction (Lamprecht 1999). We used the Friedman 2-way analyses of variance by ranks (F_r) to look for differences in the frequency of >2 paired samples, i.e., intra-age comparisons of the use of different call types during selected behavioral contexts; and intra-age comparisons of the vocal and behavioral responses to the selected long-distance calls/initial vocalizations. When appropriate, we carried out a multiple comparisons procedure (Dunn's test) suitable for analysis *post hoc* after the Friedman test (Siegel and Castellan 1988). For 2 paired samples we used the Wilcoxon T test. We show the percentages of each call type or behaviors for each specific behavioral context or initial vocalization. All tests are 2-tailed and we set significance at $p \leq 0.05$.

Table 2 Features of the vocal signals emitted by wild common marmosets

Vocal sign	Age	n_c	N_i	Call Dur	SE	Num Syl	SE	Syl Dur	SE	ISI	SE	↑ Freq	SE	↓ Freq	SE	Δ Freq	SE	← Freq	SE	→ Freq	SE	Dur start-peak	SE	Dur peak-end	SE	NH	SE	IBH	SE	Obs.
Trill	A	106	12	0,37	± 0,03	1,00		0,37	± 0,03	n/a		8,13	± 0,12	6,37	± 0,12	1,77	± 0,06	7,03	± 0,15	7,23	± 0,12	0,21	± 0,03	0,16	± 0,03	up to 1		n/a		
	J	66	9	0,37	± 0,05	1,00		0,37	± 0,05	n/a		9,03	± 0,20	6,95	± 0,14	2,08	± 0,10	8,18	± 0,33	7,80	± 0,21	0,20	± 0,05	0,17	± 0,03	up to 1		n/a		
	I	13	2	0,37	± 0,07	1,00		0,37	± 0,07	n/a		9,78	± 0,65	± 7,29	± 0,18	2,49	± 0,48	8,85	± 0,32	7,71	± 0,13	0,16	± 0,08	0,21	± 0,01	up to 1		n/a		
Twitter	A	39	9	1,12	± 0,10	9,63	± 0,76	0,06	± 0,00	0,09	± 0,02	13,08	± 0,22	5,49	± 0,12	7,60	± 0,18	8,43	± 0,18	8,04	± 0,39	0,10	± 0,09	1,03	± 0,12	up to 1		n/a		
	J	10	4	0,96	± 0,17	8,29	± 0,14	0,05	± 0,01	0,08	± 0,00	12,75	± 0,31	5,82	± 0,09	6,94	± 0,30	8,61	± 0,31	8,74	± 0,67	0,13	± 0,00	0,83	± 0,00	up to 1		n/a		
Tsik	A	84	9	n/a		n/a		0,05	± 0,00	n/a		14,63	± 0,63	2,72	± 0,39	11,91	± 0,57	12,05	± 0,95	2,80	± 0,45	0,02	± 0,00	0,03	± 0,00	up to 2		n/a		
	J	30	7	n/a		n/a		0,04	± 0,00	n/a		14,96	± 0,78	3,58	± 0,73	11,38	± 0,83	13,27	± 0,91	3,59	± 0,73	0,02	± 0,00	0,02	± 0,00	up to 2		n/a		
	I	68	2	n/a		n/a		0,04	± 0,01	n/a		14,09	± 0,91	3,64	± 0,40	10,45	± 0,51	11,76	± 0,95	4,36	± 0,12	0,03	± 0,01	0,04	± 0,00	up to 2		n/a		
Tsê	A	22	6	n/a		n/a		0,04	± 0,01	n/a		16,91	± 0,76	11,82	± 0,65	5,10	± 0,31	12,04	± 0,59	15,44	± 0,90	0,03	± 0,01	0,01	± 0,00	0,00		n/a		
	J	9	3	n/a		n/a		0,04	± 0,00	n/a		16,47	± 0,56	13,65	±0,68	2,83	± 0,24	13,65	± 0,68	14,90	± 0,39	0,03	± 0,00	0,01	± 0,00	0,00		n/a		
Egg	A	14	3	n/a		n/a		0,04	± 0,00	n/a		9,79	± 1,67	0,82	± 0,06	8,98	± 1,62	n/a		n/a		n/a		n/a		12,29	± 0,86	0,61	± 0,07	The higher frequency is the frequency of the last harmonic
	J	19	4	n/a		n/a		0,04	± 0,01	n/a		11,74	± 1,45	0,90	± 0,06	10,83	± 1,41	n/a		n/a		n/a		n/a		11,33	± 1,57	0,68	± 0,04	The higher frequency is the frequency of the last harmonic
Chatter	A	47	4	n/a		n/a		0,06	± 0,01	0,06	± 0,02	21,96	± 0,57	0,25	± 0,00	21,71	± 0,57	n/a		n/a		n/a		n/a		n/a		n/a		

Submissive squeal	J	25	4	n/a	n/a	0,49 ± 0,04	n/a	20,55 ± 0,32	1,49 ± 0,10	19,06 ± 0,33	n/a	n/a	n/a	n/a	31,68 ± 1,28	0,43 ± 0,09	The higher frequency is the frequency of the last harmonic
Loud squeal	I	39	2	n/a	n/a	0,93 ± 0,26	n/a	21,69 ± 0,64	1.12 ± 0,60	20,58 ± 0,04	n/a	n/a	n/a	n/a	39,02 ± 0,87	0,26 ± 0,00	The higher frequency is the frequency of the last harmonic
Moaning	J	10	3	n/a	n/a	0,27 ± 0,00	n/a	15,57 ± 0,60	0,81 ± 0,02	14,76 ± 0,58	n/a	n/a	n/a	n/a	39,02 ± 1,71	0,26 ± 0,07	The higher frequency is the frequency of the last harmonic
Very brief whistle	A	6	1	n/a	n/a	0,11 ± 0,01	n/a	17,39 ± 0,24	14,68 0,29	2,72 ± 0,17	14,68 ± 0,29	17,51 ± 0,35	0,09 ± 0,02	0,02 ± 0,01	up to 1	n/a	
Alarm 1	A	8	4	n/a	n/a	0,12 ± 0,01	n/a	10,85 ± 0,10	8,66 ± 0,14	2,19 ± 0,07	8,76 ± 0,12	8,31 ± 0,18	0,07 ± 0,01	0,05 ± 0,01	± 0,00	n/a	
Alarm 2	A	4	2	n/a	n/a	0,10 ± 0,02	n/a	16,86 ± 0,49	10,25 ± 0,25	6,61 ± 0,74	10,25 ± 0,25	16,38 ± 0,03	0,09 ± 0,02	0,00 ± 0,00	n/a	0,00	
Scream	I	2	1	n/a	n/a	0,63 ± 0,05	n/a	20,00 ± 0,75	1,90 ± 0,10	18,10 ± 0,65	n/a ±	n/a ±	n/a ±	n/a ±	n/a	n/a	Maximum intensity between 6 and 10,75kHz
Long phee call	A	68	8	n/a	n/a	1,38 ± 0,04	n/a	8,80 ± 0,08	7,07 ± 0,08	1,73 ± 0,10	7,21 ± 0,12	7,87 ± 0,14	1,15 ± 0,06	0,23 ± 0,05	up to 2	n/a	
Brief phee call 1	A	38	6	n/a	n/a	0,80 ± 0,03	n/a	8,91 ± 0,08	7,24 ± 0,10	1,67 ± 0,09	7,24 ± 0,10	8,35 ± 0,15	0,69 ± 0,04	0,10 ± 0,03	up to 2	n/a	
Brief phee call 2	A	4	1	n/a	n/a	1,04 ± 0,05	n/a	10,06 ± 0,36	7,65 ± 0,31	2.41 ± 0,55	7,99 ± 0,41	9,79 ± 0,49	0,98 ± 0,05	0,06 ± 0,01	up to 1		
Brief phee call 3	A	16	5	n/a	n/a	0,54 ± 0,10	n/a	8,61 ± 0,24	7,47 ± 0,15	1.14 ± 0,15	7,48 ± 0,16	8,41 ± 0,21	0,48 ± 0,09	0,06 ± 0,02	up to 1		

Age: A = adults; J = juveniles; I = infants. n_c = Number of vocal signals analyzed via sonograms; N_i = number of individuals; Call dur = call duration; Num syl = number of call unit; Syl dur = duration of call unit; ISI = intercall unit interval; ↑Freq = higher frequency; ↓Freq = lower frequency; ΔFreq = range of frequencies; ←Freq = start frequency; →Freq = end frequency; Dur start-peak = duration from the start to the higher or peak frequency of the vocal signal; Dur peak-end = duration from the higher or peak frequency to the end of the vocal signal; NH = number of harmonics; IBH = interval between harmonics; n/a = not applicable. Time in seconds; frequencies in kHz.

Results

Description of Vocal Repertoire

Wild common marmosets possess 13 different call types, all distinguishable via both sonogram analyses (Fig. 1; Tables 2 and 3) and by ear. These are: 1) trill; 2) twitter; 3) *tsik*; 4) *tsê*; 5) *egg*; 6) chatter; 7) squeal (consisting of the loud squeal and of the submissive squeal); 8) moaning; 9) very brief whistle; 10) alarm 1; 11) alarm 2; 12) scream; 13) *phee* (consisting of long *phee*, brief *phee* call 1; brief *phee* call 2; brief *phee* call 3).

1) Trill (whirrs: Pook 1976, 1977; phee call: Epple 1968; Winter 1977; Winter and Rothe 1979; trill call: Norcross *et al.* 1994): a quiet call uttered with the mouth almost closed. It is uttered in isolation or in combination with squeal or *tsik* or both.
2) Twitter (Epple 1968; Pook 1976; Winter 1977; Zwitscher-laute: Winter and Rothe 1979; gorgeio decrescivo: Camarotti and Monteiro da Cruz 1997): a loud sound, characterized by a series of short call units at intervals of <0.1 s. It is uttered like a warble.
3) *Tsik* (Epple 1968; *tsak*: Pook 1976; Winter 1977, Winter and Rothe 1979): uttered singly or in series. In the wild, *tsik*, when uttered in series, is used as a mobbing call against conspecifics from other social groups, unfamiliar humans, and potential predators moving along the ground or in the trees, e.g., coati (*Nasua nasua*) and Tayra (*Eira barbara*): Bezerra *et al.* 2008). In the case of predators, all individuals of the group except infants continue to emit *tsik* calls and follow the potential predator until it retreats. Finally, an individual distressed by an unusual noise, e.g., the falling of a large branch in the forest, may emit *tsik* calls in series.
4) *Tsê*: sound similar to, but distinguishable from, the *tsik*. The end frequency and lower frequency of the *tsê* call are higher than those of the *tsik* call. In addition, the frequency range is lower in the *tsê* call than in the *tsik* call. The call is uttered singly, or in combination with the *egg* call or *tsik* call, or both.
5) *Egg* (*egg*: Epple 1968, Winter 1977, Winter and Rothe 1979): a very short call with a few harmonics. In the wild it can be uttered singly, in series (≤3 call units) or in combination with *tsê* or *tsik* calls (usually 1 tsê or 1 tsik call is followed by ≤3 *egg* calls). Normally, the *egg* call is associated with vigilance behavior, e.g., when a strange human approaches the group or when the calling marmoset must go to the ground in an area of sparse vegetation (Souto *et al.* 2007).
6) Chatter (chatter call: Epple 1968; Winter 1977; Kecker-laute: Winter and Rothe 1979; *erh-erh*: Stevenson and Poole 1976; *que que que*: Alonso and Langguth 1989): given in series with very short intervals between the call units. Associated with intra- and intergroup aggression (Table 4).
7) Squeal (squeal call: Epple 1968; Winter 1977; Quärr-laute: Winter and Rothe 1979; *nhe-nhe*: Alonso and Langguth 1989; cry: Pistorio *et al.* 2006): there are 2 distinguishable squeal calls: submissive squeal and loud squeal. The latter

has a higher number of harmonics and lasts longer than the submissive squeal (Table 2). Both variations of the squeal are uttered in combination with *tsik* and trill calls. We termed the combination of submissive squeal plus *tsik* and trill a submissive cry. In contrast, we termed the combination of loud squeal plus *tsik* call plus trill call a loud cry.

8) Moaning: a faint call that can be uttered singly or in series (usually ≤3 call units). Mainly young individuals utter this call during play when play appears to become too intense.
9) Very brief whistle: a short, high-pitched call uttered in series and with the mouth wide open. The sonogram of this call is similar to that of the alarm 2. However, the frequency range of the latter is higher. The call is relatively rare and tends to be emitted when the marmosets have found a relatively large amount of food, e.g., an open jackfruit or a mango on the ground. This behavioral situation happened 18 times. Adults emitted very brief whistles 17 times and a juvenile uttered it once. Individuals that heard the call tended to approach the vocalizing individual.
10) Alarm 1 (warning call: Epple 1968; alarm call: Pook 1977): a short, sharp whistle, which has lower frequencies (Hz) than those of alarm 2 and therefore sounds different (to the human ear) from the latter. Usually after hearing it (generally emitted upon the sudden appearance of a potential bird predator), group members moved to denser vegetation.
11) Alarm 2 (warning call: Epple 1968; alarm call: Pook 1977; Lautgruppen 02: Winter and Rothe 1979): a short, sharp whistle emitted while the individual is making a soft *haa*-like exhalation of breath. After hearing an alarm 2, group members tend to remain motionless for several seconds until the potential predator (usually a domestic dog) disappears.
12) Scream (scream call: Epple 1968; Winter 1977; Schrei-laute: Winter and Rothe 1979): uttered singly or in series. The call is relatively rarely observed and is usually uttered by individuals either trying to steal food or being seriously injured by a conspecifc.
13) *Phee* (*phee* call: Epple 1968; Winter 1977; shrill call: Pook 1076, 1977; *phii*-laute: Winter and Rothe 1979; long call: Snowdon 1989; silvo longo: Camarotti and Monteiro da Cruz 1997): easily divided into 4 types: long *phee* (>1 s duration, loud and uttered with the mouth wide open), brief *phee* call 1 (<1 s duration, loud and uttered with the mouth wide open); brief *phee* call 2 (often >1 s in duration, less loud than the long *phee* call and uttered with the mouth less open); brief *phee* call 3 (usually <0.7 s duration, faint and uttered with the mouth less open). They generally used *phee* calls i) to make contact with conspecifics when in the presence of another group of common marmosets or an unknown individual; ii) to begin to bring group members together before nightfall, iii) when the vocalizing individual has been alone, relatively far from the rest of the group for a relatively long time (in this case, marmosets usually utter a long *phee* call and a brief *phee* call 1); and iv) when the vocalizing marmoset is in close visual contact with a conspecifc (under such circumstances, brief *phee* calls 2 and 3 are usually uttered).

Table 3 Comparisons between physical characteristics of different call types

	Twitter	Tsik	Egg[a]	Tsê	Chatter[a]	Moaning[a]	Alarm 1	Long phee	Sub squeal[a]
Trill	(↑Freq: U=0; **.0001**) (↓Freq: U=0; **.0001**) (ΔFreq: U=0; **.0001**) (Syl dur: U=0; **.0001**) (←Freq: U=24; .0339) (→Freq: U=38; .2773) [n_1=12, n_2=9]	(↑Freq: U=0; **.0001**) (↓Freq: U=8; **.0004**) (ΔFreq: U=0; **.0001**) (Syl dur: U=0; **.0001**) (←Freq: U=5; **.0001**) (→Freq: U=6; **.0002**) [n_1=8, n_2=14]	(↑Freq: U=14; **.0070**) (↓Freq: U=0; **.0001**) (ΔFreq: U=0; **.0001**) (Syl dur: U=0; **.0001**) [n_1=14, n_2=7]	(↑Freq: U=0; **.0001**) (↓Freq: U=0; **.0001**) (ΔFreq: U=0; **.0001**) (Syl dur: U=0; **.0001**) (←Freq: U=0; **.0001**) (→Freq: U=0; **.0001**) [n_1=15, n_2=9]	(↑Freq: U=0; **.0003**) (↓Freq: U=0; **.0003**) (ΔFreq: U=0; **.0003**) (Syl dur: U=0; **.0003**) [n_1=18, n_2=4]	(↑Freq: U=0; **.0013**) (↓Freq: U=0; **.0013**) (ΔFreq: U=0; **.0013**) (Syl dur: U=8; .0532) [n_1=19, n_2=3]	(↑Freq: U=0; **.0002**) (↓Freq: U=0; **.0002**) (ΔFreq: U=11.5; .0301) (Syl dur: U=3.5; **.0053**) (←Freq: U=8.5; **.0164**) (→Freq: U=22; .1826) [n_1=20, n_2=4]	(↑Freq: U=44.5; .2446) (↓Freq: U=38.5; .1258) (ΔFreq: U=44; .2381) (Syl dur: U=0; **.0001**) (←Freq: U=44; .2381) (→Freq: U=34; .0702) [n_1=16, n_2=8]	(↑Freq: U=0; **.0007**) (↓Freq: U=0; **.0007**) (ΔFreq: U=0; **.0007**) (Syl dur: U=24; .7209) [n_1=14, n_2=4]
Twitter		(↑Freq: U=8; **.0031**) (↓Freq: U=0; **.0001**) (ΔFreq: U=0; **.0001**) (Syl dur: U=21; .1011) (←Freq: U=8; **.0031**) (→Freq: U=0; **.0001**) [n_1=8, n_2=10]	(↑Freq: U=10; .1709) (↓Freq: U=0; **.0016**) (ΔFreq: U=8; .0932) (Syl dur: U=0; **.0016**) [n_1=8, n_2=5]	(↑Freq: U=0; **.0004**) (↓Freq: U=0; **.0004**) (ΔFreq: U=0; **.0004**) (Syl dur: U=0; **.0004**) (←Freq: U=0; **.0004**) (→Freq: U=0; **.0004**) [n_1=6, n_2=9]	(↑Freq: U=0; **.0011**) (↓Freq: U=0; **.0011**) (ΔFreq: U=0; **.0011**) (Syl dur: U=14; .2615) [n_1=12, n_2=4]	(↑Freq: U=0; **.0055**) (↓Freq: U=0; **.0055**) (ΔFreq: U=0; **.0055**) (Syl dur: U=0; **.0055**) [n_1=11, n_2=3]	(↑Freq: U=0; **.0011**) (↓Freq: U=0; **.0011**) (ΔFreq: U=0; **.0011**) (Syl dur: U=0; **.0011**) (←Freq: U=11; .1330) (→Freq: U=20; .6835) [n_1=12, n_2=4]	(↑Freq: U=0; **.0002**) (↓Freq: U=0; **.0002**) (ΔFreq: U=0; **.0002**) (Syl dur: U=0; **.0002**) (←Freq: U=0; **.0002**) (→Freq: U=22; .4278) [n_1=10, n_2=6]	(↑Freq: U=0; **.0028**) (↓Freq: U=0; **.0028**) (ΔFreq: U=0; **.0028**) (Syl dur: U=0; **.0028**) [n_1=9, n_2=4]
Tsik			(↑Freq: U=9; **.0097**) (↓Freq: U=0; **.0001**) (ΔFreq: U=0; **.0001**) (Syl dur: U=0; **.0001**) [n_1=10, n_2=7]	(↑Freq: U=22; .0653) (↓Freq: U=0; **.0001**) (ΔFreq: U=0; **.0001**) (Syl dur: U=30; .2362) (←Freq: U=36; .4967) (→Freq: U=0; **.0001**) [n_1=10, n_2=9]	(↑Freq: U=0; **.0007**) (↓Freq: U=0; **.0007**) (ΔFreq: U=0; **.0007**) (Syl dur: U=0; **.0007**) [n_1=14, n_2=4]	(↑Freq: U=0; **.0007**) (↓Freq: U=0; **.0007**) (ΔFreq: U=0; **.0007**) (Syl dur: U=0; **.0007**) [n_1=14, n_2=4]	(↑Freq: U=2; **.0026**) (↓Freq: U=0; **.0007**) (ΔFreq: U=0; **.0007**) (Syl dur: U=0; **.0007**) (←Freq: U=4; **.0078**) (→Freq: U=2; **.0026**) [n_1=14, n_2=4]	(↑Freq: U=0; **.0001**) (↓Freq: U=8; **.0018**) (ΔFreq: U=0; **.0001**) (Syl dur: U=0; **.0001**) (←Freq: U=1; **.0001**) (→Freq: U=6; **.0008**) [n_1=11, n_2=8]	(↑Freq: U=4; **.0062**) (↓Freq: U=0; **.0005**) (ΔFreq: U=0; **.0005**) (Syl dur: U=0; **.0005**) [n_1=15, n_2=4]
Egg[a]				(↑Freq: U=2; **.0381**)	(↑Freq: U=0; **.0095**)	n/a	(↑Freq: U=8; .4762)	(↑Freq: U=7; **.0262**)	(↑Freq: U=0; **.0061**)

				(↓Freq: U=0; **.0095**) (ΔFreq: U=0; **.0095**) (Syl dur: U=0; **.0095**) [n_1=4, n_2=6]	(↓Freq: U=0; **.0095**) (ΔFreq: U=0; **.0095**) (Syl dur: U=0; **.0095**) [n_1=6, n_2=4]		(↓Freq: U=0; **.0095**) (ΔFreq: U=0; **.0095**) (Syl dur: U=0; **.0095**) [n_1=6, n_2=4]	(↓Freq: U=0; **.0006**) (ΔFreq: U=0; **.0006**) (Syl dur: U=0; **.0006**) [n_1, n_2=7]	(↓Freq: U=2; **.0288**) (ΔFreq: U=0; **.0061**) (Syl dur: U=0; **.0061**) [n_1=7, n_2=4]
Tsê					(↑Freq: U=0; **.0040**) (↓Freq: U=0; **.0040**) (ΔFreq: U=0; **.0040**) (Syl dur: U=0; **.0040**) [n_1=8, n_2=4]	n/a	(↑Freq: U=0; **.0040**) (↓Freq: U=0; **.0040**) (ΔFreq: U=0; **.0040**) (Syl dur: U=0; **.0040**) (←Freq: U=0; **.0040**) (→Freq: U=0; **.0040**) [n_1=8, n_2=4]	(↑Freq: U=0; **.0003**) (↓Freq: U=0; **.0003**) (ΔFreq: U=0; **.0003**) (Syl dur: U=0; **.0003**) (←Freq: U=0; **.0003**) (→Freq: U=0; **.0003**) [n_1=7, n_2=8]	(↑Freq: U=4; .1143) (↓Freq: U=0; **.0095**) (ΔFreq: U=0; **.0095**) (Syl dur: U=0; **.0095**) [n_1=6, n_2=4]
Chatter[a]						n/a	(↑Freq: U=0; **.0286**) (↓Freq: U=0; **.0286**) (ΔFreq: U=0; **.0286**) (Syl dur: U=0; **.0286**) [n_1, n_2=4][b]	(↑Freq: U=0; **.0040**) (↓Freq: U=0; **.0040**) (ΔFreq: U=0; **.0040**) (Syl dur: U=0; **.0040**) [n_1=4, n_2=8]	n/a
Moaning[a]							n/a	(↑Freq: U=0; **.0121**) (↓Freq: U=0; **.0121**) (ΔFreq: U=0; **.0121**) (Syl dur: U=0; **.0121**) [n_1=3, n_2=8]	n/a
Alarm 1								(↑Freq: U=0; **.0061**) (↓Freq: U=0; **.0061**) (ΔFreq: U=1.5; **.0232**) (Syl dur: U=0; **.0061**)	n/a

Table 3 (continued)

	(←Freq: U=0; **.0061**) (→Freq: U=7; .2303) [n_1=4, n_2=7]	
Phee		(↑Freq: U=0; **.0040**) (↓Freq: U=0; **.0040**) (ΔFreq: U=0; **.0040**) (Syl dur: U=0; **.0040**) [n_1=8, n_2=4]

The final numbers inside each set of parentheses represent the p values of the Mann-Whitney U test (in bold are those that are significant, $p \leq 0.05$, after the sequential Bonferroni α correction). ↑Freq = higher frequency; ↓Freq = lower frequency; Δ Freq = range of frequencies; ←Freq = start frequency; →Freq = end frequency; Syl dur = duration of call unit; n/a = not applicable: too few data points from both vocalizations to run the U test or the sequential Bonferroni method.

[a] We did not analyze the start and end frequencies for egg, chatter, moaning, and submissive squeal (subsqueal).

[b] Because of the small sample size, we could not use the sequential Bonferroni method; however, as all results of the set are $p < 0.05$ we consider them significant. We did not include alarm 2, very brief whistle, and scream owing to their small sample sizes. Only the most common type of phee is presented.

Table 4 Definition of behavior categories

Behavior category	Behaviors
Foraging behavior	Saltatory search: Searching for animal prey in a stop-and go pattern (Souto *et al.* 2007). Careful search: Carefully watching and, simultaneously, manipulating a leaf, branch, or tree hole.
Vigilance	Looking around into the surrounding vegetation while stationary, moving the head quickly side to side and up and down (adapted from Halsey *et al.* 2006; Hardie and Buchanan-Smith 1997).
Rest	Solitary rest: Remaining temporarily still, quiet, inactive or self-grooming with no other marmoset within ≥2 m. Social rest: Stationary with another marmoset in bodily contact, the former either remaining temporarily still, quiet, inactive, grooming the conspecific, or being groomed.
Play	Solitary play: Undertaking frisk-hops or locomoting over short distances (<1 m) alone. Social play: Consists of pretend fighting, either on the ground or in the trees; chasing each other around tree trunks or over branches. Play interacting with conspecifics.
Eat	Consumption of either animal prey (e.g., cicada, grasshopper, ant, small frogs, small lizards) or vegetable matter (e.g. fruit, flowers, seeds).
Capture	The act of catching a prey item (Maier *et al.* 1982; Schiel 2000).
Aggression	Intragroup aggression: Chasing a group member; vocalizing chatter call; performing piloerection while looking at a group member; giving angry little slaps or bites to a group member (Stevenson and Poole 1976) Intergroup aggression: Chasing a nongroup member; showing genitals; performing piloerection while looking at a non-group member; engaging in a physical fight with a nongroup member (Stevenson and Poole 1976).
Social watch	Watching a group conspecific: Stationary, looking at a group member that is behaviorally active (Schiel and Huber 2006). Watching a conspecific from other group: Stationary, looking at an individual of another social group behaviorally active
Locomote to caller	Moving in the direction of a caller.
Locomote away from caller	Moving in the direction opposite that of the caller.
Approach	Approach only: Locomoting to get closer to another individual (1 m distance) without physical contact. Approach with interaction: Getting physically close to another marmoset and then interacting with it by grooming it, carrying it (when it is an infant) or through aggressive behaviors.
Look at call direction	Looking in the direction from which a call has emanated (either being able to see the caller or otherwise).
Pause	Stopping the current behavior and remaining stationary for several seconds.
Flee	Moving away rapidly from a negative stimulus.
Frozen	Staying in a stationary position and not moving any body parts, including the head.

Vocal Repertoire of Adults, Juveniles, and Infants

The vocal repertoire of adults consisted of 12 calls; that of juveniles, 11 calls; and that of infants, 9 calls (Table 1). Owing to background noise, we were unable to obtain sonograms of adequate quality for the following vocal signs: 1) juveniles: *phee* calls, very brief whistle, and submissive squeal; 2) infant: *phee*, *tsê*, *egg*, chatter, and moaning. Table 2 contains information on the physical characteristics of the vocalizations emitted by adult, juvenile, and infant common marmosets in the wild.

Context of Vocalizations

In some cases, there are significant differences in the frequency with which the call types were emitted. They depended on: 1) the behavioral context of the individual (Tables 4 and 5); and 2) the initial vocalizations to which individuals responded (Table 6).

During foraging behavior, adults uttered trill calls significantly more often than other vocalizations (94.4% of the 7 call types) and for both juveniles and infants they seemed also an important vocalization (83.3% of 10 call types uttered by juveniles and 86.2% of 4 call types by infants: Table 5). During vigilance behavior, adults uttered most frequently a combination of *tsê* and *egg*, which constituted 89.2% of the 4 call types uttered. The Friedman test did not detect significant differences between the 4 call types juveniles uttered during vigilance behavior. However, *tsê* + *egg* represented 80.4% of the calls (Table 5). Infants did not display vigilance behavior. During periods of solitary rest, only adults and juveniles vocalized. Among the vocalizations that individuals of both age classes uttered during solitary rest were twitter, trill, and *phee* calls. We detected no significant difference in the frequency with which they were uttered (Table 5). During periods of social rest, only adults vocalized, and we recorded twitter, trill, and *phee* calls (F_r: significant; Dunn's test: not significant; Table 5). When capturing prey or eating, *Callithrix jacchus* did not vocalize (Table 5).

When watching conspecifics of the same social group, individuals of all age classes vocalized. The loud cry was the call combination infants uttered more often under these circumstances; juveniles and adults never uttered it. There is no significant difference in the frequency of the 6 call types juveniles uttered when watching conspecifics of the same social group (Table 5). Only juveniles used the submissive cry under the circumstances. Adults emitted various call types or call combinations when watching conspecifics of the same social group (F_r: significant; Dunn's test: not significant; Table 5). When watching conspecifics from other social groups, only adults and juveniles vocalized, and we detected no significant difference in the frequency in which they uttered call types. However, adults seemed to utter the long *phee* call quite frequently (61.8%), whereas it represented only 1.5% of the calls juveniles emitted under these circumstances (Table 5). The production of chatter was especially pronounced during bouts of intragroup aggression. Adults, juveniles, and infants emitted it, which constituted 93.7%, 85.7%, and 75%, respectively, of the calls individuals of the 3 age classes made in such situations. Adults emitted it significantly more often than they did the *tsê*, the only other vocalization detected from adults under similar circumstances (Table 5). During bouts of intragroup aggression, both juveniles and infants emitted only 1 call, in addition to chatter: respectively, *egg* and submissive cry (Table 5).

Only the adults vocalized during bouts of intergroup aggression. They emitted 3 call types (chatter, 64.3%; twitter and *tsê* + *egg*, 14.3%; scream, 7.1%), with no significant difference between them (Table 5).

The vocal responses of individual marmosets to vocalizations of others were highly dependent on the call types they perceived (Table 6). For example, in adults, twitters were more likely to be responded to with another twitter (93%) than with another call type, e.g., the brief *phee* call 1, 6.7%; Wilcoxon *T* test: significant. In terms of behavioral response, receivers performed pause behavior (74%) or locomoted to caller (16%) significantly more often than 2 other behaviors (Table 6). In all recorded cases juveniles responded to twitters with twitters. Such calls usually also elicited pause behavior (82.4%), though without a statistical difference when compared to the behavior locomote to caller (17.6%; Table 6).

Infant loud cries mostly elicited the following responses in adults: 1) it approached and physically interacted with the infant caller (60%), 2) it only approached the infant caller but did not physically interact with it (10%), or 3) it looked in the direction of the call, but did not approach (10%; F_r: not significant). In juveniles to approach and to interact seemed to be an important response (60%), followed by simple approach (10%), though there is no significant difference between their frequencies (Table 6).

Adults tended to respond to the combination of long *phee* calls plus brief *phee* call 1 mainly with a twitter (59.4%; F_r: significant; Dunn's test: not significant), and also resulted in the receiver either locomoting in the direction of the initial caller (51%), or pausing (46.3%; F_r: significant; Dunn's test: locomote to caller and pause were similar and both are significantly greater than look at call direction; Table 6).

Discussion

We recorded 13 different calls from the vocal repertoire of wild common marmosets. Wild adult, juvenile, and infant common marmosets showed quantitative differences in the call type-composition of their respective vocal repertoires (for 12, 11, and 9 call types, respectively). In addition, some calls were age specific, e.g., loud squeals by infants and alarm calls by adults, twitter only by adults and juveniles. There are reports of age-related variations in call types of captive common marmosets (Epple 1968; Pistorio *et al.* 2006; Winter 1977; Winter and Rothe 1979), and in the vocal repertoires of other primates species, including Japanese macaques (*Macaca fuscata*: Itani 1963); vervets (*Cecopithecus aethiops*: Struhsaker 1967); squirrel monkeys (*Saimiri sciureus*: Ploog 1967); and pygmy marmosets (*Cebuella pygmaea*: Snowdon 1988); and also in the vocal repertoires of nonprimate species such as red foxes (*Vulpes vulpes*: Newton-Fisher *et al.* 1993). The age-related variation may be due both to physical development (Snowdon 1988) and to behavioral changes with age, which may at least partially explain the age-related variation recorded here in the vocal repertoires of wild *Callithrix jacchus*.

The vocal repertoire of common marmosets that we recorded appears similar to that previously recorded in captives (Epple 1968; Pook 1977; Winter 1977; Winter and Rothe 1979). However, there are some differences. For instance, we did not record the *tsee* call that Epple (1968) described. In this sense our study was more comparable to the ones of Pook (1977), Winter (1977), and Winter and Rothe (1979), who also did not record the *tsee* call in their captives. Epple (1968) described the *tsee* call as sounding similar to the *tsik* call, and indeed we also recorded a

Table 5 Behavioral contexts and the vocalizations that were more likely to be uttered

Behavioral context	N_i	Age	Friedman (F_r; with Dunn's test) or Wilcoxon (T) test	n_2	n_3	% of vocalizations related to the behavioral context
Foraging	14	A	F_r=50.969*** (N=14) (Dunn's test = trill greater than other call types, $p<0.05$)	738	525	94.3% trill; 3.6% brief *phee* call 3; 2.5% twitter; 2.3% brief *phee* call 2; 0.38% *tsik*; 0.38% brief *phee* call 1; 0.19% *tsê* + egg
	6	J	F_r=23.842** (N=6) (Dunn's test = failed in detecting differences)	284	114	83.3% trill; 7.9% brief *phee* call 3; 2.6% twitter; 1.75% *tsik*; 0.88% egg, *tsik*, 0.88% *tsik* + egg, 0.88% tsê + egg, 0.88% submissive cry and 0.88% brief *phee* call 2
	5	I	F_r=8.727* (N=5) (Dunn's test = failed in detecting differences)	176	29	86.2% trill; 6.9% brief *phee* call 3; 3.45% *tsê* and 3.45% submissive cry
Vigilance	10	A	F_r=18.088** (N=10) (Dunn's test = failed in detecting differences)	71	158	89.2% *tsê* + egg; 3.8% twiter, 3.8% very brief whistle; 1.9% brief *phee* call 2; 0.6% brief *phee* call 1 and 0.6% *tsik* (mc test = *tsê* + egg greater than all other uttered calls)
	5	J	F_r=3.868 (N=5) (Dunn's test = n/a)	26	46	80.4% *tsê* + egg; 10.9% very brief whistle; 6.52% *tsik*; 2.17% tsik + egg
Solitary rest	13	A	F_r=10.892 (N=13) (Dunn's test = n/a)	105	51	60.8% twitter; 11.8% trill; 7.8% long *phee* call, 7.8% brief *phee* call 3; 5.9% brief *phee* call 1; 3.9% long *phee* call + brief *phee* call 1; 1.96% brief *phee* call 2
	5	J	Fr=3.000 (N=5) (Dunn's test = n/a)	49	21	85.7% twitter; 9.5% brief *phee* call 3; 4.76% trill
	4	I	–	21	–	The infants did not vocalize during the times they were observed.
Social rest	11	A	F_r=10.069* (N=11) (Dunn's test = failed in detecting differences)	106	64	32.8% trill; 31.2% twitter; 28,1% brief *phee* call 3; 4.7% brief *phee* call 2; 3.1% brief *phee* call 1 (mc test failed in detecting statistical differences).
	5	J	–	8	–	The juveniles did not vocalize during the times we observed them.
	5	I	–	115	1	The infants did not vocalize during the times we observed them, except for 1 single time in which 1 infant uttered a singly trill.
Solitary play	2	A	–	2	0	–
	6	J	–	26	3	From the 26 times that we observed the juveniles on solitary play, 23 times they were in silence, and only 3 times one of the juveniles uttered a single trill
	5	I	–	108	0	–
Social play	8	A	–	24	0	–
	6	J	F_r=8.643 (p=0.07) (N=6) (Dunn's test = n/a)	72	19	47% moaning; 26.3% *tsik*; 15.8% trill; 5.3% twitter; 5.3% egg (mc test failed in detecting statistical differences)
	5	I	–	111	36	100% moaning

Eat	14	A	–	137	0	
	6	J	–	158	1	All juveniles maintained silence while eating, except for 1 that uttered a *tsê* + egg once.
	5	I	–	77	0	
Capture	14	A	–	79	0	
	6	J	–	82	0	
	5	I	–	10	0	
Intra-group aggression	6	A	$T=0^*$ ($N=6$)	19	16	93.75% chatter; 6.25% *tsê*
	2	J	N/a	12	7	85.7% chatter; 14.3% egg
	3	I	N/a	8	8	75% chatter; 25% submissive cry
Inter-group aggression	6	A	$F_r=11.000^*$ ($N=6$) (Dunn's test = failed in detecting differences)	32	14	64.3% chatter; 14.3% twitter, 14.3% *tsê* + egg; 7.14% scream
Watching a group conspecific	11	A	$F_r=19.954^*$ ($N=11$) (Dunn's test = failed in detecting differences)	39	49	32.6% twitter; 18.37% very brief whistle; 12.24% brief *phee* call 3; 6.12% *tsê* and submissive cry; 4.08% brief *phee* call 1; 2.04% *tsik* + egg and 2.04% brief *phee* call 2 (mc test = twitter greater than *tsik* + egg and brief *phee* call 2)
	5	J	$F_r=11.478$ ($N=5$) (Dunn's test = n/a)	59	54	35.18% submissive cry; 20.4% twitter; 18,5% *tsik*; 14.8% trill; 3.7% *tsik* + egg, 3.7% brief *phee* call 1; 1.85% *tsê* and 1.85% *tsê* + egg
	5	I	$F_r=24.182^{**}$ ($N=5$) (Dunn's test = failed in detecting differences)	178	172	61.05% loud cry; 18.02% submissive cry; 1.74% *tsik* + egg; 1.16% *tsê*, 1.16% *tsê* + egg; 1.16% brief *phee* call 2 and 0.58% moaning
Watching a conspecific from other group	4	A	$F_r=9.659$ ($N=4$) (Dunn's test = n/a)	36	61	68.8% long *phee* call; 11.5% twitter; 6.56% brief *phee* call 1; 4.92% *tsik*; 1.64% long *phee* call + brief phee call 1; 1.64% brief *phee* call 3; 1.64% chatter; 1.64% *tsik* + egg and; 1.64% *tsik* serie
	4	J	$F_r=7.402$ ($N=4$) (Dunn's test = n/a)	64	66	31.8% twitter; 25.8% brief *phee* call 3; 22.7% trill; 7.58% brief *phee* call 1; 6.06% submissive cry; 3.03% brief *phee* call 2; 1.5% long *phee* call

n_1 = Number of individuals; n_2 = number of times the behavior was performed; n_3 = number of vocalizations performed. Age: A = adult; J = juvenile; I = infant.
$^*p \leq 0.05$; $^{**}p \leq 0.01$; $^{***}p \leq 0.001$.

Table 6 Initial vocalizations and their vocal and/or behavioral responses

Initial vocalization	N_i	Age	Freedman (F_r; with Dunn's test) or Wilcoxon (T) test	n_2	n_3	% Vocal responses	Behavioral responses; Freedman (F_r; with Dunn's test) or Wilcoxon (T) test	n_4	% Behavioral responses
Twitter call	10	A	T=0** (N=10)	71	60	93% twitter; 6.7% brief *phee* call 1	F_r=23.231*** (N=10) (Dunn's test = Pause greater than Look at call direction and Locomote away from caller).	88	74% Pause; 16% Locomote to caller; 6% Approach with interaction; 2% Look at call direction; 2% Locomote away from caller.
	5	J	–	29	23	100% twitter	F_r=3.000 (N=5) (Dunn's test = n/a)	31	82.4% Pause; 17.6% Locomote to caller;
Loud cry	10	A	–	27	5	80% very brief whistle; 20% twitter.	F_r=4.361 (N=10) (Dunn's test = n/a)	30	60% Approach with interaction; 10% Approach only; 10% Look at call direction; 3.3% others.
	4	J	–	15	0		–	16	56% Approach with interaction; 18.75% Approach only; 6.25% Locomote to caller, 6.25% Look at call direction; 6.25% others.
Long *Phee* call (ALA) + brief phee call 1 (ABA)	11	A	F_r=18.198** (N=11) (Dunn's test = failed in detecting differences)	49	32	59.4% twitter; 18.75% long *phee* call + brief *phee* call 1; 6.25% brief *phee* call 1; 6.25% brief *phee* call 2.	F_r=12.200** (N=11) (Dunn's test = Locomote to caller and Pause greater than Look at call direction).	41	51.3% Locomote to caller; 46.3% Pause; 2.4% Look at call direction.

N_i = Number of individuals; n_2 = number of times the initial vocalization was performed; n_3 = number of times that vocal responses were performed; n_4: number of times the behavioral responses were performed. Age: A = adult; J = juvenile; I = infant.

*$p \leq 0.01$; **$p \leq 0.001$; ***$p \leq 0.001$.

vocalization that sounded similar to the *tsik*. However, the sonograms obtained from the vocalization are clearly different from that reproduced in Epple (1968). Consequently, we named this new call *tsê*.

Epple (1968) described warning calls from captives. Pook (1977) described similar calls as alarm calls, and Winter and Rothe (1979) described as Lautgruppen. We recorded 2 different kinds of warning calls in the wild: alarm 1 and alarm 2. The calls were easily distinguished both aurally and when viewed as sound sonograms. The sonogram of alarm 2 is very similar to the sonograms Epple (1968) and Pook (1977) presented for alarm calls in captives. The sonogram of alarm 1 looked very similar to one of the sonograms Winter and Rothe (1979) presented in a group of calls termed Lautgruppen 02 (or call group 02). We considered alarm calls 1 and 2 as warning calls because they were connected to the sudden appearance of potential predators. The circumstances were similar to those that elicited such calls in captive studies (Barros *et al.* 2002; Pook 1977).

According to Cheney and Wrangham (1987), the antipredator behavior of small primates (<1 kg body mass) consists mainly of concealment, vigilance, and flight rather than attack, even though many species exhibit mobbing behavior. They suggested that diurnal callithrichid species are adapted to avoid rather than to challenge predators. Researchers have reported alarm calls for almost all primate species as an antipredator behavior, with apparently different alarm calls for different types of predators (Cheney and Wrangham 1987). Common marmosets are small, diurnal primates and the antipredator behaviors of wild individuals support some of the predictions for antipredator behavior. Our subjects emitted alarm 1 when aerial raptors (potential predators) and smaller, but still aggressive birds, e.g., rufous-bellied thrushes (*Turdus rufiventris*) and greater kiskadee (*Pitangus sulphuratus*) suddenly appeared in the surrounding area. It was common to see *Turdus rufiventris* and *Pitangus sulphuratus* mobbing and attacking common marmosets in the study site (Bezerra *et al.* 2007). After hearing alarm 1, common marmosets fled to more dense vegetation, presumably making it more difficult for the birds to attack them. Individuals emitted alarm 2 only when domestic dogs appeared suddenly very close to the edge of the forest. The stillness of the marmosets in response to hearing an alarm 2 is probably an attempt to limit the chances of being spotted by a dog. In another fragment of Atlantic rain forest, the Dois Irmãos Forest (08°04′00″S, 34°52′00″W) 20 km far from the study site, Mendes Pontes and Soares (2005) reported predation on common marmosets by domestic dogs. Similarly, Pook (1977) reported that captive common marmosets respond to alarm calls by instantaneous alertness and by fleeing to a more secure position, such as nest boxes or under branches and platforms. Like common marmosets, tamarins (*Saguinus fuscicollis* and *S. mystax*) also have predator-specific alarm calls and show specific reactions to them. For example, when confronted with aerial predators, tamarins tend to look upward more frequently than usual and move to lower parts of the tree, whereas when confronted with terrestrial predators, they tend to look downward and sometimes mob the predator (Kirchhof and Hammerschmidt 2006).

Another call type connected to the appearance of a potential predator in the wild is the *tsik*. Given in series, it serves as a mobbing call. A mobbing call also occurs in captive common marmosets (Epple 1968) and in black-tufted marmosets (*Callithrix* *penicillata*: Barros *et al.* 2002), and wild pygmy marmosets (*Cebuella pygmaea*: Soini 1988), buffy-headed marmosets (*Callithrix flaviceps*: Ferrari and Lopes Ferrari 1989), and Geoffroy's marmosets (*Callithrix geoffroyi*: Passamani 1995). Camaragibe marmosets repeatedly emitted the mobbing vocalization in the presence of coati and tayra. Once a tayra captured a juvenile marmoset (Bezerra *et al.* 2008).

Some of the *phee* calls Epple (1968), Winter (1977), and Winter and Rothe (1979) presented as a *phee* call for infant common marmosets had a sine-like ascending and descending frequency. We observed the same vocalization in wild adult, juvenile, and infant common marmosets. Pook (1977) also recorded adult captive common marmosets emitting the vocalization, which he termed whirrs call. However, like Norcross *et al.* (1994), we term the vocalization a trill. The sonogram of the vocalization for common marmosets looks similar to the sonograms of trills lately described for other primate species: *Callithrix argentata* (Epple 1968; Omedes Regas 1983), *Cebuella pygmaea* (Snowdon 1988), *Leontopithecus rosalia* (Epple 1968; McLanahan and Green 1977), *Cebus capucinus* (Boinski and Campbell 1995; Gros-Louis 2002), and *Microcebus* ssp. (Zimmermann and Hafen 2001).

Several of the calls Camaragibe common marmosets emitted were often in >1 behavioral context, as in other neotropical primates (Snowdon 1988). One was the trill. Though individuals very frequently emitted trills when they were foraging for prey items, they also did so during solitary rest, social rest, social play, or while watching conspecifics. It seems then that certain vocalizations in wild common marmosets can be carriers of general information irrespective of the specific behavioral activity at the time (Gros-Louis 2002; Weiss *et al.* 2001). The arboreal habitat of wild common marmosets probably makes visual contact less efficient than auditory contact; thus, we assume that the trills wild foragers emit may help to maintain group cohesion, in a variety of social contexts, as in captive common marmosets (Pook 1977). Conversely, chatter was almost the only call emitted during intragroup aggression. It did not occur in other behavioral contexts, with the exception of intergroup aggression, where it also occurred with other calls.

The conditional nature of vocal communication in wild common marmosets was not restricted to some call types being more likely to be uttered within specific behavioral contexts. Other calls types or call combinations were age specific or much more common in particular age classes. For instance, the loud cries were emitted only by infants and then mostly when in the vicinity of older individuals of the same social group. Infants emit them usually when begging for food or attention from older individuals of the same social group. Because wild infants seem to be tolerated by adults and juveniles from other social groups (Bezerra *et al. unpub. data*), and because they vocalized only toward members of their group, but not toward older individuals from other social groups, it is possible that they were already able to discriminate members of their own social group from members of other groups. Also, one could compare the loud cries of infant common marmosets to the babbling behavior in other primate species, e.g., pygmy marmosets (Snowdon and Elowson 2004). Loud cries and babbling behavior seems to result in increased social interactions with other individuals.

The vocal data obtained from juvenile marmosets also allow a greater understanding of their social lives: At 6–10 mo (Stevenson and Rylands 1988) their vocal repertoire seems to become adapted to their new status in the group. Indeed, juveniles uttered submissive cries when watching conspecifics, a call combination that probably reflects their social situation, i.e., that they are no longer so easily tolerated by older conspecifics as when they were infants (Bezerra and Souto, *pers. obs.*; Stevenson and Poole 1976). Thus, one can see the submissive cry as an attempt to get closer to or receive assistance from adults without being rejected.

Capturing a prey or eating it was not accompanied by vocalizations. Also, after capturing cicadas, grasshoppers, or small frogs, wild common marmosets tended to go to a secluded area apparently to be able to consume the prey undisturbed (Souto *et al.* 2007). However, when finding a relatively large amount of vegetable food, such as an opened jackfruit or mango, they tended to utter the very brief whistle call. It seemed to be a recruitment call, because upon hearing it, other group members approach and consume it along with the individual that called.

During vigilance behavior, individuals were more likely to utter the combination of *tsê egg*. The call types are relatively high-pitched and very short and, therefore, may serve to coordinate vigilance between group members, while minimizing the possibility of discovery by a predator. Uster and Zuberbühler (2001) recorded a similar situation in *Cercopithecus diana*.

The ways in which wild subjects uttered contact calls seemed to be affected by the behavior of the caller and to some extent by the behaviors or the vocalizations in which other conspecifics were engaged. Pook (1976, 1977) also reported this for captive *Callithrix jacchus* and Snowdon and Hodun (1981) for free-living *Cebuella pygmaea*. Moreover, as reported from captivity (Epple 1968; Yamamoto 1991), the age of the individual affected both the vocalization and the response to it. Thus, in adults and juveniles twitters elicited another twitter, while the reaction pause was their main behavioral response to the call. However, infants did not emit twitters or show a perceivable reaction when hearing a twitter made by an adult or juvenile of their group. Interestingly, captive infants twittered (Winter 1977; Winter and Rothe 1979). However, the twitters of captive infants differed from those of captive adults, being comprised of 2 call units, compared to the multiple units (≤21) of adult twitters.

Loud cries are a combination of call types that only infants emitted. Whereas adult and juvenile group members responded to loud cries, other infants apparently did not, which indicates that age specificity in wild common marmosets is related not only to the caller but also to the receiver. Indeed, because loud cries usually also involve an attempt to beg captured food from older group members, and because infants are less capable than adults of capturing prey, the targets of the call should be older and more experienced individuals. As expected, juveniles and adults responded by moving toward the caller.

In conclusion, the vocal repertoire of wild common marmosets is both large and varied, with vocal signals that have complex physical characteristics. Our results indicate that common marmoset communication is related mostly to the transmission of internal motivational states (Burling 1993). However, the distinctive alarm calls in response to birds and dogs and concomitant differentiated defensive actions suggest that vocalizations can also convey information about the environment. The ages of the individuals and the behavior of the caller and that of conspecifics surrounding individuals influence the production of call types in the repertoire. Moreover, the combination of different call types shows a flexibility that should be the topic of future studies.

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