Vocal Response of Captive-reared *Saguinus oedipus* During Mobbing

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Abstract Mobbing is an important component of antipredator behavior for animals from many taxa. Callitrichids are small-bodied primates that mob multiple types of predators. Though there have been several observations of callitrichids mobbing predators in the wild, their anecdotal nature provides only rough descriptions of behavior and vocalizations. Researchers could neither spectrographically identify nor quantify vocalizations owing to the limitations of observing predation in the field. We examined in detail the mobbing response of 1 callitrichid species, the cotton-top tamarin, in captivity. We recorded vocalizations for quantitative analysis and observed behavior qualitatively. We report 3 new vocalizations that had not been described in the original repertoire for the cotton-top tamarin. Analysis of the time course of a mobbing session yielded a pattern in which the highest intensity mobbing vocalizations decreased over the session even though lower intensity vocalizing continued, which may reflect a shifting strategy from mobbing to vigilance. The rate of calling during mobbing sessions differed from the rate of calling during control sessions. We discuss the vocalizations in relation to 2 hypotheses of form and function of antipredator calls. The newly described mobbing vocalizations may have an important impact on the study of mobbing because they represent a class of vocalizations that researchers have largely ignored in studies of callitrichids, thus raising new issues concerning past and future research on antipredator behavior in the family.

Keywords antipredator vocalizations · cotton-top tamarin · mobbing · vocal repertoire

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Introduction

Mobbing, defined as animals converging at a potential predator (Ostreiher 2003), is a common antipredator behavior across many taxa, and researchers have hypothesized it has several potential, nonexclusive functions (Curio 1978). That Callitrichidae are prey for a wide variety of predators, and mobbing is an important component of their antipredator behavior. Callitrichids most commonly mob snakes and mammals (Bartecki and Heymann 1987; Buchanan-Smith 1990; Corrêa and Coutinho 1997; Passamani 1995; Shahuano Tello *et al.* 2002), but they have also mobbed perched raptors (Ferrari and Lopes Ferrari 1990). Researchers have typically described their behavior in notable detail, but have only rarely given the same attention to vocalizations emitted during mobbing. Precise descriptions of vocalizations are important because different calls have different functions and represent different motivations.

Several authors have hypothesized that the functions of antipredator vocalizations have shaped their structures. Marler (1955) proposed that high-pitched, narrowband calls are cryptic and harder for predators to localize than more conspicuous low-pitched, broadband ones. Thus when a prey wants to evade detection (we use evasion throughout to refer to the combined flight/freezing response), a high-pitched, whistle-like call could alert group mates to the danger while putting the caller at relatively low risk of detection by the predator. The opposite is true for low-pitched, raspy calls, which have characteristics that make them easier for both predators and group mates to localize. Marler predicted that mobbing calls would be low-pitched notes to facilitate group mates finding the caller and joining in mobbing the predator. Owings and Morton (1998) offered an alternative hypothesis that essentially predicted the same structural pattern, but for a different reason. Under the motivational-structural code, mobbing calls, being inherently aggressive, are low-pitched and harsh to advertise large size. Evasive calls, which Owings and Morton included with appeasing calls, signify smallness to try to reduce the possibility of an attack. Under either hypothesis, high-pitched, narrowband calls are reserved for evasion, and low-pitched, broadband calls are used for mobbing predators. The hypotheses are important for the study of callitrichid antipredator behavior because they can provide information on the probable function of a given vocalization, which we can then test.

Cotton-top tamarins are native to Colombia and are one of the few callitrichid species for which researchers have documented the vocal repertoire (Cleveland and Snowdon 1982). Using the repertoire to identify calls, we provoked mobbing responses in captive-reared cotton-top tamarins to analyze the vocalizations emitted during mobbing. We identified, via recording equipment and sonograms, the specific calls emitted during the mobbing response as well as illustrated how the pattern of calling changed over time. As a control, we recorded sessions in which we did not stimulate mobbing. We predicted that the rate of vocalizing would be greater during the mobbing session than in the controls, and that individuals may emit specific vocalizations during mobbing that controls do not.

It is extremely difficult to obtain such a level of vocal analysis in the field. Natural predatory encounters are rare, fleeting, and unpredictable. Though numerous researchers have observed callitrichids encountering a predator in the wild, none have

been fortunate enough to have recording equipment set up and running at the time of the event. One option would be to simulate predator encounters experimentally, e.g., via stuffed specimens, but we are aware of no attempt to use such procedures with callitrichids. Thus, studies of captive subjects can fill in detail missing from field observations. As captive primates mob under certain circumstances, the response of captive-reared subjects ought to be qualitatively similar to that of wild-born individuals. Many variables could influence the duration of the response in the wild, including type of predator, whether an actual attack occurred, severity of threat, distance from predator, and time of day (esp. close to retirement). The precise duration of the response occurring in captivity may not correspond to the duration of responses in the wild, but the overall pattern of the response ought to correspond to the pattern of response in the wild, even if it is temporally stretched or compressed.

Understanding callitrichid antipredator behavior has important implications for the study of predator recognition. The more complete picture of the mobbing response we have, the better we can relate studies of captive-born subjects to the existing observations from the field. For example, authors of studies of captive-born callitrichids have reached conflicting conclusions about whether predator naïve subjects mobbed a terrestrial predator (Barros *et al.* 2002; Castro 1990; Hayes and Snowdon 1990). A more thorough understanding of the callitrichid mobbing response may help us to reconcile the differences among studies. Specifically, the lack of clearly defined mobbing behavior and vocalizations may have led different researchers, both in captive and in field studies, to label functionally different behavior as mobbing.

Methods

Subjects

We studied 5 families of cotton-top tamarins. All subjects were born in captivity and had spent their entire lives indoors; hence they had never seen a predator. Each family consisted of 1 adult reproductive pair and 3–6 offspring. Four of the families lived in large $3 \times 2.3 \times 1.8$ m cages, and 1 smaller family lived in a $2.3 \times 1.1 \times 1.8$ m cage. Each of the 5 families lived in a separate room. Two of the families had multiple cages of paired tamarins in their rooms, with each group visually isolated from the others. We equipped all cages with natural branches and ropes as the main climbing structures, and offered food and water at *ca*. 1 m above the floor to approximate the natural arboreal habitat of cotton-top tamarins. The main noon feed consisted of commercial foods (Zu-Preem Marmoset Diet and Lab Diet's New World Primate Diet), fresh fruits and vegetables, and a starch. We provided supplemental protein-rich foods at lights-on and in the late afternoon and water *ad libitum*. All subjects were on a 12-h light-dark cycle (Ginther *et al.* 2001).

Equipment and Procedure

We tape-recorded 11 sessions across 5 families (range 1–4) in which we provoked a mobbing response. The 2 stimuli we used to elicit mobbing responses were an

unfamiliar human dressed in specific clothing used only during capture of tamarins for veterinary treatment and a bristly, blue light fixture duster. The tamarins are caught and handled only for veterinary treatment, so they are not habituated to the procedure. Presenting a blue duster also elicited a mobbing response qualitatively identical to the response given to the capture situation. We do not know why the tamarins mob the duster. Apparently, they began mobbing it spontaneously the first time animal care staff attempted to clean with it. We conducted control sessions consisting of 9 recordings with the same 5 families (range 1–3). During the control sessions, we tape-recorded the subjects' vocalizations via the same methods, except that we did not present either of the mobbing stimuli. Thus, the control sessions represent baseline rates of vocalizing under no provocation. Earlier researchers had presented novel stimuli that might evoke curiosity or fear (Cleveland and Snowdon 1982; Hayes and Snowdon 1990), so we did not replicate the procedure. A human who was familiar to the tamarins was present during both mobbing and control sessions to make qualitative observations.

We recorded vocalizations via a Sennheisser ME 66 directional microphone and a Marantz PMD221 tape recorder placed outside of the subjects' cage. Sessions lasted between 3 and 7 min and comprised ≥1 exposure to the stimulus, with each group experiencing between 1 and 4 sessions (only 1 session/d). Because our goal was to elicit the strongest mobbing response possible to document vocal behavior fully, we intentionally varied sessions, both to prevent habituation and to find the optimal conditions to elicit responses from groups.

The session began with the experimenter setting up the equipment and beginning recording. We then brought the stimulus into the room-but left it outside of the subjects' cage. The human in veterinary garb moved around and waved about the blue duster, as movement helped stimulate a response. If we conducted multiple exposures within a session, we removed the stimulus from the room for a brief period and then reintroduced it. At the end of a session, we removed the stimulus and ceased recording. Control sessions consisted of the same procedure, except that no stimulus was present.

Data Analysis

We analyzed recordings via Avisoft SASLab Pro for Microsoft Windows. We filtered recordings (1 kHz high pass, 14 kHz low pass), digitized them into a .WAV file, and then visualized them in a spectrogram (frequency: FFT length = 512, Hamming window, bandwidth = 81 Hz, resolution = 62 Hz; temporal: 1/bandwidth = 12.3 ms, resolution = 4 ms). The analysis yielded the unexpected discovery of 3 vocalizations that were not described in the original published repertoire of cotton-top tamarins (Cleveland and Snowdon 1982): the bark, growl, and high-chirp trill. Barks typically occurred in bouts of calling; from each bout we sampled ≤3 individual bark notes for detailed analysis. For bouts >3 notes, we sampled 1 note from the beginning, middle, and end of the bout. We defined the beginning as the first 3 notes of the bout; the middle as the 3 or 4 (in the case of an even number) notes around the midpoint; and the end as the last 3 notes of the bout. We selected the notes to sample by chance, except that we ignored presumed background notes (due to chorusing) because their lower fidelity on the sonogram meant that we could not take precise measurements.

We analyzed 1 growl note, selected randomly, per string of growls or bark bout. We labeled each growl as alone, preceding a bark bout, occurring in the middle of a bark bout, or ending a bark bout. Notes of all types had to occur ≤.3 s of each other to be scored within the same bout. This was an arbitrary decision corresponding to the threshold of a noticeable pause in the calling. We took measurements of frequency and duration variables that differed for each of the new calls based on the major structural aspects of each call. For example, upsweep duration is an important part of the structure of the bark, but it is not a feature of either of the other calls. A uniform set of variables would fail to describe the unique structures of the different calls. We ignored noise in the measurements because we focused on the part of the vocalization with the highest energy. However, as the bark and growl overlap in some characteristics, we ran independent samples *t*-tests on the frequency measurements to test whether the bark and growl are indeed distinct calls.

To analyze the time course of the mobbing response, we identified calls and counted them in 15-s blocks (hence 4 blocks/min) across the duration of the session. This yielded rates of calling for all vocalizations across blocks, minutes, and sessions. To facilitate analysis, we corted call types into 4 classes based on structural and functional similarities (Cleveland and Snowdon 1982), which appeared to represent similar motivational states. We compared the 4 call classes over time and between mobbing and control sessions. We did not count calls that were not associated with mobbing or antipredator behavior. For analysis of the time course of the response, we used only the first 5 min from each session. Each family had ≥1 session that reached 5 min (or longer), but not all families reached 6 or 7 min. Thus, 5 min was the maximum length of time for which we could compare all families. We computed statistics via SPSS 12.0.

Results

Mobbing sessions were characterized by rapid, attack-like lunges directed at the stimulus. Immediately on stimulus presentation, tamarins piloerected, leapt to the front mesh wall of the cage, and threatened the stimulus by vocalizing with an open mouth. The tamarins typically threatened the stimulus for a while, and then retreated in the cage before making another lunge. Only adults and subadults seemed to make lunges; juveniles typically watched from a distance, and independent infants were even seen to hide at the very back corner of the cage, behind their nest box. The frequency of lunges decreased over the course of a session as the tamarins began to habituate to the stimulus. We observed none of the behaviors during control sessions. We did not take quantitative data on the behaviors, so we can report only qualitative descriptions.

Newly Described Vocalizations

The first newly described vocalization is the bark, which is a low, noisy call with an upward frequency modulation (Fig. 1). Subjects most often emitted barks in bouts consisting of repeated bark notes (Fig. 2). Bark bouts were associated with piloerection of the head, body, and tail, and attack-like lunges at the stimulus. We

Fig. 1 Sonogram showing a single growl followed by a single bark.
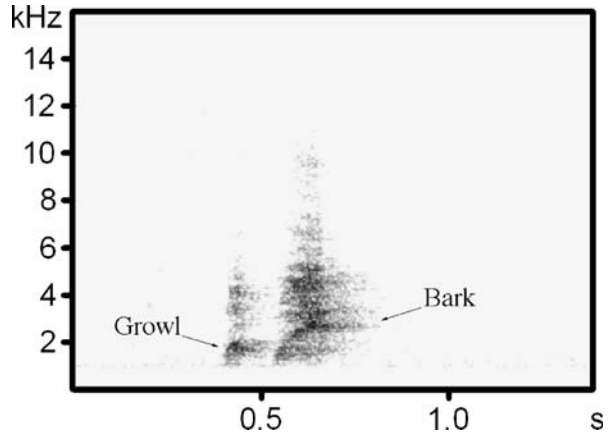
recorded 90 bark bouts from the 11 sessions, with ≥1 bark bout recorded in each session (and therefore from each family). Sampling yielded a total of 234 notes for detailed analysis. For each sampled note, we measured the start frequency, stop frequency, duration of the upsweep, and the overall duration of the note (Table I). Our measurements showed no difference between notes sampled at the beginning, middle, or end of a bout, or between families; therefore, we combined all notes and treated them as independent in the analysis.

The second call newly identified is the growl, a low, noisy call that subjects emitted as a single note and in short strings (Fig. 1). Growls were frequently associated with bark bouts; growls began bouts, occurred in the middle of a string of barks, or ended a bout (Fig. 2). Sampling yielded a total of 127 analyzed growls, with every family represented at least once. Growls were shorter, had little to no frequency modulation, and were much less intense than the bark (Table II). A small percentage of growls approach bark-like structure, in that they tend to be longer, have a higher maximum frequency, and display some of the curved shape of the bark. There is no difference in structure between growls occurring alone, preceding bouts, in the middle of bouts, or ending bouts, or between families; therefore we combined all notes and treated them as independent in the analysis. Independent

Fig. 2 Sonogram of a bark bout. This bout contains a mixture of bark and growl notes. Growls both lead into the barks and end the bout as calling trails off. There is also one growl note in the middle of this bout. Note the slightly different time scale than in Fig. 1.
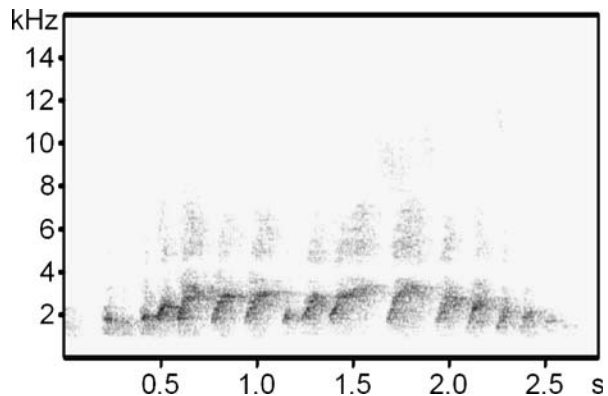
Table I Characteristics of a single bark note (*N*=234)

	Mean ± SD	Median (range)	Coefficient of variation (%)
(Start frequency (Hz)	1417±210	1400 (930–2340)	14.8
Stop frequency (Hz)	2714±325	2750 (1310–3460)	12.0
Upsweep (s)	.051±.018	.050 (.012–.124)	34.5
Duration (s)	.139±.055	.132 (.050–.378)	39.7

samples *t*-tests comparing the bark starting frequency to the growl maximum frequency (T_{359}=14.53, 2-tailed *p*<.001), and the bark maximum frequency to the growl maximum frequency (T_{359}=24.04, 2-tailed *p*<.001) are both highly significant.

The third newly identified call, the high-chirp trill (Fig. 3), fits into the trill category of the pulsed vocalizations class (Cleveland and Snowdon 1982). The trill begins at a higher frequency than the trills described previously. We recorded and analyzed 57 high-chirp trills distributed across all 5 families. For each high-chirp trill we measured the start frequency, peak frequency of the first note, maximum peak frequency of the trill (sometimes 2 or even all 3 of the measures came from the same point), lowest peak frequency of the trill, number of notes, duration, and number of inflection points (e.g., a trill that only descended would have 0 inflection points, a trill that descended and then ascended would have 1 inflection point, etc.). Values are in Table III. There was no difference among families, so we combined all trills and treated them as independent in the analysis.

Bark Bout Characteristics

We calculated mean and median values for the number of bark notes in a bout, bout duration, and the number of growls preceding, in the middle of, and ending a bout (Table IV). In addition to growls, high-chirp trills preceded bark bouts on occasion. As mobbing is a social behavior, it was common for several individuals to chorus during a bark bout. We logged noticeable chorusing, defined as detection of overlapping notes. We may have underestimated the frequency of chorusing; if multiple individuals called in a bout but never overlapped notes, we would not be able to detect the chorus. Table V contains the frequency of growls, high-chirp trills, and chorusing.

Overall Session Characteristics

We identified a total of 11 different vocalizations associated with fear or antipredator behavior emitted during the mobbing response. In addition to the 3 newly described

Table II Characteristics of growls (*N*=127)

	Mean ± SD	Median (range)	Coefficient of variation (%)
Maximum frequency (Hz)	1838±340	1810 (1120–2710)	18.5
Duration (s)	.070±.025	.066 (.032–.190)	35.4

Fig. 3 Sonogram of a high-chirp trill. This trill has 3 inflection points.
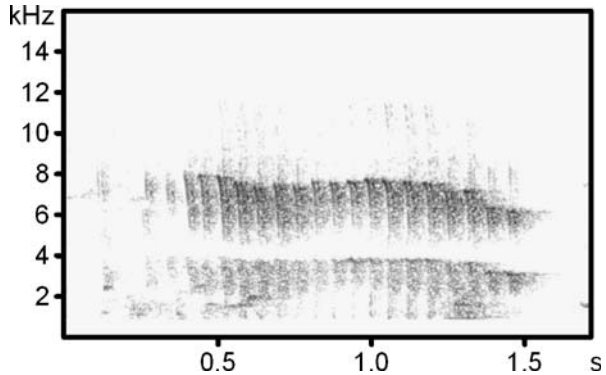
calls, barks, growls, and high-chirp trills, we also observed previously described H chirp trills; chevron chatters; chirp bursts; A, E, and H chirps; chevrons (single notes); and quiet long calls. We sorted barks and growls into the mob class; high-chirp trills, H chirp trills, chevron chatters, and chirp bursts into the pulsed class; all 3 chirps into the chirp class; and chevrons and quiet long calls into the contact class. When calculating means for numbers of calls per family, we corrected for the number of adults and subadults in the group (number of calls/[number of adults + number of subadults]). Juveniles and infants watched from a distance and did not seem to perform any of the high-intensity mobbing behaviors. Because juveniles and infants seemed to be more observers than actors in the mobbing response, we assumed that they did not add substantially to the vocalizing.

Averaged across families, contact calls were the most frequently emitted call class at a mean rate of 12 calls/min. Because contact calls remained fairly constant throughout a mobbing session, and subjects emitted them at a consistently higher rate than the other classes, they are not shown in Fig. 4a. An ANOVA examining the change in mob calls over time is significant ($F_{4,16}=6.57$, $p=.003$), and there is a significant contrast between min 1 and min 2–5 ($F_{1,4}=17.54$, $p=.014$). Single-factor ANOVAs on the other call types are nonsignificant ($F\leq1$).

The control sessions revealed a different pattern (Fig. 4b). The most important feature of the control sessions is that we recorded no bark or growl in any of the sessions. Whereas every family emitted ≥1 bark during the mobbing sessions, none of the families emitted a bark during the control sessions ($\chi^2=6.4$, $p<.02$, 1 sample with Yates correction for continuity). Subjects emitted pulsed and contact calls at

Table III Characteristics of high-chirp trills ($N=57$)

	Mean ± SD	Median (range)	Coefficient of variation (%)
Start frequency (Hz)	7197±1723	7530 (3960–11,400)	23.9
First note peak frequency (Hz)	7356±1692	7530 (3960–11,400)	23.0
Maximum peak frequency (Hz)	7622±1624	7930 (4460–11,400)	21.3
Minimum peak frequency (Hz)	5299 ± 1769	5430 (1870–8650)	33.4
Notes	7.2±4.3	6 (3–20)	59.3
Inflection points	1.05±1.12	1 (0–5)	106.9
Duration (s)	.430±.237	.348 (.130–1.214)	55.1

Table IV Characteristics of bark bouts (*N*=90)

	Mean ± SD	Median (range)	Coefficient of variation (%)
Bark notes	8.0±7.1	5 (1–28)	89.1
Duration (s)	1.974±1.641	1.368 (.070–7.302)	80.2
Growls-pre	1.8±1.5	1 (1–8)	60.5
Growls-mid	2.7±1.6	2 (1–6)	60.4
Growls-post	2.6±1.5	2 (1–7)	83.2

For the growl data, mean and median values are given for each category when ≥1 growl was given in a bout.Table V. Frequency of bout

very low rates, and gave only chirp calls with any frequency. Planned comparisons of paired *t*-tests reveal significantly more mob and pulsed calls during the mobbing sessions than in the controls (mob: T_4=3.35, 1-tailed *p*=.014; pulsed: T_4=4.90, 1-tailed *p*=.004), and an almost significant trend for contact calls in the same direction (T_4=1.80, 1-tailed *p*=.07).

Discussion

We discovered 3 vocalizations—bark, growl, and high-chirp trill—that had not been previously described for the cotton-top tamarin. Subjects used the vocalizations in the mobbing response and have important implications for the study of mobbing behavior. The results generally supported our prediction that calling would be more frequent during mobbing than in control sessions.

The frequency parameters of the 3 new calls tended to have low levels of variability (coefficient of variation ≤ 30%), similar to values reported for chirps from cotton-top tamarins (Snowdon 1988). The length of a call or bout, measured in either notes or seconds, had much higher variation (coefficient of variation >30%), most likely owing to the fluctuating motivation of the caller. The presence and frequency of other features of the bark bout, such as growls and high-chirp trills, is probably also related to motivation. The classification of the bark and the growl as distinct calls is based on the analysis of prototypical notes, which are quite different (Fig. 1) and supported by our statistical analysis. However, there may in fact be a graded nature between these calls. The bark bout in Fig. 2 contains a few notes that appear to be intermediary between the 2 types. The intermediary forms appeared only in bark bouts, so all of the growls given alone had the typical structure. Thus we think that it is useful to classify the

Table V Frequency of bout characteristics (*N*=90)

Growls-any	Growls-pre	Growls-mid	Growls-post	High-chirp trill-pre	Chorusing
90.0%	57.8%	38.9%	61.1%	16.7%	51.1%

Frequencies calculated as the percentage of bark bouts that contained ≥1 observation of each category. We scored multiple observations during a single bout as a single occurrence. Example: 57.8% of all of the bouts began with ≥1 growls, and the remainder began with no growls

Fig. 4 (a) Mean calls per min-
ute for mobbing sessions. There
was a significant contrast for
mob calls between the 1st min
and min 2-5. (b) Mean calls per
minute for control sessions.
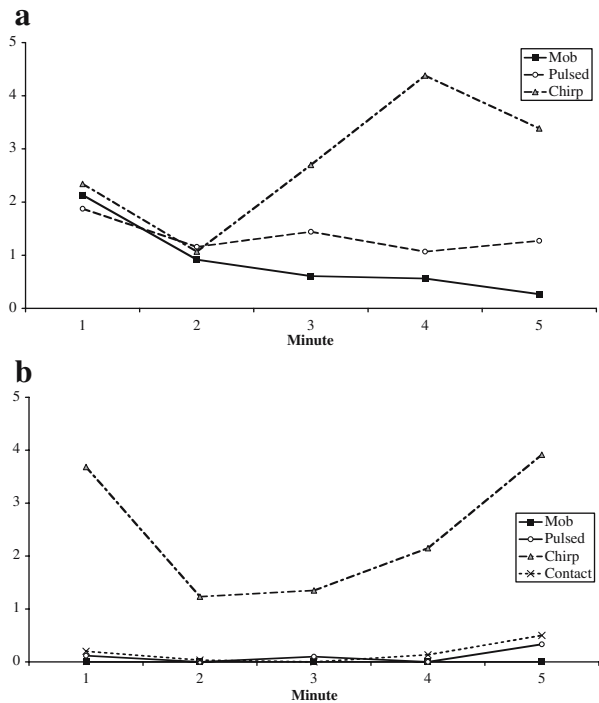
2 calls as distinct, but with the caveat that they may blend into each other in some
circumstances.

Motivational factors appear to underlie the pattern of calling during the mobbing
and the control sessions. In the mobbing sessions, subjects emitted the high-intensity
mob calls early, which then waned, but continued to give the lower intensity pulsed,
chirp, and contact calls continued with the same frequency throughout a session.
This may signal a transition in the motivation of the tamarins from primarily
mobbing to primarily vigilance. It seems that the tamarins were still aroused by the
stimulus in the 5th min, but to a much lesser extent than the 1st min. The behavior
seems to have shifted from outright attack to monitoring the situation.

During the control sessions, we recorded no vocalization from the mob class,
even though all of the other call classes were represented. Authors of previous
studies presented cotton-top tamarins with a variety of novel stimuli and did not
record any call from the mob class (Cleveland and Snowdon 1982; Hayes and
Snowdon 1990) but did record calls from the pulsed, chirp, and contact classes. This
reinforces our distinction that barks and growls are mobbing calls because they were
never given in other contexts. Very specific stimuli must be presented before cotton-
top tamarins will emit barks and growls, which may explain why researchers had not
previously recorded them. Various stimuli in their captive environment will elicit
vigilance (chirps), contact calling, and potentially even higher arousal vocalizing (pulsed
calls, typically when the stimulus persists or when multiple groups begin calling), but
the ambiguous sources of arousal never lead to mobbing behavior. It is only when 1 of 2

known stimuli are present, or an individual is caught and handled, that cotton-top tamarins will mob.

To our knowledge, the findings represent the most detailed examination of mobbing vocalizations in any callitrichid. Observations from the field have reported the circumstances of mobbing and provided rough descriptions of vocalizations and behavior, but none identified, measured, or counted vocalizations in the detail we have presented. Our description of the bark vocalization and the corresponding bout structure, while new to our colony, may not be the first published observation of this call type in the Callitrichidae. Epple (1968) reported a scream vocalization for 7 callitrichids (*Callimico goeldii*, *Callithrix geoffroyi*, *C. jacchus*, *Leontopithecus rosalia*, *Mico argentatus*, *Saguinus geoffroyi*, and *S. oedipus*) that matches 1 context (handling) of the bark (taxonomy updated to correspond to Rylands *et al.* 2000). The only discrepancy is the duration of the call (1–1.5 s) Epple described, which is much longer than the duration we have reported. Because Epple (1968) presented no sonogram, the duration represents a subjective estimation. Owing to the lack of sonograms, there is no frequency measurement.

Two other studies also seem to report analogous calls in the screech of golden lion-tamarins (McLanahan and Green 1978), and the scream of red-bellied tamarins, (*Saguinus labiatus labiatus:* Coates and Poole 1983). Both vocalizations have the same context (handling by humans), similar durations (mean of 0.230 s±.150 for *Leontopithecus rosalia*; range of .180–.550 s for *Saguinus labiatus labiatus*), and similar frequency ranges (0–7 kHz for *L. rosalia*, 1.5–8 kHz for *S. l. labiatus*); all of which are consistent with our description of the bark (Table I). While it may seem that the maximum frequency differs between the 2 species and the cotton-top tamarin, we found a similar maximum around 7–8 kHz if we included noise in our measurements (Fig. 1).

Looking broadly at the published vocal repertoires of the Callitrichidae, it is evident that similar classes of calls exist for all of the species studied (Cleveland and Snowdon 1982; Coates and Poole 1983; Epple 1968; McLanahan and Green 1978; Moody and Menzel 1976). The main barrier to comparisons is the nonstandardized terminology for obviously similar calls. All 8 of the species produce vocalizations we have called chirps (tsik in Epple 1968; chucks and sudden calls in Moody and Menzel 1976; clucks in McLanahan and Green 1978; seek, seep, and tsak in Coates and Poole 1983). The same can be said of the trills and contact calls. Therefore, based on the wide range of analogous calls in the various species of Callitrichidae, and hints at the existence of an analogue to the bark in 3 previous studies, it seems likely that analogues of the bark and growl vocalizations exist in many, if not all, callitrichid species.

Marler (1955) proposed that high-pitched, narrowband vocalizations are harder to localize than low-pitched, broadband ones, and that a gradual onset and offset are harder to localize than a sudden onset and offset. He illustrated this with the antipredator vocalizations of male chaffinchs (*Fringilla coelebs*), which uses a call *ca.* 7 kHz that begins and ends imperceptibly for the flight response, and a call *ca.* 4 kHz with sharp discontinuities for mobbing. Owings and Morton (1998) described the same pattern, in the Carolina wren (*Thryothorus ludovicianus*) with their hypothesis of the motivational-structural code. The hypothesis predicts high-pitched whistles for extreme fear (evasion) and low-pitched, harsh calls for extreme

aggression (mobbing). In relation to both hypotheses, the bark fits well with the characteristics of mobbing calls, but the chirps do not. Under the motivational-structural code, chirps are at most weakly aggressive, but they may belong with calls intermediary between fear and aggression (Owings and Morton 1998). The evasion call of cotton-top tamarins is a form of E chirp (Cleveland and Snowdon 1982), so other chirps used in an antipredator context may contain fear as part of the motivation. The E chirp does not contain the hypothesized whistle-like elements of evasion calls, but it has a much shorter duration than whistles (Cleveland and Snowdon 1982); a very short duration may accomplish the same goals of being cryptic or signifying smallness/fearfulness. The high-chirp trill is consistent with the description of moderately aggressive calls (Owings and Morton 1998). On the basis of the findings that 1) barks were associated with mobbing behaviors, 2) subjects never emitted barks spontaneously, and 3) the structure of the bark was consistent with 2 separate hypotheses of form and function in vocal communication, we conclude that the bark represents the highest intensity mobbing call of cotton-top tamarins (with the growl representing slightly lower arousal), and thus potentially for all of the Callitrichidae.

The discovery of the bark vocalization has important implications for the study of antipredator behavior in callitrichids. Several studies have exposed captive-born callitrichids to predators or predator models (Barros *et al.* 2002; Caine 1984, 1988; Caine and Marra 1988; Castro 1990; Hayes and Snowdon 1990; Hankerson and Caine 2004). However, the only studies that report bark-like calls recorded them in the context of capture and handling (Coates and Poole 1983; Epple 1968; McLanahan and Green 1978), and now in response to a blue duster. It is unclear from the captive studies how the bark relates to natural antipredator behavior.

Field observations of mobbing by callitrichids have not clarified the situation owing to the limitations of measuring encounters in the wild. Most of the time the vocalizations are relegated to statements such as alarm calls, mobbing calls, excitement calls, squeals, or screams (Bartecki and Heymann 1987; Buchanan-Smith 1990; Heymann 1987, 1990; Izawa 1978; Passamani 1995; Peres 1993; Shahuano Tello *et al.* 2002; Stafford and Ferreira 1995). Similarly, vague descriptions accompany encounters with raptors. The lack of specificity of vocal types in field reports may have led some experimenters to equate a relatively low-intensity vocal response in captive-born subjects to a potentially high-intensity vocal response of natural encounters.

Only 2 publications report the precise vocalizations the subjects emitted in the context of mobbing (Corrêa and Coutinho 1997; Ferrari and Lopes Ferrari 1990). Ferrari and Lopes Ferrari (1990) reported 2 different intensities of mobbing by buffy-headed marmosets (*Callithrix flaviceps*) with snake mobbing relegated to the lower intensity type (pattern 2a). The response of the marmosets was to approach the snake and emit low-intensity tsak vocalizations, which correspond to chirps. This response was different from the mobbing response to terrestrial mammals (pattern 2b), which consisted of higher intensity tsak calls. Observers of closely related buffy-tufted-ear marmosets (*Callitrix aurita*) mobbing a pit viper (*Bothrops jararaca*) reported similar low-intensity behavior and vocalizations (Corrêa and Coutinho 1997). Ferrari and Lopes Ferrari (1990) speculated that predation in their study area may be lower than that for other callitrichids, or that predation pressure is

lower for marmosets than for tamarins in general. It is possible for the intensity of response to a predator to vary with predation pressure, if the difference in pressure results from differences in prey vulnerability and not predator density. Thus, we do not know if the low-intensity mobbing response to snakes by the 2 marmoset groups is 1) a product of lower predation pressure for the populations alone, 2) typical for marmosets but not tamarins, owing to differing predation pressures, or 3) universal for all callitrichids. A similar principle applies for the description of high-intensity mobbing of mammals (Ferrari and Lopes Ferrari 1990).

Many questions remain unanswered in the study of the antipredator behavior of the Callitrichidae. First, we need to know whether the bark vocalization indeed has analogues in other callitrichids. The most reliable method to elicit the calls seems to be capture and handling, though as with the cotton-top tamarins we studied and the blue duster, there may be idiosyncratic stimuli that elicit these calls. Second, we need more detailed descriptions of the vocalizations given during natural predator encounters, as Ferrari and Lopes Ferrari (1990) and Corrêa and Countinho (1997) have done. Even if no one is fortunate enough to tape record an encounter, familiarity with the subjects' vocal repertoire will allow for qualitative descriptions of the precise calls given. This is important because we have detailed vocal descriptions for only 2 closely related marmoset species. Several studies on captive-born callitrichids have reported some degree of anxiety toward predators. What we do not know is whether this anxiety is part of the full, natural response to the predator, implying innate recognition, or a less intense fear of novelty, implying learned recognition. Ultimately, the question of innate vs. learned predator recognition has important implications for reintroductions of captive-born callitrichids (as well as other primates) and the prerelease training they receive.

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