

RESEARCH ARTICLE

The Effect of Habitat Acoustics on Common Marmoset Vocal Signal Transmission

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Noisy acoustic environments present several challenges for the evolution of acoustic communication systems. Among the most significant is the need to limit degradation of spectro-temporal signal structure in order to maintain communicative efficacy. This can be achieved by selecting for several potentially complementary processes. Selection can act on behavioral mechanisms permitting signalers to control the timing and occurrence of signal production to avoid acoustic interference. Likewise, the signal itself may be the target of selection, biasing the evolution of its structure to comprise acoustic features that avoid interference from ambient noise or degrade minimally in the habitat. Here, we address the latter topic for common marmoset (*Callithrix jacchus*) long-distance contact vocalizations, known as phee calls. Our aim was to test whether this vocalization is specifically adapted for transmission in a species-typical forest habitat, the Atlantic forests of northeastern Brazil. We combined seasonal analyses of ambient habitat acoustics with experiments in which pure tones, clicks, and vocalizations were broadcast and rerecorded at different distances to characterize signal degradation in the habitat. Ambient sound was analyzed from intervals throughout the day and over rainy and dry seasons, showing temporal regularities across varied timescales. Broadcast experiment results indicated that the tone and click stimuli showed the typically inverse relationship between frequency and signaling efficacy. Although marmoset phee calls degraded over distance with marked predictability compared with artificial sounds, they did not otherwise appear to be specially designed for increased transmission efficacy or minimal interference in this habitat. We discuss these data in the context of other similar studies and evidence of potential behavioral mechanisms for avoiding acoustic interference in order to maintain effective vocal communication in common marmosets. *Am. J. Primatol.* 75:904–916, 2013. © 2013 Wiley Periodicals, Inc.

Key words: *Callithrix jacchus*; vocal communication; behavioral ecology; sound broadcasts; sound window

INTRODUCTION

Animal vocalizations evolved in response to a myriad of selection pressures. These include constraints imposed on signal structure by the species' vocal-motor and auditory systems, as well as environmental constraints on effective exchange of communicative information [Bradbury & Vehrencamp, 2011]. In noisy acoustic environments, interference from both biotic and abiotic sources, such as the density of foliage, forest structure, humidity and heterospecific acoustic signals can distort and ablate the spectro-temporal structure of vocal signals [Morton, 1975; Wiley & Richards, 1978, 1982], thereby degrading the communicative content of vocal signals. There are at least two dimensions along which selection may act in order to improve commu-

nication in these environments. One is selection for auditory feedback-mediated vocal-motor control that allows callers to monitor the acoustic environment and initiate vocalizations during periods of low acoustic interference [Roy et al., 2011; Waser &

Contract grant sponsor: NIH; contract grant numbers: K99/R00 DC009007, R01 DC012087; contract grant sponsor: UCSD Academic Senate Grant.

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Received 30 October 2012; revised 1 March 2013; revision accepted 5 March 2013

DOI: 10.1002/ajp.22152

Published online 16 April 2013 in Wiley Online Library (wileyonlinelibrary.com).

Brown, 1984]. Another is selection for acoustic adaptations in the signal structure. Vocalizations may comprise acoustic characteristics that result in decreased interference by ambient sound or otherwise resist degradation in particular ecosystems [Waser & Brown, 1984, 1986; Waser & Waser, 1977; Wiley & Richards, 1982]. Ultimately, a species' vocal communication system is likely to have evolved both behavioral and acoustic adaptations for improving communicative efficacy to varying degrees. The exact relationship between the two, however, is likely species-specific. The current study sought to complement ongoing behavioral experiments investigating common marmoset (*Callithrix jacchus*) feedback-mediated vocal control [Roy et al., 2011] with a comprehensive characterization of the species' habitat acoustics and vocal signal transmission. Broadly defined, our aim was to better understand the potential evolutionary and extant strategies employed by marmosets to maintain effective communication in their natural habitat.

The quantification of species' habitat acoustics has occurred for several decades, with a wealth of data available [Brown et al., 1995; De la Torre & Snowdon, 2002; Kime et al., 2000; Marten & Marler, 1977; Marten et al., 1977; Zimmerman, 1983]. These studies have traditionally sought to characterize the acoustic landscape in which communication occurs, and, by comparison with extant species-typical vocalizations, determine the plausibility of selection for an acoustic structure that improves signal transmission in this environment. Waser and Brown [1984] speculated that selection would favor nonhuman primate long-distance vocalizations that occurred within a specific spectral "sound window." In other words, long-distance vocalizations comprising a fundamental frequency (F0) in a particular frequency range may avoid acoustic interference from other species, such as birds, thereby increasing transmission efficacy. Alternatively, signalers could avoid acoustic interference by taking advantage of a temporal "sound window." Callers could monitor the ongoing acoustic events in the forest and control the timing and occurrence of vocal behaviors to initiate during periods with little interference from heterospecific vocalizations. Several Old World monkeys, for example, show increased vocalization rates early in the morning when other species are less acoustically active [Brown et al., 1995; Waser & Brown, 1986; Waser & Waser, 1977]. Exploiting windows in both the frequency and time domains can improve communication in noisy acoustic environments.

The common marmoset (*C. jacchus*) is a small (~200–400 g), arboreal New World monkey, endemic to Northeastern Brazil. This species potentially represents a unique case study for communicating in complex acoustic environments for at least the following reasons. Despite living in noisy forest

habitats, the vocal repertoire of the species is relatively high in frequency, with most calls having a F0 of ~6–9 kHz [Bezerra & Souto, 2008; Miller et al., 2010; Pistorio et al., 2006]. This includes their long-distance contact call, known as the "phee" [Miller et al., 2010; Norcross & Newman, 1993]. The physics of sound transmission suggest that signals of at this frequency are likely to significantly degrade in forest habitats [Morton, 1975; Wiley & Richards, 1978]. One potential reason for the high frequency of these calls may be related to the species' small body size (~200–400 g). Indeed many Callitrichids of similar body size produce vocalizations in this frequency range. There are, however, exceptions. The closely related and similarly sized cotton-top and Geoffroy's tamarins (*Saguinus oedipus*, *S. geoffroyi*) produce a long-distance contact call with a F0 of ~1.5–1.8 kHz [Cleveland & Snowdon, 1982; Weiss et al., 2001], well below the F0 of common marmoset calls. Furthermore, the high frequency of the marmoset vocal repertoire presumably places them in direct acoustic conflict with many of the avian, insect, and anuran species inhabiting the same forests, but direct evidence to this end is limited. A single study of pygmy marmosets (*Cebuella pygmaea*), another Callitrichid species that produces high frequency vocalizations [Elowson & Snowdon, 1994; Pola & Snowdon, 1975], provided evidence of significant acoustic competition from the natural habitat acoustics within the species-typical vocal range [De la Torre & Snowdon, 2002]. Comparable habitat acoustic data are not available for other Callitrichids. Field data on common marmosets have indicated little change in calling rate over the course of a day [Bezerra et al., 2009], suggesting that marmosets do not alter vocalization rate to take advantage of times of day with low acoustic interference. Nevertheless, other behavioral strategies or acoustic adaptations may serve to reduce acoustic competition. More data are needed on the habitat acoustics of common marmosets in order to better understand the scope of potential interference and the presence of available spectral and temporal sound windows.

The aim of this study was to characterize the effects of habitat acoustics on vocal signal transmission in common marmosets. The study consisted of two parts. First, we recorded the ambient acoustics of a typical forest inhabited by the species in Northeastern Brazil during both the rainy and dry seasons over a 2-year period. The aim here was to quantitatively characterize differences in biotic and abiotic acoustic sources over different time intervals (i.e., hours, seasons, and years). Given the strong seasonal variability of this forest for precipitation and species diversity [Santos et al., 2004] and density, as well as the activity patterns of most vertebrates, we predicted that significant differences in the ambient acoustics of the forest would be evident along

multiple time scales. Second, we also performed a series of experiments in which acoustic stimuli were broadcast and rerecorded at different distances to test the effects of sound degradation on different types of sounds. This study comprised two broad stimulus sets. The first set consisted of synthetically generated tones and clicks at different frequencies. Consistent with previous work [Morton, 1975; Wiley & Richards, 1978, 1982], these stimuli were designed to measure the effects of degradation and reverberation on sound transmission and provided a comparison with previous work. We predicted that these stimuli would likely show a similar rate of deterioration found in similarly forested habitats from previous work. The second stimulus set comprised naturally produced and synthetically manipulated marmoset phee calls. This long-distance contact call comprises a F0 of ~6-9 kHz [Fig. 1; Miller et al., 2010]. By broadcasting naturally produced and selectively manipulated versions of this call type, we sought to determine how the habitat acoustics affected specific acoustic features during sound transmission. Because of the relatively high frequency of the marmoset phee call, we postulated that the call may not be specifically adapted to limit signal degradation in the habitat. Rather, marmosets may maintain effective communication by limiting degradation through other means, such as acoustic monitoring and vocal timing.

METHODS

Study Site

All work was carried out at the Tapacurá Field Station (09°07'S, 34°60'W), a region of semi-deciduous Atlantic Forest near the northeastern city of Recife, Pernambuco, Brazil. Permission to conduct this research was granted by the Federal Rural University of Pernambuco (Recife, Brazil). All research adhered to the ASP principles for the ethical treatment of primates and the laws governing animal research in Brazil.

The field site is 208 m above sea level, has an average annual temperature of 26°C and an average annual humidity of 80% [Santos et al., 2004]. The 382 ha of forest serves as habitat for a large, native population of common marmosets, which have been the subject of several previous studies of feeding ecology and behavior [Hubrecht, 1985; Santos et al., 2004; Scanlon et al., 1989]. During the present study, common marmosets were frequently observed and heard vocalizing throughout the forest, indicating a dense resident population of this species at this location. The site has a distinct rainy season from April to September and dry season from October to March. As per definition, this semi-deciduous forest loses part of its foliage during the dry season. This is also associated with a fluctuation in insect abundance [Nocedal, 1994]. Such variation in both foliage and

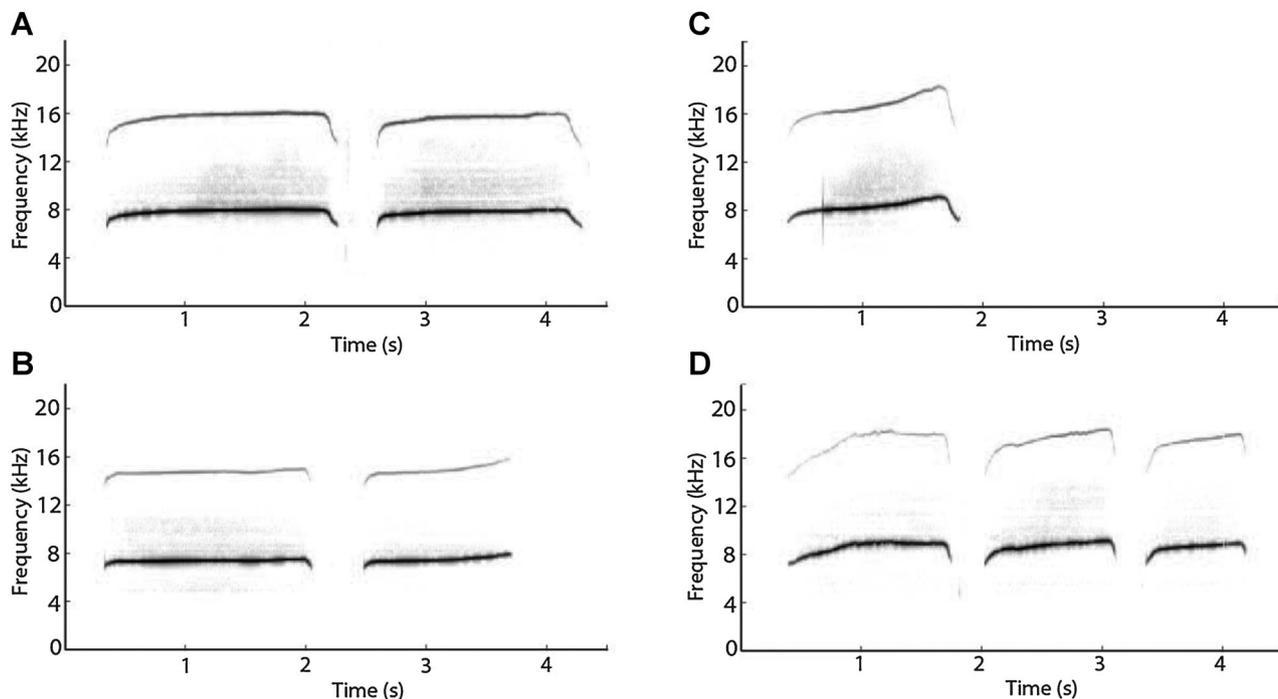


Fig. 1. Phee call spectrogram exemplars, same scale used on all plots. A: Common marmoset two-pulse phee call of an adult male; B: Two-pulse phee call, adult female; C: one-pulse phee call, adult female; D: three-pulse call, adult male.

insect populations is expected to result in season-specific habitat acoustic patterns. For this reason, four trips to the field site were made: twice during the wet season, in March 2010 and 2011, and twice during the dry season, in late August–September 2010 and September 2011.

Ambient Recordings

Ambient recordings were performed throughout the day at 2 hr intervals from 0600 to 1800 hours at forested locations within the field site. Each ambient recording was 10 min in length. Three full days of recordings were gathered during each of the four trips to the field site. Recordings were made by an observer holding the microphone and recorder at arm height with the microphone pointed vertically. Great care was taken to avoid recording human-generated sounds of any sort, and recording sessions were restarted in the event of such sound interference.

Ambient recordings were made using a Marantz PMD660 digital recorder with a Sennheiser ME-62 omni-directional condenser microphone (foam wind-screen attached) positioned vertically. All audio used a 44.1 kHz sample rate, stored in 16-bit WAV format on SD cards.

Ambient Acoustic Analysis

All analyses were performed in MATLAB v7.10 and v7.11. To analyze changes in the frequency spectrum throughout the day, we used a multi-taper fast Fourier transform (FFT) method from the Chronux MATLAB toolbox (www.chronux.org). Three sections of 1 min each were randomly sampled from the 10 min raw recordings, and the power spectra were averaged to represent each recording.

To confirm similarities apparent the power spectra, we used discriminant function analysis (DFA). This analysis builds a linear model from past experience with a dataset, and then uses the model to predict membership, based on a given variable, in naturally occurring data groupings. Here, DFA was used to determine if the spectral signature of an ambient recording could predict the following attributes of the recording: time of day, time of day by season, season, season by year, and year. DFA was performed using algorithms from the MATLAB Statistics Toolbox.

Sound Broadcasts

To investigate sound transmission properties of the habitat, a set of sounds were broadcast and re-recorded at three locations within the field site. Locations were chosen to represent possible variations in vegetation density at the Tapucara Field Station. Each location was marked using physical markers and GPS during the first usage (March 2010)

and reused for the sound broadcasts during the subsequent trips. Average vegetation density was determined by employing the nearest neighbor method, in which we measured the distance to the nearest neighbor of each tree (with at least 5 cm circumference) at 1 m height, in two 5 m² areas [Souto et al., 2007]. Broadcast location 1 had a high tree density of 3.7 trees/m² and a high mean nearest neighbor distance of 86.2 cm. Location 2 had a lower density of 2.3 trees/m² and a nearest neighbor distance of 58.7 cm. Location 3 also had lower density of 2.3 trees/m² and a nearest neighbor distance of 73.7 cm.

Broadcasts were made using a Roland Micro-Cube amplified speaker. The speaker was hung from a tree branch at a height of approximately 5 m, at a location with no interfering trees or branches immediately in front of the speaker. The height of the speaker was positioned to be within the canopy layer at each location, as this is the level of the forest that marmosets were observed to travel at this location. Before the beginning of each broadcast session, the system was calibrated such that a 1 kHz sine wave tone measured 1 m distance from the speaker registered 90 dB SPL on an Extech dual-range sound level meter (Model 407732).

Recordings of broadcast sounds were made at four distances from the sound source: 10, 20, 40, and 80 m. All recording sites lay on an approximately straight line from the sound source, as confirmed by GPS mapping. To re-record broadcast sounds, we used the Marantz PMD660 recorder and Sennheiser ME66 directional microphone (foam windscreen attached) aimed in the direction of the broadcast speaker. Recordings were made using previously mentioned recording settings.

Two playlists of sounds were broadcast. The first playlist, broadcast during the 2010 wet and dry seasons, consisted of the following components: (1) twenty-five marmoset phee calls (recorded from a captive colony at University of California, San Diego), (2) seven click train stimuli, each consisting of three 20-cycle trains of 30 msec click and 70 msec silence, with click F0s nearly logarithmically spaced at 125 Hz, 250 Hz, 500 Hz, 1 kHz, 2 kHz, 4 kHz, 6 kHz, and 8 kHz, and (3) seven sine-wave tones, 1 sec each, at the same frequencies as the click trains.

The second playlist, broadcast only during the 2010 dry season, consisted of acoustic manipulations of marmoset phee calls. Manipulations were either in the time domain—that is, calls were sped up or slowed down, while maintaining frequency—or in the frequency domain—that is, the fundamental frequency was shifted up or down, while maintaining the original length of the call. This playlist consisted of the following components: (1) five unmodified marmoset phee calls, (2) frequency manipulations of these five calls such that the mean F0 was at 250 Hz,

500 Hz, 1 kHz, 2 kHz, 4 kHz, 8 kHz, and 16 kHz, with harmonics scaled appropriately, and (3) time manipulations of the five calls, such that frequency was not altered, but call lengths were scaled by factors of 0.2, 0.6, 0.8, 0.9, 1.1, 1.2, 1.4, and 1.8.

Analysis of Broadcast Sounds

Re-recorded broadcast sounds were primarily analyzed using normalized cross-correlation with the original broadcast stimulus as the template. This analysis produces an array of correlations as a function of time lag between the template waveform and the sample waveform. As such, the maximum cross-correlation value, presumably located at the time lag where the original template stimulus is found in the recording, was used for each broadcast sound, and all other values were discarded. Cross-correlation values were compared using multivariate repeated measures ANOVA, implemented with SPSS 20.0 software. A repeated measures analysis was used because of the likelihood of dependency between correlation values at different distances during the same recording session. As such, the within-group variable was distance from broadcast site (i.e., 10, 20, 40, or 80 m). Between-group variables analyzed were stimulus frequency, recording site, time-of-day, and season. Wilks' lambda was used to test for within-group effects.

The click train is a signal with rapid fluctuation between acoustic energy and periods of silence. This allows for analysis of reverberative habitat effects as a function of both click frequency and distance. To calculate reverberation in the click train, first the rerecorded signal was band-pass filtered using an equiripple Parks-McClellan FIR filter, pass bands ± 100 Hz from the click carrier frequency, designed with MATLAB Signal Processing Toolbox. From this filtered signal, the ratio of the mean amplitude during the 70 msec period of post-click silence to the mean amplitude of the 30 msec click section was used as a reverberation index [Naguib, 2003]. This measurement indicates the amount of energy in the silent sections that remains from the previous click as it reverberates. Thus, a reverberation index of 1.0 indicates no mean amplitude difference between click and nonclick sections. For each broadcast click train, the reverberation indices of all click-silence cycles were averaged to obtain a mean reverberation index value.

RESULTS

Ambient Acoustics

Spectral analysis of these data revealed trends in ambient noise by time of day and season (Fig. 2). The dry season was characterized by elevated biotic noise,

especially in the morning hours. The period from 0600 to 1000 hours was marked by increased sound in a wide spectral band (2–16 kHz), likely due to insect, bird, and anuran sounds in these morning hours. Noon (1200 hours) was relatively quiet, showing few peaks in sound frequency distribution, except for one near 4 kHz during the 2011 dry season. At 1400 hours in the 2010 dry season, sound attributable to insects such as crickets, locusts, or cicadas generated a peak between 2 and 14 kHz. Due to decreased presence of these insects, this trend was not evident in the 2011 dry season, which only showed a continued peak around 4 kHz. The late afternoon (1600 hours) showed a relative lull in ambient sound, although one high frequency sound around 18 kHz was consistently present. At the latest daily time sampled, 1800 hours, there was a sharp increase in 2–10 kHz sound due primarily to early evening anuran calling, as well as some insect-generated sound.

The wet seasons were generally characterized by less overall biotic acoustic activity. This is most evident during the morning periods when high levels of vocalizations were typical in the dry season. In the early morning (0600 hours), the 2011 wet season spectrum showed strong peak at 6 kHz while in 2010, a weaker peak was located near 8 kHz. Morning through midday (0800–1400 hours) was a period of relative quiet. At 1600 hours, the ~ 18 kHz high frequency sound, notable in dry season, was also present in the wet season. Early evening (1600 hours) was marked by an increase in anuran and insect-generated noise (2–8 kHz), which was slightly decreased in bandwidth when compared with the corresponding dry season recordings.

To explore the consistency of such trends, we used DFA, which uses a measured variable to categorize members of a dataset into groups. Categorization is based on a linear model built from previous experience with the data. In other words, DFA can be used to determine if a model can accurately categorize a dataset into its inherent categories. We used DFA to determine the suitability of spectral signature to classify each ambient acoustic recording by the following categories: time of day, time of day by season, season, season by year and year. The accuracy of the predictions shows whether the power spectrum is a unique signature for categorization. Accuracy was calculated as the percentage of correct classifications in a category minus the expected correct categorization by chance. In the categorization of frequency spectra by season, for example, one would expect 50% correct by chance, and the percentage correct beyond this level is a measure of the suitability of spectral signature to classify in this category. In all categories, DFA was able to classify correctly beyond chance (Fig. 3). Time of day by season (e.g., "0600 hours wet season" vs. "0600 hours dry season") had the highest percentage correct above

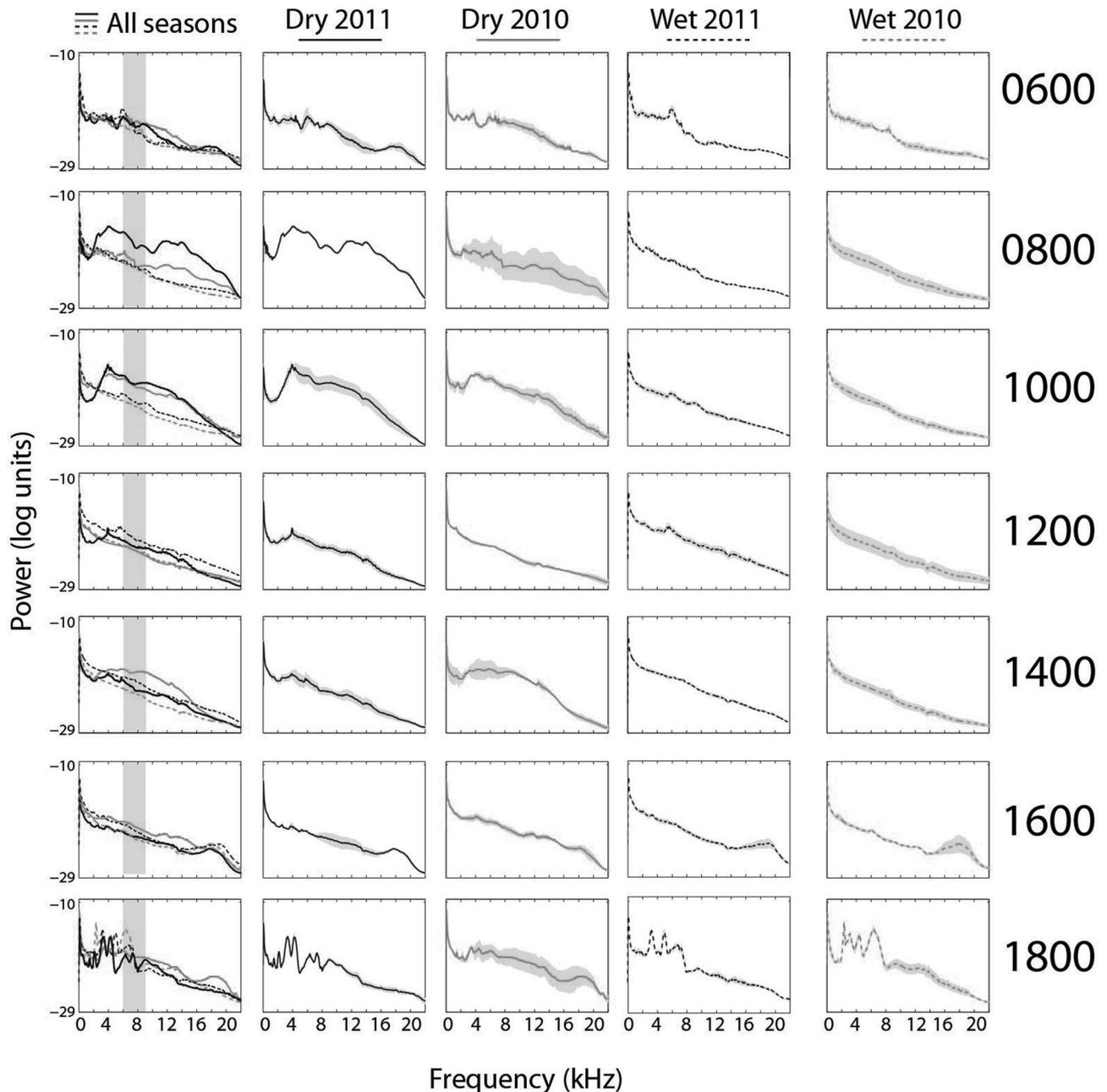


Fig. 2. Power spectra of ambient habitat acoustic recordings by time of day and season. Right margin indicates time of day. On all plots, X-axis shows frequency from 0 to 22.05 kHz while Y-axis shows power units, logarithmically transformed. Leftmost column shows the mean spectra by time of day from each season on one plot for comparison. Shaded gray area indicates the approximate range of the fundamental frequency of the common marmoset phee call, ~6–9 kHz. The other four columns show the mean spectrum by time of day for the season indicated at the top, with each plot representing an average spectrum from 3 days of recordings. Shaded error bars represent ± 1 SEM.

chance. Time of day alone had the lowest correct beyond chance rate, suggesting that seasonal difference by time of day is an important habit acoustic factor. Overall, these DFA data confirm the qualitative differences observable in the ambient acoustic spectra, demonstrating that ambient acoustics vary predictably over several timescales.

Broadcasts—Tones and Clicks

To characterize sound transmission in the habitat, we used a series of sound broadcasts designed to test whether certain spectral or temporal properties offered increased transmission efficacy. We first sought to determine how frequency affects sound

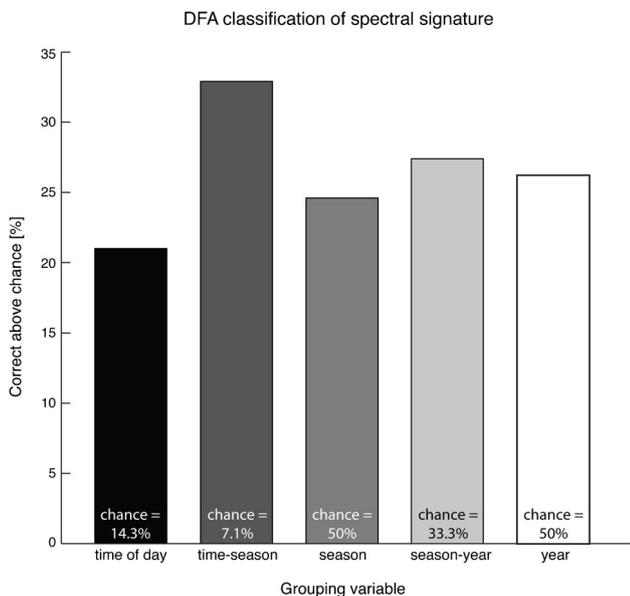


Fig. 3. Results of discriminant function analysis (DFA) in classifying the mean spectral signature of each recording correctly into various categorical variables, shown on the X-axis. DFA is an analysis that shows the suitability of a given variable (here, power spectrum) in discriminating data into categories. To compare results across categories of different size, plotted is the percentage correctly classified above the expected correct classification by chance. For example, “season” represents two groups, “wet” and “dry,” and correct classification, if left up to chance, would be 50%. DFA correctly classified 74% of samples by season, so the 24% difference is plotted. Chance levels for each group are indicated at the base of each bar.

transmission in the habitat by broadcasting a series of 1 sec sine wave tones at varied frequencies (250 Hz, 500 Hz, 1 kHz, 2 kHz, 4 kHz, 6 kHz, and 8 kHz), and then testing correlation of rerecorded sounds with the original broadcasts. Generally, lower frequencies had a higher correlation coefficient than higher frequencies (Fig. 4), as verified by repeated measures ANOVA (main effect of frequency, $F[3, 68] = 6.31, P > 0.001$). Post hoc analysis revealed that lower frequency tones at 250 and 500 Hz differed significantly in correlation value from all others, but those 1 kHz and higher did not differ significantly (Tukey’s HSD test, significance at $P < 0.05$ for all tests). The dry season showed higher mean correlation values (main effect of season, $F[3, 1] = 5.30, P = 0.024$) with more variability. Distance affected correlation values during the dry season ($F[3, 33] = 6.26, P = 0.001$). Although 10 and 80 m were not significantly different, 20 m was significantly higher than 40 m (Tukey’s test, $P < 0.05$). During the wet season, overall effect of distance was nearly significant ($F[3, 33] = 2.54, P = 0.073$).

In addition to pure tones, we sought to examine whether rapid amplitude fluctuations had an effect on transmission efficacy. We also broadcast click trains with pulses at varied fundamental frequen-

cies, with the same frequencies as used for tones. Clicks generally decreased in transmission efficacy as F_0 increased (Fig. 4), which we again confirmed through repeated measures ANOVA (main effect of frequency, $F[3, 6] = 90.96, P < 0.001$). Clicks at 1 kHz and below differed significantly from all other frequencies, decreasing in correlation as frequency increased, while clicks 2 kHz and above did not differ in correlation values from each other higher frequencies (Tukey’s test, $P < 0.05$). In the dry season, clicks decreased in correlation over distance ($F[3, 33] = 141.38, P < 0.001$), and 10 m correlation values were significantly higher than 80 m (Tukey’s test, $P < 0.05$). A similar trend held for the wet season ($F[3, 33] = 92.32, P < 0.001$), again with 10 m correlations significantly higher than 80 m (Tukey’s test, $P < 0.05$). Overall, variability of transmission efficacy in the wet season was lower than in the dry season. While the main effect of season was not significant ($F[3, 1] = 3.43, P = 0.068$), the interaction between season and distance was highly significant ($F[3, 68] = 20.54, P < 0.001$).

Click train broadcasts were also analyzed for reverberation to determine how frequency and distance from source affect this acoustic factor. As a reverberation index, we measured the ratio of mean sound pressure between click and silence sections of each click train broadcast. Reverberation index predictably increased with distance from source during the wet and dry seasons together (Fig. 5; $F[3, 68] = 68.52, P < 0.001$). Furthermore, reverberation index generally increased with increasing frequency of click train during both seasons (main effect of frequency, $F[3, 6] = 3.57, P = 0.004$). Clicks at 250 Hz did not differ significantly from 500 Hz, 1 kHz, or 2 kHz, but differed significantly from all higher frequencies. Likewise, the highest frequency clicks, 4, 6, and 8 kHz, did not differ significantly from each other (Tukey’s test, $P < 0.05$). Seasonal differences were not a significant factor for sound reverberation (main effect of season, $F[3, 1] = 1.822, P = 0.181$).

Broadcasts—Marmoset Phee Calls

Recordings of naturally produced marmoset phee calls were broadcast during both wet and dry seasons (Fig. 6). For both seasons, cross-correlation analysis indicated that phee call transmission efficacy degraded predictably with increasing distance, as confirmed by repeated measures ANOVA ($F[3, 248] = 470.34, P < 0.001$). Unlike tone and click stimuli, broadcast phee calls differed significantly at each distance from all other distances (Tukey’s test, $P < 0.05$). Generally, phee call correlations were less variable than the artificial sound broadcasts during both seasons. Phee call broadcasts during the wet season showed significantly higher correlations than those in the dry season (main effect of season, $F[3, 1] = 161.59,$

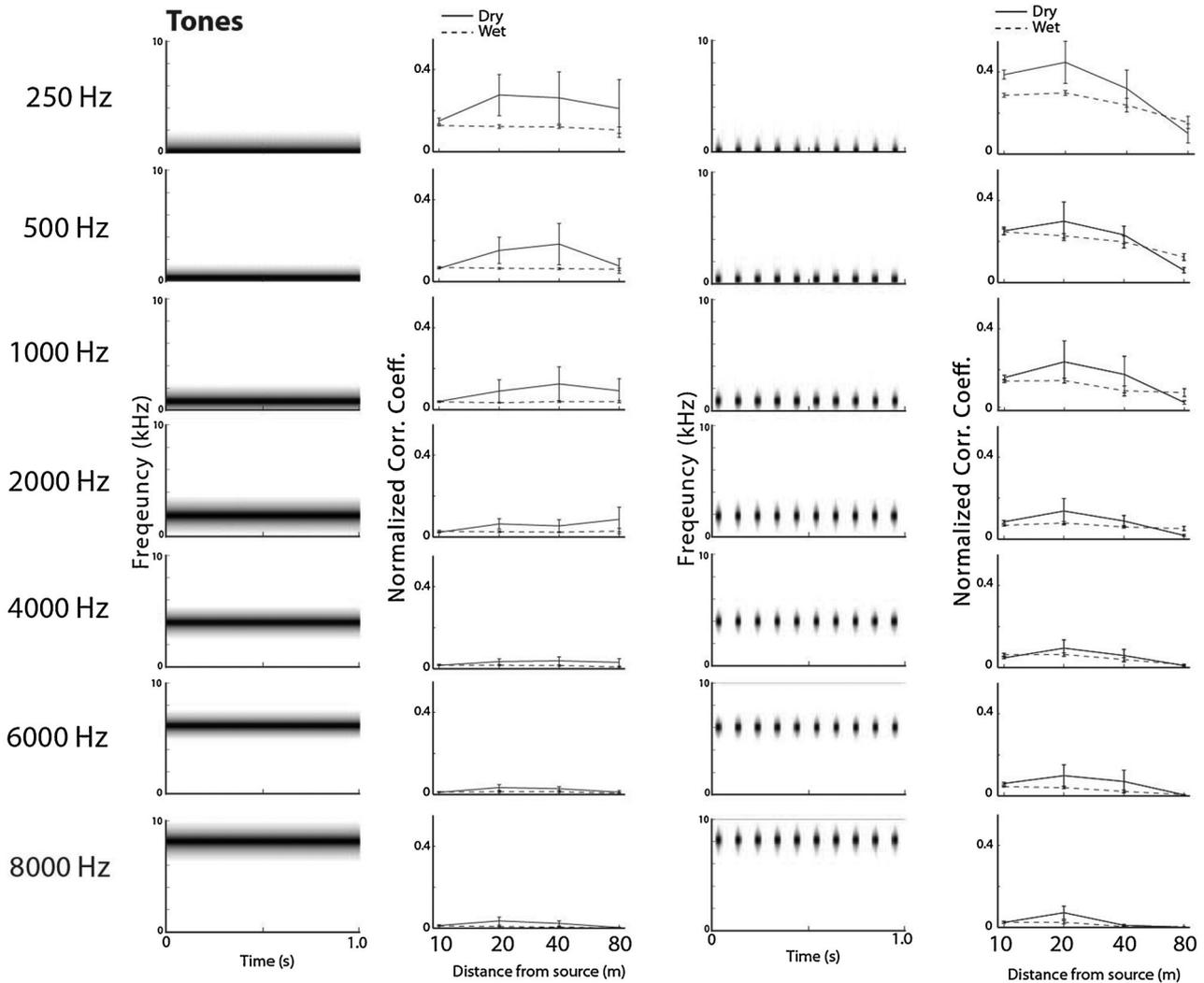


Fig. 4. Tone and click broadcasts, cross-correlation analysis. Spectrograms are visualizations of original broadcast sounds, X-axes show time from 0 to 1.0 sec, and Y-axes show frequency from 0 to 10 kHz. Columns to the right of spectrogram plots are correlations by distance of adjacent broadcast sounds. Y-axes of all plots show mean normalized correlations between original broadcast sounds and the re-recorded sounds, where 0 would be uncorrelated and 1.0 would be perfect direct correlation. Actual Y-axis scale is 0–0.55. Error bars indicate ± 1 SEM. Dashed lines indicate wet season, solid lines indicate dry season. X-axes show measurement distance, logarithmically spaced at 10, 20, 40, and 80 m.

$P < 0.001$). In addition, the interaction between season and distance was significant ($F[3, 248] = 41.48, P < 0.001$), suggesting that seasonal acoustic differences may modulate the effects of distance on call degradation.

Two characteristic properties of the phee call are its F0 and pulse length [Miller et al., 2010]. To determine whether these variables affect transmission efficacy, we artificially manipulated frequency (while keeping length constant) or pulse length (while keeping frequency constant), and broadcast these calls using the same methods as tone and click broadcasts. As above, normalized cross-correlation analysis was carried out to determine transmission efficacy. Due to equipment failure, this playlist was only broadcast during the 2010 dry season.

For frequency manipulations, we observed the expected decrease in transmission efficacy as frequency increased (Fig. 7), again verified by repeated measures ANOVA (main effect of frequency, $F[3, 3] = 72.90, P < 0.001$). Post hoc analysis showed that all frequencies (2, 4, 8, and 16 kHz), differed in cross-correlation values from all others (Tukey’s test, $P < 0.05$). Transmission efficacy also decreased with distance ($F[3, 106] = 240.49, P < 0.001$), and this pattern was significant at all distances (Tukey’s test, $P < 0.05$).

Between manipulations of phee length, there was no significant difference in transmission efficacy (Fig. 8; main effect of phee length, $F[3, 7] = 1.089, P = 0.371$). A consistent pattern of decreased correlation by distance was observed ($F[3, 214] = 675.82,$

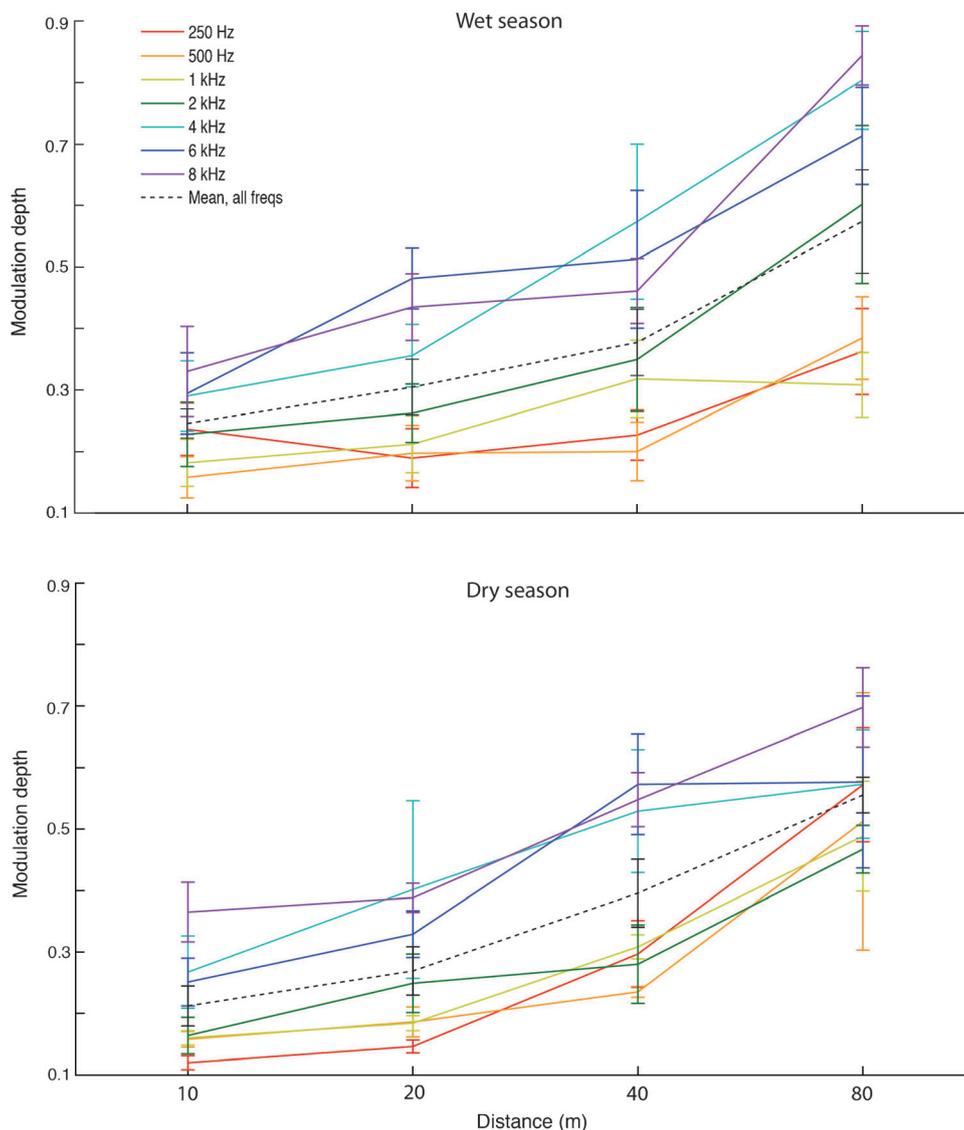


Fig. 5. Reverberation analysis on click broadcasts. Upper plot shows wet season, lower plot shows dry season. Click pulse fundamental frequency (F0) is indicated by colors, see inset figure legend. Y-axis shows modulation depth, the ratio of mean amplitude during the 70 msec silent inter-pulse intervals to mean amplitude of the preceding 30 msec click pulse. This provides a measurement of how much sound is left reverberating during the silence from the previous click pulse. To spectrally isolate the broadcast signal and its reverberations, all recordings were bandpass filtered with filter corners ± 100 Hz from the click F0. X-axis shows measurement distance.

$P < 0.001$), which was significant at all distances (Tukey's test, $P < 0.05$). For all phee manipulations (time and frequency), this decrease was highly predictable, with lower variability than observed for tone and click broadcasts in the dry season.

DISCUSSION

Here, we characterized the acoustic landscape of a typical common marmoset habitat in Northeastern Brazil. Combining recordings of the ambient habitat acoustics with sound broadcast experiments, we sought to test whether the common marmoset long-distance contact call—the phee call (Fig. 1)—com-

prises acoustic characteristics that may have been selected to improve signal transmission, and therefore communicative efficacy, in the species' natural history. Previous acoustic analyses indicated that, similar to those of many other Callitrichids, common marmoset vocalizations consist of a fundamental frequency (~ 6 – 9 kHz) that degrades quickly in forest environments [Bezera & Souto, 2008; Miller et al., 2010]. It is possible, however, that additional acoustic characteristics augment signal transmission. Our analyses indicated that phee call degradation was much less variable relative to other acoustic signals, suggesting that the rate of acoustic distortion may be predictable to conspecific signal receivers.

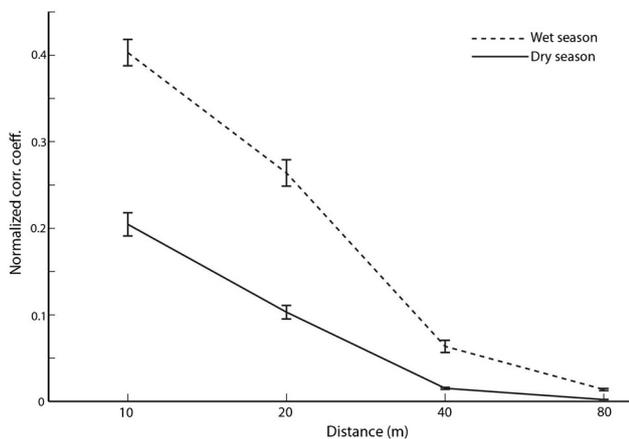


Fig. 6. Phee call broadcasts, cross-correlation analysis. Axes as in Figure 4 cross-correlation plots, except that Y-axis range is 0–0.45. Dashed lines indicate wet season, solid lines indicate dry season.

Furthermore, selection may not have acted only on the signal structure per se, but on behavioral mechanisms for monitoring the acoustic environment and initiating vocal production during periods of low acoustic interference.

Based on previous work [De la Torre & Snowden, 2002; Waser & Brown, 1986], we predicted that habitat acoustics at Tapacurá would show patterns by time of day and season, and, as such,

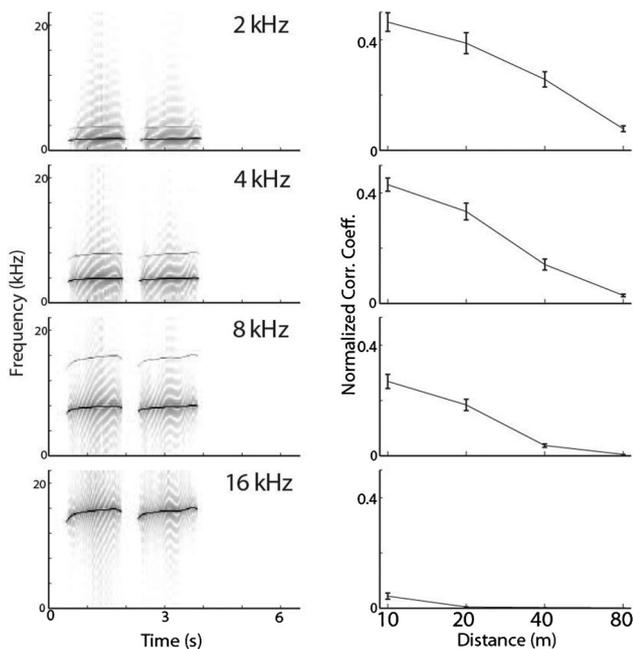


Fig. 7. Frequency-manipulated phee call broadcasts, cross-correlation analysis. Broadcast sounds had digitally manipulated mean fundamental frequencies, altered as indicated on spectrogram plots. Spectrogram plots show one example of the five different manipulated calls. Spectrogram axes as in Figure 4, except that Y-axis range is 0–22.05 kHz and X-axis range is 0–6.0 sec. Adjacent line plots show correlation analysis results, axes as in Figure 4, except that Y-axis range is 0–0.5.

recordings were carried out across the wet and dry seasons. Indeed, comparison of frequency spectra from ambient recordings showed that such temporal regularities exist. On the circadian scale, mornings and evenings were generally dominated by broadband biotic noise from insects, birds, and anurans, while the midday showed a lull in ambient noise. Seasonally, biotic noise generally played a more significant role in ambient acoustics during the dry season than the wet. This does not necessarily suggest decreased general calling activity during the wet season, as damping of biotic noise due to increased vegetation and foliage may also play a role. Such a conclusion is supported by decreased transmission efficacy of some broadcasts during this season. Despite these temporal regularities in potentially interfering habitat sound, initial data suggest that average calling rate for common marmosets does not fluctuate significantly throughout their waking hours [Bezerra et al., 2009]. Data specifically on the occurrence of phee production over the course of the day, however, are not available. Such a dataset is necessary in order to fully explicate this possibility.

Past work on habitat acoustics tested for a spectral “sound window,” a frequency band with minimal interference from other sound sources in the habitat, providing a clear channel for communication [Waser & Brown, 1984, 1986]. The phee call, the most important common marmoset long-distance call, has a fundamental frequency of ~ 7 kHz [Miller et al., 2010], a high range which confers the seemingly disadvantageous property of rapid degradation over distance [Morton, 1975]. Although spectral analysis of marmoset habitat acoustics showed most peaks in the frequency spectrogram lie either outside or on the fringes of this band (Fig. 2), we found no clear evidence of a spectral “sound window;” much energy is still concentrated between ~ 6 and 9 kHz. This suggests that, in contrast to Old World monkeys [Brown et al., 1995; Waser & Brown, 1986], the frequency range of common marmoset vocalizations may not have been selected for transmission properties. Many factors may have contributed to such variability in the environment-acoustic signal relationship between New and Old World primates. For example, differences in the density of endemic and migratory birds in these forest environments may affect the occurrence and consistency of spectral sound windows. As discussed earlier, two Callitrichid species—cotton-top and Geoffroy’s tamarins (*S. oedipus*, *S. geoffroyi*)—produce long-distance vocalizations with significantly lower F0 than common marmosets and the other members of the family [Cleveland & Snowden, 1982; Weiss et al., 2001]. Importantly, these two tamarin species are the only Callitrichids endemic to forests north of the Amazon. As such, the biotic and abiotic sources of acoustic interference that faced these species during their

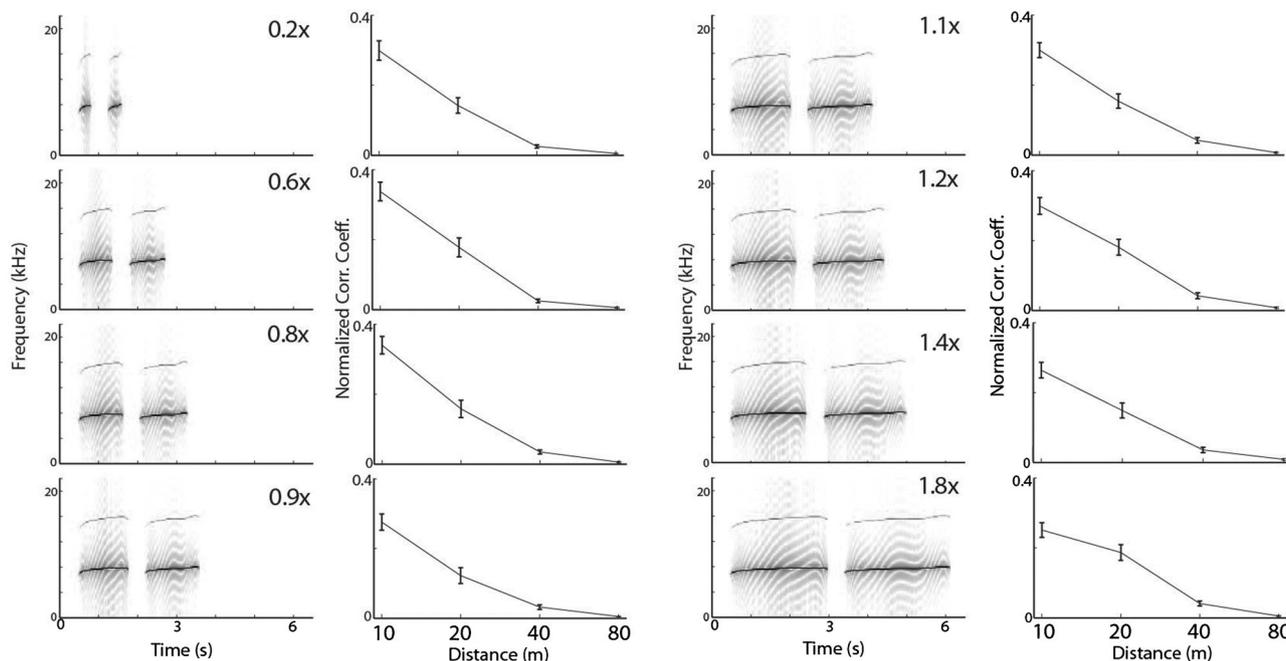


Fig. 8. Length-manipulated phee call broadcasts, cross-correlation analysis. Broadcast sounds had digitally manipulated pulse lengths, with lengths scaled as indicated on spectrogram plots. Inter-pulse interval length was not altered. Spectrogram plots show one example of the five different manipulated calls. Spectrogram axes as in Figure 4, except that Y-axis range is 0–22.05 kHz and X-axis range is 0–6.0 sec. Adjacent line plots show correlation analysis results, axes as in Figure 4, except that Y-axis range is 0–0.4.

respective evolution are likely to be different from the other Callitrichid species. While this may not be the sole contributor to the observed differences in this family, it is a reasonable factor. Furthermore, New World primates seem to exhibit a higher degree of vocal learning and plasticity than Old World primates [Egnor & Hauser, 2004], which may allow for individual callers to more readily modify their calling behavior in response to the immediate acoustic environment. More empirical work, however, is necessary to confirm either of these possible explanations.

Analysis of phee call broadcast data generally confirmed our predictions for signal degradation trends. Transmission efficacy for phee calls decreased as a function of distance, as well as with increasing fundamental frequency. These trends were highly consistent with little variability between repeated broadcasts. Surprisingly, tones and clicks, our artificial broadcast sounds, did not show the same trend by distance. Instead, these sounds generally showed greatest transmission efficacy at intermediate distances of 20 and 40 m. Tones and clicks broadcast in the dry season showed higher overall transmission efficacy, but also higher variance, than in the wet season. Taken together with the ambient acoustic analysis, these data suggest that the dry season provides an environment for increased signal propagation but also higher interference due to biotic sound from heterospecific vocalizations, resulting in both increased transmission efficacy and variability. The

wet season, which is defined by increased foliage density, results in decreased and less variable signal transmission.

The drastically different patterns found for phee broadcasts (a natural sound) versus tones and clicks (artificial sounds) may indicate at least some acoustic dimensions of the phee call were selected for sound transmission. Broadcast phee calls showed highly predictable degradation over distance, a property that may be crucial for a long-distance contact call by providing the call receiver(s) with locational information about the calling animal. Without these predictable degradation patterns, the receiver would not be able to aurally calculate the position of the sender. In addition, this study demonstrates that certain properties of the phee call may be unrelated to sound transmission in the natural marmoset habitat. For example, our analyses indicated that increasing or decreasing the length of the phee call pulse does not affect transmission efficacy. Ruling out such a role, we may hypothesize that pulse length variations instead play a social role in communicating caller identity or some other informational feature of the phee call [Miller et al., 2010]. While the design of the current study precludes strong conclusions about the functional role of specific properties of the phee call, subsequent studies in the field and laboratory will further test this possibility.

Maintenance of effective communication in a noisy acoustic landscape is unlikely to rely entirely on

selection for the properties of a vocal signal. Sound transmission can also be improved through complementary behavioral control during vocal communication. For example, a calling marmoset may monitor the acoustic landscape and initiate vocal production based on temporal windows with little biotic interference. This capacity requires mechanisms for auditory feedback and vocal control, two processes historically thought to be limited in nonhuman primates. Recent work in common marmosets, however, has provided evidence to the contrary. Behavioral experiments indicate some degree of vocal control over the acoustic structure of vocalizations [Miller et al., 2009], as well as an ability to communicate in the presence of experimentally controlled noise events [Roy et al., 2011]. Roy et al. [2011] broadcast bursts of white noise at different temporal patterns to pairs of visually occluded common marmosets. Subjects quickly began to only initiate vocal production during silent periods. In one test condition, consisting of alternating periods of 8 sec white noise followed by 8 sec of silence, the callers coordinated their vocal behavior in order to complete a vocal exchange within the 8 sec silent window. The capacity for vocal behavior mediated by environmental acoustic monitoring may be based on neural mechanisms in the auditory system for sensory-motor integration [Eliades & Wang, 2003, 2008]. Marmosets' ability to exploit temporal windows suggests that they may have evolved mechanisms for a mixed communication strategy in noisy forest environments. They monitor the acoustic environment for periods of silence and produce calls with highly predictable degradation rates, thereby emitting signals with the best opportunity for effective communication. More data are needed, however, on the timing and occurrence of marmoset vocalizations in the presence of natural habitat acoustic interference.

Animal vocalizations, of course, are not evolutionarily selected solely for signal transmission properties in noisy environments. Communication systems evolve in response to a myriad of selection forces ranging beyond purely ecological constraints, such as each signal's social function, predation avoidance, etc. Relative to anuran and songbird communication [Bradbury & Vehrencamp, 2011; Gerhardt & Huber, 2002; Ziegler & Marler, 2004], little remains known about the various ecological, social, and neural factors that affect nonhuman primate communication. However, ongoing behavioral and neurobiological research on the mechanisms underlying common marmoset vocal perception and production has positioned this species as an emerging model system. Field research complimentary to such laboratory studies provides a powerful approach to enhance our understanding of the various forces that shaped the evolution of nonhuman primate communication.

ACKNOWLEDGMENTS

This work supported by grants to C.T.M. from NIH (K99/R00 DC009007; R01 DC012087) and a UCSD Academic Senate Grant. We thank the Federal Rural University of Pernambuco for permission to conduct this research at Tapacurá Ecological Field Station (Recife, Brazil). We also thank Camile Bione and Monique Bastos for their help during field experiments, and Paulo Martins for support at the field station. All research adhered to the ASP ethical principles for treatment of nonhuman primates in research and the Brazilian laws.

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