STRUCTURE AND FUNCTION OF SONGBIRD COMMUNICATION: THE RELATIONSHIP BETWEEN SOUND PROPAGATION AND SOCIAL USE OF VEERY (*CATHARUS FUSCESCENS*) CALLS

LAURA R. BLOCK
Bowdoin College, Brunswick, ME 04011 USA

MENTOR SCIENTIST: DR. KARA BELINSKY
State University of New York, New Paltz, NY 12561 USA

Abstract. Veeries (*Catharus fuscescens*) are a species of North American thrush with a large repertoire of calls that they use to communicate with one another. To gain insight into the behavioral role of calls in this species, I examined connections between the acoustic structure and the social function of veery calls. I identified three common call categories (named veer, chatter, and peu) and compared their acoustic features to determine which calls propagate well in veery habitats and which attenuate the most over distance. I used acoustic structure data to create a quantitative and qualitative method of categorizing veery calls, and conducted two experiments: a sound transmission experiment to test how the three calls degrade over distance in veery habitat, and a playback experiment to examine how veeries respond to each of the three calls. Of the three call types tested, the veer call transmitted the best across veery habitat, followed by the peu call. The chatter call degraded the most of the three. When exposed to playback stimuli, veeries generally responded with calls that had a similar acoustic structure and therefore a similar ability to propagate. My categorization of veery calls can be used as a method to identify and analyze veery calls in future work, and the results of the sound transmission and playback experiments demonstrate a relationship between call structure and function. This relationship is a key step toward discovering the function of various veery calls and prompts many questions about how and why birds vocalize.

INTRODUCTION

Animal communication is the transfer of signals from a sender to a receiver. A signal can be in the form of sound, light, touch, or chemicals. Once the sender produces the signal, it transmits through a medium—air, water, or a solid—until it reaches the receiver, who interprets it using sense organs (Dugatkin 2009). Although communication varies greatly between different species, each species generally has signals for aggression, mating, parenting, coordinating social behaviors, and locating food or other resources. Signals also often contain information about the sender's sex, age, location, and identity. Communication is crucial for mating and reproduction, so it is an important area of study in order to create effective plans for wildlife conservation and property management.

Acoustic communication is one of the most commonly used and complex signal modalities. Many species, including birds and humans, create the majority of their signals by forcing air from the respiratory system through a valve like the glottis or the syrinx to generate periodic, non-sinusoidal vibrations. These sounds have harmonic frequencies at several integer multiples of the lowest, or fundamental, frequency. Sound propagates away from its source through changes in pressure; molecules experience condensation and rarefaction in waves, radiating the change in pressure outward from the initial location of the vibration (Bradbury and Vehrencamp, 1998).

Sound degrades as it propagates away from the sender as a result of both the environment though which it travels and the acoustic elements of the signal itself. Richards (1978) identified two key primary sources of environmental degradation: amplitude fluctuations from atmospheric turbulence, and reverberations from surfaces like vegetation that scatter sound. The acoustic elements of the signal itself also greatly influence sound propagation. These elements include the frequency range, relative amplitude (the change in pressure caused by the sound waves), harmonic structure (the presence of overtones with frequencies at integer multiples of the fundamental), intra-syllable syntax (the arrangement of acoustic units), and general acoustic structure of the sound. Degradation of animals' acoustic signals as they transmit can limit communication (Wiley 1978). For acoustic communication to be effective, the receiver must be able to discriminate the variations in the acoustic structure of the signal (Wiley 1978). As the signal degrades over distance, the receiver becomes less able to discriminate the important structures.

Signal degradation can be more or less consequential for the sender depending on which aspects of the acoustic signal are necessary for the communication (Richards 1978). Many species produce signals whose acoustic structures correlate with their communicatory purpose. In other words, the structure and function of animal signals are often linked, so that the acoustic elements that propagate best in a habitat are those that encode the information. This connection between structure and function is related to the acoustic adaptation hypothesis, which states that evolution favors acoustic signals that will propagate well without degrading in the sender's specific habitat (Bradbury and Vehrencamp, 1998). Studying sound degradation and the connection between structure and function in acoustic signals can provide insight into how animals interact and the purpose of various signals.

Many studies have suggested that there is a strong connection between the acoustic structure of bird songs and their communicatory function. Sound propagation is especially important for songbirds, as their communicatory signals are often at high frequencies and involve rapid amplitude and frequency modulations that can cause their sounds to degrade, especially in dense, forested environments (Boncoraglio and Saino, 2007). Acoustic signals have elements that will degrade predictably, and birds may be able to judge the degradation of these elements to determine how far away the sender is, using a tactic called ranging (Wiley 1978; Naguib 2001; Morton 1986). Many birds do not regularly need to communicate over great distances that would require them to have different signal structures. Instead, they use signals that degrade differently over short distances depending on the function of each signal (Wiley 1978). The difference in the propagation ability of various sound features is likely related to each feature's communicatory purpose. For long distance signals, signals used to find a mate, or signals that need to overcome acoustic competition to be received, sounds that propagate well in the bird's habitat are advantageous. However, there are also signals that are adapted to degrade over shorter distances; for example, some birds use signals that degrade rapidly when predators or other eavesdroppers may be nearby (Richards 1978). The acoustic structure that determines how well a signal propagates in a specific habitat is often associated with that signal's social function. This association can then be used to determine the social functions of many forms of animal communication.

The veery (*Catharus fuscescens*) is a species of North American thrush that migrates north from South America for its mating season and nests on the ground in dense, wet deciduous forests. They have a very unusual song that incorporates two distinct melodies at different frequencies in tandem. The dominant high frequency "voice" in veery song, intra-syllable syntax, and rapid frequency and amplitude modulations are features of the veery song that communicate species identity, an important function, and these elements are transmitted across veery habitats with the least degradation (Weary et al. 1986). This presents a clear relationship between the acoustic structure of veery songs (including their ability to propagate in veery habitat) and their social function (in this case, communicating species identity).

Although there have been many studies regarding veery song, there have been relatively few regarding veery calls. Dilger (1956) detailed several of the veery's hostile vocalizations, including three calls that he referred to as "veer, pheu, and a high pitched, windy, squealing sound." He discussed several possible agonistic uses of these sounds and described how veeries often combine them with visual cues when under duress, but did not examine the calls' acoustic structures or their other social functions. Samuel (1972) identified nine veery calls and examined their sonogram images as well as the context in which they were often used. He speculated about the purpose of several of the calls in high-intensity hostile encounters, but did not come to any definitive conclusions about call functionality. Heckscher (2007) conducted a more comprehensive study of veery calls. He recorded adult veery calls over seven breeding seasons in a banded population and organized them visually based on similarities in sound structure. He used low frequency and call duration as properties to compare call types in scatterplots and box plots. He found that the repertoire was comprised of two different call continua (a tonal continuum and a harsh continuum), as well as four separate call structures that did not fit into either continua. He called these four structures the whistle, the downward call, the u-call, and the chatter. This contrasts with Samuel's (1972) nine dissimilar veery call types, although Heckscher argues that five of these nine calls fit into one of his two continua, and the other four of Samuels' nine calls are variants of two of the discrete call types Heckscher identified.

Veeries have a large repertoire of calls that are difficult to name as distinct sounds because veeries often modulate various acoustic aspects and produce sounds that are a combination of different standard calls. It is therefore more straightforward to refer to their calls as call families or categories—groups of call sounds that may be slightly different, but all have important identifying similarities in acoustic structure. The three call families examined in this study are the veer call, the chatter call, and the peu call (Figure 1).

I studied the relationship between the acoustic structure and the social function of veery calls, and examined how these calls propagate through veery habitat. I had three research questions:

1) What acoustic measurements define and categorize each call type?
2) How do these three call types transmit and degrade in veery habitat and how far does each call travel before it degrades?
3) How do veeries respond vocally to these call types?

To address these questions, I first categorized veery calls based on a quantitative and qualitative description of the features that comprise each call family, and determined criteria for a "degradation tipping point," or the loss of various acoustic structures that render a call degraded. I conducted a sound transmission experiment to test how the three calls degrade over distance in veery habitat, as well as a playback experiment to examine how veeries respond to each of the three calls to obtain more insight into the function of veery acoustic signals. I hypothesized that these three veery calls transmit and degrade differently in veery habitat, and that their acoustic structure plays a role in their social use.

METHODS

This study was conducted in oak- and maple-dominated deciduous forests at the Cary Institute of Ecosystem Studies in Dutchess County, New York, U.S.A. Playback trials were conducted between 6:00am and 10:00am in June and July 2015. Study subjects were territorial male veeries identified by their songs.

Categorization and evaluation of call families

I used recordings of natural veery songs and calls from previous years at the Cary Institute and isolated the calls to create a database of call recordings. The recordings were taken by Kara Belinsky and Ethan Duke between 2010 and 2014. The recording tracks were predominantly veery song with calls mixed in. I sampled over 40 tracks, but only used the 8 that had more than a full minute of uninterrupted calling behavior for quantitative acoustic structure measurements. After extensive review of the various types of veery calls on these tracks, I categorized the sounds into three major call families: the veer call, the peu call, and the chatter call. I used Raven software (Cornell Laboratory of Ornithology, Ithaca, New York, U.S.A.) to measure the frequency range (Hz), maximum frequency (Hz), duration (seconds), average power (dB), peak power (dB), and the acoustic structure or shape of each call. Using these data, I made a quantitative and qualitative list of criteria that define members of each call family. I then determined what changes in acoustic structure must take place for a call to be considered degraded. In other words, I defined the criteria for a degradation tipping point (Table 1). I based these criteria off of the degradation models described by Wiley et al. (1978). Acoustic signals degrade in four distinct ways: overall attenuation, attenuation of frequencies, reverberation/scattering, and amplitude fluctuations (Wiley et al., 1978). I defined degradation using a loss of frequency range, duration (due to reverberation), and peak power (due to amplitude fluctuations). If a call met two of the three criteria at a tested distance away from the speaker, that call was altered enough that it could not be easily recognized, and its acoustic structure had changed enough to render it degraded.

Experiment # 1 (Sound transmission)

I created an audio track consisting of one minute of natural recordings of each of the three call types (veer, chatter, and peu) using past recordings taken by Kara Belinsky and Ethan Duke on Cary Institute property. The exemplar track had 14 veer calls, 21 chatter calls, and 19 peu calls. The calls were all spaced naturally—I did not change the time between each call from the original bird— and the interim between the calls was only silence. I then played the calls at a consistent volume from a speaker 1m off of the ground and recorded them with a microphone held at distances of 5, 20, 35, and 50 yards away from the speaker (measured with a Range Finder that measured in yards). I repeated this process over eight trials, each in forest locations that are known veery habitat. The forest locations were all at least 200m apart. There were a total of 1728 calls analyzed (448 veer calls, 672 chatter calls, and 608 peu calls) over the eight trials at all four distances.

I analyzed the recordings using Raven software and calculated the duration, frequency range, maximum frequency, average power, and peak power of the recorded calls at each of the four distances to measure how the three different calls degraded. I ran 2-way ANOVA tests, and all statistical analyses were performed using R software (R Core Team 2015).

Experiment # 2 (Playback)

I conducted a playback experiment on ten actively singing male veeries. The playback audio track consisted of four minutes of pre-playback silence, one minute of call A, one minute of silence, one minute of call B, one minute of silence, one minute of call C, and four minutes of post-playback silence. I changed the order of calls A, B, and C for each trial to eliminate possible error. Each exemplar track had 14 veer calls, 21 chatter calls, and 19 peu calls. For each trial, I identified an actively singing veery male, played the exemplar track on a speaker 1m off of the ground at a set volume, and recorded the bird's responses. I was always approximately 50m away from the bird, and I waited for four minutes before starting the exemplar track to give the bird time to adjust to my presence and to record its natural singing or calling behavior before the playback. I minimized the chances of recording the same male twice by performing many of my trials on the same day and having a distance of at least 200 meters between each trial location. The veeries were also part of a banded population, and I recorded all color bands I saw. I also took qualitative and anecdotal notes on the birds' behavior during the trials. I then analyzed the sound recordings using Raven software and measured the latency of each response, as well as the duration, frequency range, maximum frequency, average power, and peak power.

RESULTS

Categorization and evaluation of calls

In addition to quantitative acoustic measurements (Table 2), each call must also fit a qualitative acoustic structure description. A veer call must have an acoustic structure that forms a straight negative slope with an even power distribution and at least one upper harmonic with a parallel slope. A chatter call must have an acoustic structure that consists of close vertical frequency bands that do not curve, and high upper harmonics that extend the frequency bands. Finally, a peu call must have an acoustic structure of negative slope that curves and levels off into a slope of zero, several upper frequency bands that mirror the fundamental, and the majority of the power (dB) of the sound concentrated in the curve or bend of the shape (see Figure 1 for sonogram images).

Experiment #1 (Sound transmission)

Based on the degradation tipping point criteria (Table 1), the veer call had a degradation tipping point of 50 yards, the chatter call had a degradation tipping point of 35 yards, and the peu call also had a degradation tipping point of 35 yards. The veer call transmitted the farthest across veery habitat, and although the chatter and peu calls had the same tipping point, the peu call transmitted better based on percent loss calculations of its frequency range and peak power.

Although I collected data for five different acoustic structure measurements (frequency range, maximum frequency, duration, average power, and peak power), only frequency range, duration, and peak power were used to determine the degradation tipping points. The mean data for the latter three acoustic measurements at each distance mark is shown in Table 3, and the percent loss of all five of the acoustic measurements regardless of call type is shown in Figure 4.

The three call types were significantly different in their frequency ranges ($p<0.01$) and in their duration ($p<0.01$). There was a significant difference in peak power among the three call types ($p<0.01$). There was also a significant difference in frequency range, duration, and peak power among the four distances ($p<0.01$ for all). See Table 3 for standard deviation measurements. Sample size (N) was 1728 calls ($N_{Veer} = 448$, $N_{Chatter} = 672$, and $N_{Peu} = 608$).

The chatter call had a tipping point of 35 yards, as two of its three measurements crossed the degradation threshold by that distance mark, but it is important to note that it had a large loss of frequency range at a small distance. The chatter call had already lost 35.46% of its frequency range at only 20 yards away from the speaker (Figure 2a). Although the peu call also had a degradation tipping point of 35 yards, its frequency range and peak power loss were not as extreme as those of the chatter call.

For the frequency range shown in Figure 2a, there was no significant difference in percent loss of frequency among the three call types ($p=0.55$). There was a significant difference in percent loss of duration among the three call types ($p=0.027$), but there was no significant difference in percent loss of peak power among the three call types ($p=0.34$). All three charts in Figure 2 had a significant difference in the measurement by distance ($p<0.001$), and none of the charts had a significant interaction between the percent loss of the measurement and the distance ($p=0.97$, $p=0.58$, and $p=0.55$ for charts a, b, and c).

Degradation was determined with both the quantitative measurements outlined above and with qualitative measurements. Acoustic degradation causes a loss of upper harmonic structures and of general amplitude, both of which can be seen in sonogram images of the calls at increasing distances (Figure 3). Note the rapid degradation of the chatter call in comparison to the other two, as well as the loss of upper harmonic structures in all three calls by the 50-yard distance.

Experiment # 2 (Playback)

I analyzed seven of the ten playback trials. Three of the trials were discarded due to sound interference, lack of response, or counter-singing with another veery. The veeries generally sang continuously during the four minutes of pre-playback silence, were quiet for the first few playback calls (usually only 3 or 4), and then began calling continuously in response to the playback. Many birds continued calling after the exemplar track was complete, and several resumed singing with added whisper calls, which may be an agonistic signal (Belinsky et. al 2015).

In 5 out of 7 trials, veeries responded to veer calls with veer calls of a very similar frequency range, peak frequency, and duration. In 4 out of 7 trials, veeries responded to chatter calls with veer calls of a lower average frequency range than veers they used in response to veer stimuli. When exposed to peu playback, veeries responded with song 3 out of 7 times and responded with peu calls of a lower average frequency than normal peu calls the other 4 times. In every case where a veery responded to a stimulus with a call that did not match the stimulus, the acoustic structure data (frequency range, peak frequency, and duration) were very close to the acoustic structure data of the stimulus despite being a different call.

DISCUSSION

There were three main outcomes of this study: 1) a quantitative and qualitative criteria list to categorize three types of veery calls, 2) sound transmission data that show the degradation tipping point for all three call types, and 3) anecdotal and playback data regarding how veeries respond selectively and acoustically to the three call types.

Past studies have given various veery calls colloquial names that reference a certain sound or sonogram image (Dilger 1956; Samuel 1972; Heckscher 2007), but no study has ever defined veery calls in a quantitative manner as well. Heckscher (2007) divided the veery call repertoire into two separate call continua (a harsh continuum and a tonal continuum) as well as four distinct call types organized visually. Samuel (1972) identified nine separate veery calls, also grouped by visual (acoustic structure) parameters. Like Heckscher and Samuel, I examined a large collection of veery calls and categorized them, but I grouped them using different parameters, including frequency range, relative peak power, and overtone structure. This method of categorization can be used to identify unknown veery calls, and also can be used as a starting point for creating more quantitative criteria lists in the same format and style for veery calls other than veer, chatter, and peu. If an unknown call fits into the proper range for the three acoustic structure measurements and also fits the proper acoustic structure description and sonogram, then the confusion that often surrounds the naming of calls is greatly lessened. However, there are overlapping criteria among the veery calls; this method should be used in addition to the naming-by-ear system commonly in place as a way to verify predictions of call type.

The sound transmission experiment determined how veer, chatter, and peu calls transmit across veery habitat and how far each can travel before it degrades. Although there were many differences in acoustic structure measurements, in general the veer call transmitted the farthest and with the least degradation, and the chatter call degraded the most over the shortest distance. The degradation tipping points are consistent with each call’s acoustic structure; the peu call and the chatter call have the majority of their amplitude concentrated at a higher frequency than the veer call. The veer call has upper harmonic structures, but most of its amplitude is concentrated in the straight negative slope that is at a lower in frequency than the other two calls. Higher frequencies generally degrade faster than lower frequencies as they have shorter wavelengths. Longer wavelengths can more easily travel around obstacles instead of reflecting off of them and losing energy while they scatter (Morton 1975). Frequencies higher than 3 kHz are very prone to degradation by reverberation scattering in forested environments (Wiley 1978). This explains the lower degradation tipping point of the peu and chatter calls. Fast acoustic modulations like the close vertical frequency bands in the chatter call also experience more degradation than pure-tone whistles (Wiley 1978), which explains why the chatter call degrades the most in veery habitat. All three calls experience a loss of power and a loss of most of their upper harmonic structures as they degrade. However, a loss of the upper harmonic structures in the chatter call muddles the sound greatly, whereas in the veer call, a loss of the upper harmonic structures still leaves the low negative slope of the fundamental intact, so the call is not as muddled with degradation.

This knowledge of how veery calls transmit and degrade across their habitat, in combination with response evidence from the playback experiment, can lead to much speculation about call function. There is no way to prove the social function of these calls, but anecdotal evidence in combination with these data lead me to infer the following: The veer call may be used as a long-distance contact call. Veer calls transmit the farthest with the least degradation across veery habitat of the three calls tested, and I have often heard veeries "veering" back and forth across large territory sizes and almost always responding to veer calls with veer calls that degrade similarly. Samuel (1972) noted that the veer call was often used back and forth between two veeries perched far apart, and was only rarely used between birds in close quarters, an observation which supports my inference. The chatter call may be used as an alarm call regarding predators or other danger; it degrades at the shortest distance, and after hearing a chatter call, veeries usually either become quiet or respond with a quiet and low modulated peu call that also degrades rapidly. This close contact alarm call would be ideal for birds to not be overheard by a predator, and much anecdotal evidence also supports this idea. Samuel (1972) also noted that several veery calls, including the chatter call, were used only in high-intensity hostile encounters. Lastly, the peu call may be used for close contact communication between mates. It degrades after a relatively short distance, and veeries often use it back and forth, usually modulating the response to a lower average frequency range that only travels the required distance to a nearby mate. In the final chapter of his dissertation, Heckscher (2007) speculates that the four veery calls he identified (separate from the two call continua) convey aggression, location, neutral contact, and appeasement. He determined this by observing natural interactions in conjunction with calls, and found that the chatter call (which is very similar to the chatter call I present here) is used for aggression, with supports my speculation. His other three call types do not match the veer or peu calls that I present in terms of their acoustic structures or frequency ranges, so I cannot compare his conclusions about those call types to my speculations about veer or peu calls.

The results of the playback experiment inform the above inferences about veery call function and reinforce the degradation data from the sound transmission experiment. The playback results are qualitative rather than quantitative and were conducted at a small scale, so these data should be used as anecdotal evidence only. This playback study should be repeated over a larger time scale and with a much larger sample size to eliminate error and determine quantitative acoustic structure results, but this experiment is a key step toward designing this later study, and offers anecdotal evidence about veery call function.

Bird calls have often been overlooked in favor of more elaborate songs, but they are just as vital to understanding bird communication. Veeries have a complex repertoire of calls, making them an ideal study species for exploring vocal communication of passerine birds. Veeries are also important to study as a conservation species; their population is in decline, and it is necessary to understand their communication and mating behaviors to effectively plan for their conservation. The results of this study offer insights into communication that are applicable to many animal species in addition to the veery, as signal degradation plays an important role in all acoustic communication.

ACKNOWLEDGEMENTS

I would like to extend my appreciation to Dr. Kara Belinsky, Dr. Kenneth Schmidt, Elizabeth Farley-Dawson, Aude Lochet, Beau Duval, Patricia Smith, Alan Berkowitz, Lara Chodelski, Erik Arndt, the Cary Institute of Ecosystem Studies, and the National Science Foundation.

LITERATURE CITED

Belinsky, K. L., Nemes C. E., Schmidt, K. A. 2015. Two novel vocalizations are used by veeries (*Catharus fuscescens*) during agonistic interactions. PLoS ONE **10:**3.

Boncoraglio, G., Saino N. 2007. Habitat structure and the evolution of bird song: a meta-analysis of the evidence for the acoustic adaptation hypothesis. Functional Ecology **21:**134-142.

Bradbury, J. W., Vehrencamp, S. L. 1998. Principles of Animal Communication, 2nd ed. Sunderland, MA: Sinauer Associates.

Dugatkin, L. A. 2009. Communication. Pages 402-427. In: Principles of Animal Behavior, 2nd ed. New York: W.W. Norton.

Dilger, W. C. 1956. Hostile behavior and reproductive isolating mechanisms in the avian genera Catharus and Hylocichla. The Auk **73:**313-353.

Heckscher, C. M. 2007. Use of the veery (*Catharus fuscescens*) call repertoire in vocal communication. PhD Dissertation, University of Delaware.

Morton, E. S. 1975. Ecological sources of selection on avian sounds. The American Naturalist **109:**17-34.

Naguib, M., Haven Wiley, R. 2001. Estimating the distance to a source of sound: mechanisms and adaptations for long-range communication. Animal Behaviour **62:**825-837.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Richards, D. G., Wiley R. H. 1978. Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. The American Naturalist **115:**3.

Samuel, D. E. 1972. Song variation and other vocalizations of veeries. Bird-Banding **43:**2.

Weary, D. M., Lemon R. E., Date E. M. 1986. Acoustic features used in song discrimination by the veery. Ethology **72:**199-213.

Wiley, R. H., Richards, D.G. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. Behavioral Ecology and Sociobiology **3:**69-94.

APPENDIX

TABLE 1. Criteria necessary for a call to be considered degraded. A call has reached its degradation tipping point if at the tested distance, two of these three criteria are met.

Acoustic Measurement	Percent loss from 5 yards to tested point
Frequency Range (Hz)	≥30%
Duration (seconds)	≥5%
Peak Power (dB)	≥25%

TABLE 2. Quantitative criteria used to categorize each call family.

	Frequency Range (Hz)	Peak Frequency (Hz)	Duration (seconds)
Veer Call	6000-15000	2500-3500	0.28-0.35
Chatter Call	5000-12000	3000-4000	0.25-0.35
Peu Call	7000-15500	2500-3000	0.30-0.40

TABLE 3. Mean (± standard deviation) frequency range, duration, and peak power data for veer, chatter, and peu calls at 5, 20, 35, and 50 yard distances. N_{Total} = 1728 calls, N_{Veer} = 448, $N_{Chatter}$ = 672, and N_{Peu} = 608.

Veer Call	Frequency Range (Hz)	Duration (sec)	Peak power (dB)
5 yards	14683.6 ± 2059.5	0.321 ± 0.014	91.62 ± 3.38
20 yards	11403.0 ± 3210.1	0.316 ± 0.018	81.00 ± 3.67
35 yards	8929.0 ± 1558.3	0.309 ± 0.009	72.60 ± 3.34
50 yards	6448.8 ± 2980.3	0.297 ± 0.022	67.47 ± 4.25

Chatter Call	Frequency Range (Hz)	Duration (sec)	Peak power (dB)
5 yards	11680.7 ± 1830.9	0.310 ± 0.029	85.46 ± 2.75
20 yards	7538.9 ± 832.2	0.299 ± 0.021	73.20 ± 3.55
35 yards	5925.2 ± 1421.5	0.291 ± 0.023	63.80 ± 3.87
50 yards	5270.3 ± 1232.9	0.283 ± 0.027	58.73 ± 3.70

Peu Call	Frequency Range (Hz)	Duration (sec)	Peak power (dB)
5 yards	15008.5 ± 636.8	0.374 ± 0.065	91.42 ± 3.75
20 yards	11000.8 ± 2446.0	0.346 ± 0.060	79.05 ± 2.12
35 yards	8672.5 ± 1439.9	0.342 ± 0.028	71.60 ± 3.30
50 yards	7065.2 ± 2261.4	0.333 ± 0.036	67.78 ± 4.45

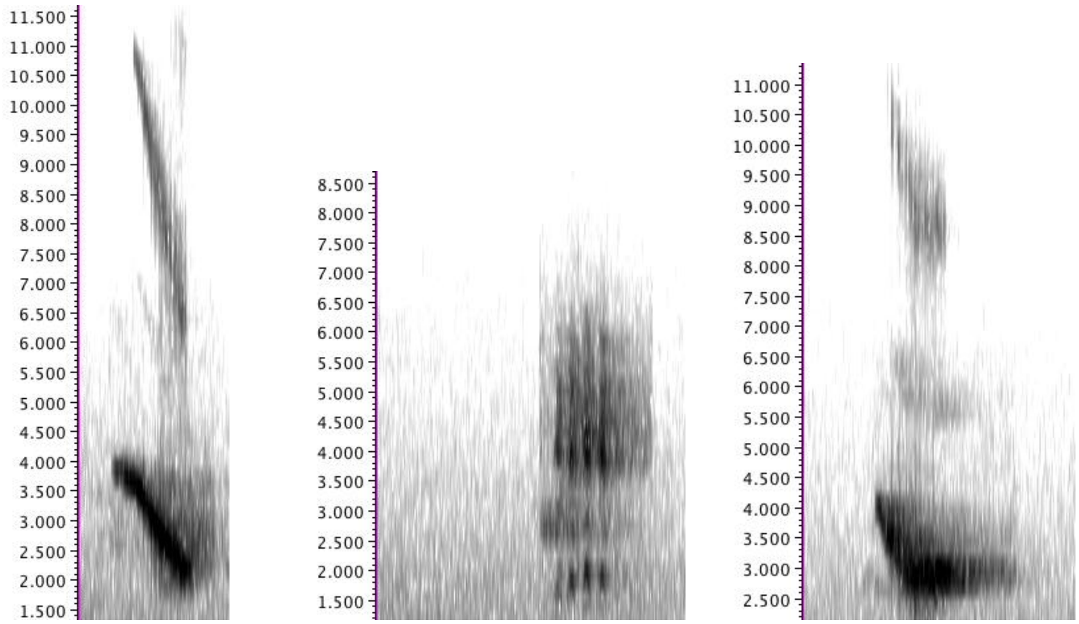

FIGURE 1. Sonogram images of the three veery call families examined in this study. From left to right: veer, chatter, peu. These images were produced using Raven Software and veery call recordings from June 2015 at the Cary Institute of Ecosystem Studies.

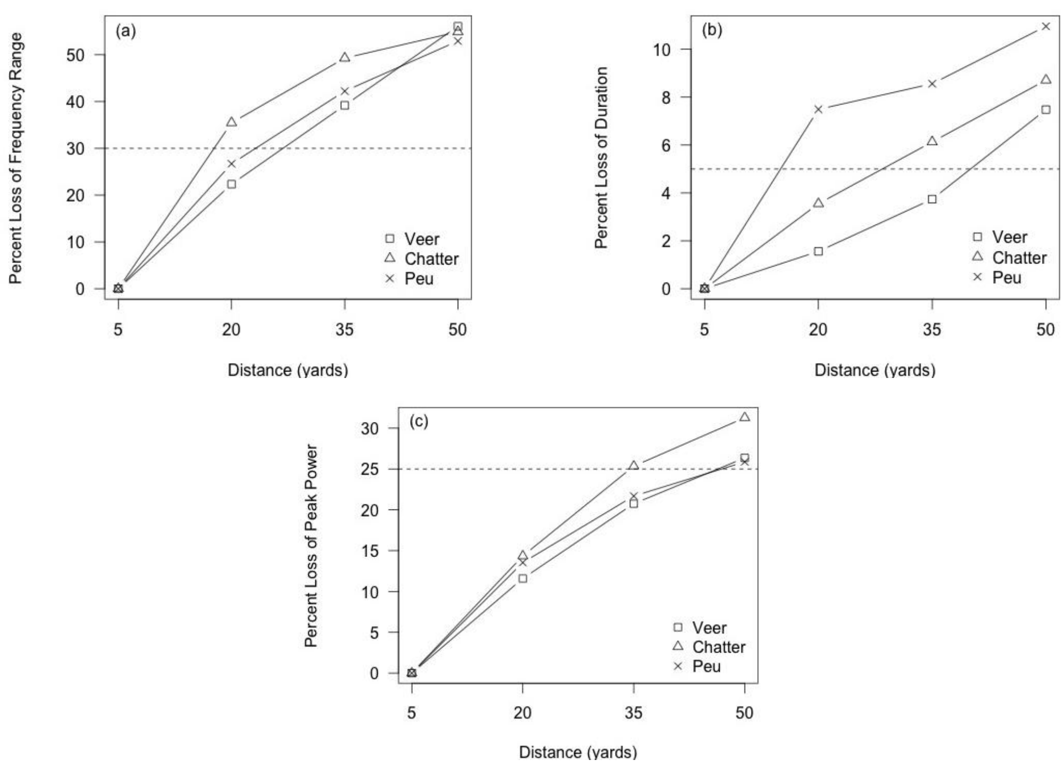

FIGURE 2. Percent loss with distance of frequency range (a), duration (b), and peak power (c) for the veer, chatter, and peu calls. The dotted lines represent the degradation tipping point measurement. See methods section for an explanation of tipping point measurements. Sample size (N) was 1728 calls (N_{Veer} = 448, $N_{Chatter}$ = 672, and N_{Peu} = 608).

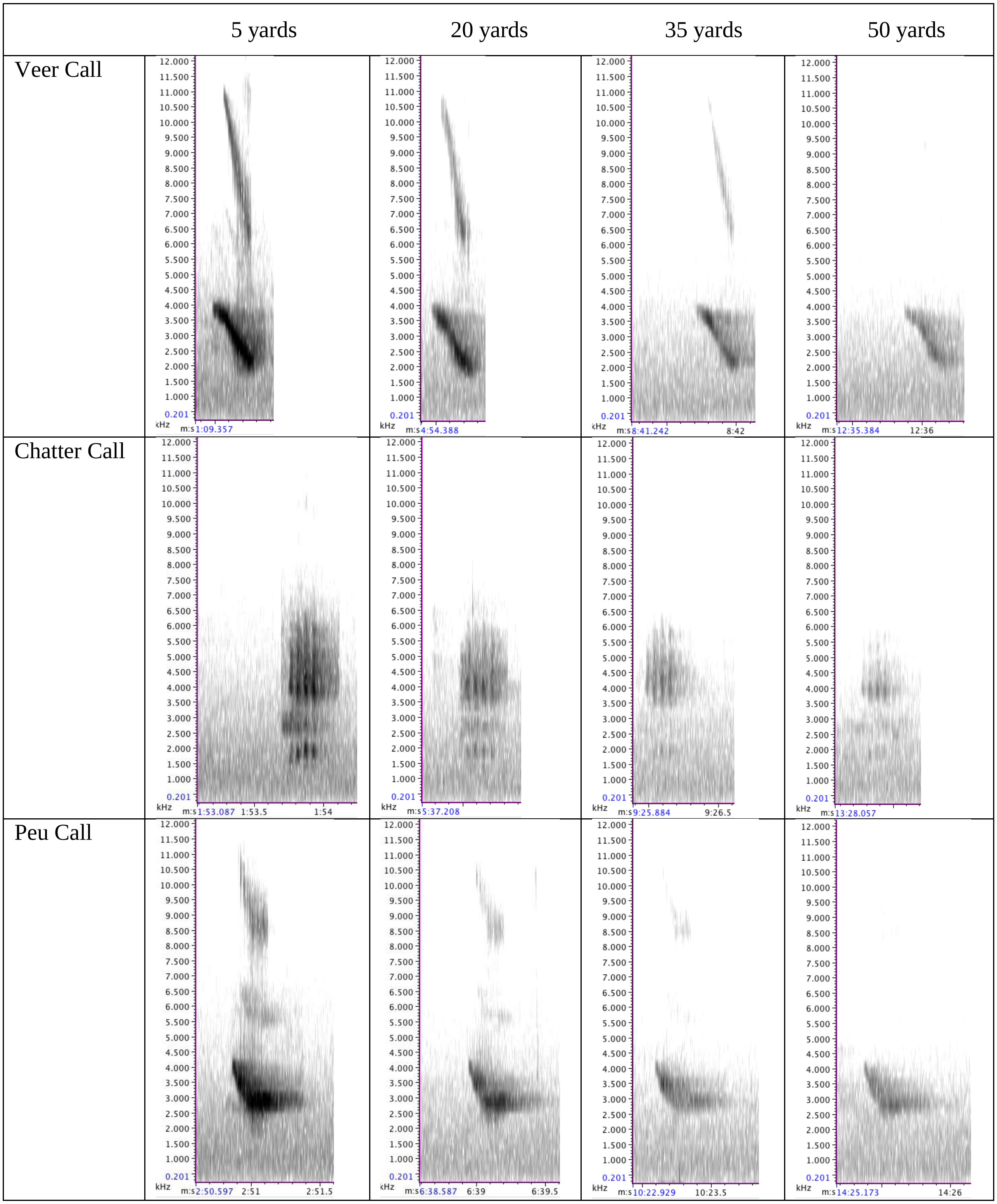

FIGURE 3. Sonogram images showing frequency (kHz) against time (seconds) for veer, chatter, and peu calls as they degrade. Each row shows the same individual call recorded at each distance.

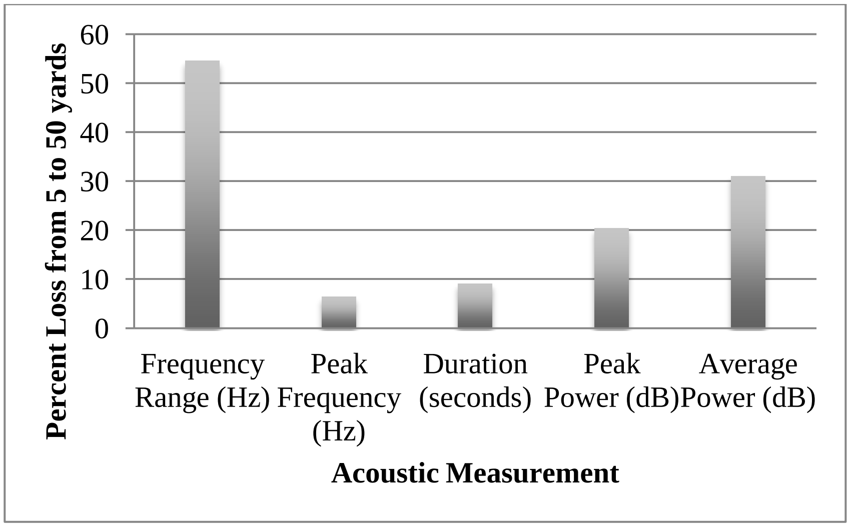

FIGURE 4. Mean percent loss considering veer, chatter, and peu calls combined for frequency range, peak frequency, duration, peak power, and average power from initial data at 5 yards from the speaker to final data at 50 yards from the speaker.