VEERY QUERIES: HYPOTHESIZED AGGRESSIVE VOCALIZATIONS IN A MIGRATORY SONGBIRD SPECIES

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Abstract. The veery *(Catharus fuscescens)* is a neotropical migratory songbird species that breeds on the Cary Institute grounds. Males use a variety of acoustically complex vocalizations during the breeding season, particularly during territorial defense and mate attraction. In previous years, Cary researchers have determined that male veeries use two vocalizations, dubbed whisper calls and no-intro songs, more frequently during agonistic encounters with rival males and have hypothesized that these may serve as signals of aggressive intent. This year's research was designed to build upon the previous investigations and determine whether these vocalizations indeed signal a bird's intent to escalate the conflict. We used a playback experiment wherein we presented territorial males in the field with two acoustic stimuli: one "control" recording of unmanipulated song, and one "treatment" recording that was altered to contain both whisper calls and songs missing the introductory note. In comparison to the pre- and post-playback periods, where no vocal stimuli were used, males uttered more whisper calls and no intro songs during both control and treatment playback. In addition, they spent more time in close proximity to the speaker during both of these playback periods, which is generally considered a reliable measure of aggression. Both whisper calls and no-intro songs were correlated with amount of time spent within 10m of the speaker across all four periods. However, we found no significant difference in veery responses to the control versus treatment playbacks, indicating that this species may use additional behaviors that we were not able to simulate during this experiment in order to signal aggressive intent.

INTRODUCTION

The veery, *Catharus fuscescens*, is a Neotropical migratory songbird species that breeds in the Northern U.S. and Canada, including on the grounds of the Cary Institute. Although the ethereal song of the veery is one of the quintessential sounds of early summer, little is known about how this species of thrush uses its vocalizations during territorial interactions with rival birds. Like many long-distance migrant species, veery populations are declining throughout their range, albeit slowly (BirdLife International 2009; McGowan & Corwin 2008). Habitat destruction appears to be the main culprit, though collisions with windows and wires during migration, predation by domestic cats, and other anthropogenic factors likely play a role as well (Bevier et al. 2005). Determining how veeries use vocal signals during territorial disputes may help provide more information about this species' overall breeding behavior.

Bird song in general serves two purposes: mate attraction and territory defense. In veeries, as in most songbird species, only the male sings, though both sexes also produce a range of calls. Males use their songs to advertise their quality to potential mates, as well as to protect their territories from intruding males. In encounters between rival birds, song is thought to function as a signal of the individual's aggression level. Through his song, each male conveys his willingness or ability to fight, and the less aggressive individual submits. Both rivals thus benefit from signaling their intentions and avoiding an actual physical attack (Searcy et al. 2006). Song type matching or switching, frequency matching, low-amplitude singing ("soft song"), high-amplitude singing, trill performance, and song overlapping are all vocalizations that may function as aggressive signals in various avian species (Forstmeier et al. 2002; Cramer & Price 2007; Searcy & Beecher 2008, 2009; Ackay et al. 2011; Anderson et al. 2012).

However, aggressive signals in birds can be difficult to identify, since both aggressive vocalizations (those that signal intent to escalate) and submissive ones (those that signal de-escalation) may be present in an agonistic context. Searcy and Beecher have therefore proposed three criteria for determining whether a given vocalization is aggressive (2009). The *context criterion* seeks evidence that the hypothesized aggressive signal is used more frequently in aggressive situations; the *predictive criterion* determines if the signal can be used to predict a subsequent escalation by the signaling bird; and the *response criterion* establishes whether a bird reacts differently to the signal than to a control.

Veery song typically consists of three parts, or phrases (see Fig. 1); these follow a relatively predictable format but are often varied by the singer by dropping or adding notes. Phrase one (the introduction) consists of a single upward-slurring note; phrase two contains several notes that generally span a range of frequencies; and phrase three contains several notes of lower frequency than the second phrase (Samuel 1972). Male veeries have small repertoires, generally consisting of only one to two songs, but these are sufficiently different from one individual to the next to allow identification on the basis of song (Stern 1956; Samuel 1972; Weary et al. 1987). The function of calls has not been studied as extensively as song; however, they are usually shorter and simpler than songs and are used by both sexes for various types of communication. In oscine songbirds like the veery, most calls appear to be innate, whereas songs are learned as young birds develop (Kroodsma & Miller 1996). Veeries are unique in that they possess a wide variety of calls, several of which, like their songs, are also complex in frequency.

Presently, we know that male veeries use certain vocalizations at higher rates during agonistic (conflict) encounters with rival males. Through previous experiments, Dr. Belinsky and her colleagues identified and described two vocalizations in particular that they believed to serve as aggressive signals. In the first, dubbed “dropped-intro” or “no-intro” songs, the bird’s typical song is performed minus phrase one, the first rising note (see Fig. 2).

The second, “whisper calls,” are relatively short, complex notes usually uttered at low amplitude and often inserted between the primary songs during agonistic contexts (see Fig. 3). Whether these vocalizations should be classified as calls or songs is somewhat unclear. In previous studies, Dr. Belinsky and her assistants had adopted this terminology, primarily due to their relatively short lengths (Belinsky pers. comm.). They seem to be used only by male birds and differ significantly in structure from the known contact and alarm calls employed by both sexes. (However, sex-specific calls have been documented in a number of bird species, both oscine and non-passerine (Gehr 2007)). Nevertheless, it bears mentioning that these “whisper calls” may indeed be songs or song elements akin to a note or phrase contained within a longer vocalization, particularly since they are sometimes substituted in place of the introductory note described above.

Dr. Belinsky and her assistants assessed Searcy and Beecher’s response and context criteria in a 2010 playback experiment conducted at the Cary Institute. During this experiment, they created two different treatment stimuli: one with whisper calls inserted between songs, and one with introductory notes removed from several of the songs. During each trial, a territorial veery was first presented with a control playback (consisting of unaltered veery song) followed by either the no-intro treatment playback or the whisper call treatment playback. If the focal male responded to this trial, the researchers returned the next day and repeated the process with the other treatment stimulus. Veeries responded to all three playback stimuli with whisper calls and no-intro songs, indicating that these vocal signals are indeed used in agonistic contexts and therefore satisfying the context criterion. However, the results did not allow the researchers to definitively distinguish whether these vocalizations are used to communicate escalating or de-escalating intentions, as veeries responded similarly to the control and both treatment stimuli—i.e. the response criterion was not met (Belinsky et al., unpublished).

The aim of our research this year has been to further investigate veery responses to no-intro songs and whisper calls, and to determine whether they exhibit graded responses to these putative aggressive signals. In the 2010 playback experiment described above, each bird was presented with acoustic stimuli that contained additional whisper calls on one day and additional no-intro songs on another. From field observations, however, it appears that veeries may use both vocalizations in concert during agonistic encounters. During this year's experiment, we combined no-intro songs and whisper calls into a single high-intensity stimulus for playback in hopes of eliciting a more extreme response, whether escalating or de-escalating. A stronger response to the combined vocalizations may indicate that veeries employ graded agonistic signals, responding progressively more or less based on the intensity of the simulated threat.

As per Searcy and Beecher, we aimed to evaluate these signals from the perspective of both the sender (producer of the signal) and the receiver (target or observer of the signal.) We again assessed the context criterion by counting how many whisper calls and no intro notes the focal male produced during an aggressive contest, a simulated territorial intrusion by a rival bird (sender's perspective). From the receiver's perspective, we also assessed the response criterion, presenting focal birds with both a control playback stimulus and a treatment playback stimulus to determine whether birds exhibited differential responses to each (Searcy & Beecher 2009).

Hypothesized aggressive signals

Searcy and Beecher note that agonistic signals may fall into one of two categories: strategic signals, which all senders are able to use, and index or performance signals, which are constrained in some way—for example, those that are energetically or mechanically demanding and thus can only be produced by senders physically capable of doing so (Searcy & Beecher 2009). Within the strategic signal category, further distinctions may be made between "conventional signals" which make the sender more vulnerable to a response by the receiver, and "classic handicaps," where all senders can produce the signal but it is more costly for some individuals than others.

From this perspective, whisper calls could potentially fall into either the strategic or index category. Because of the relatively low amplitude, Dr. Belinsky has postulated that this signal may be analogous to the soft song, a strategic conventional signal, used by song sparrows *(Melospiza melodia)* prior to attack (Ackay et al. 2011; Anderson et al. 2012). However, veeries freely insert these vocalizations between songs performed at normal amplitudes. This behavior seems antithetical to the purpose of a true soft song, which is to ensure honesty of the aggressive signal since, in order to use it, senders and receivers must be in close proximity to one another and are therefore more vulnerable to attack (Searcy et al. 2006). Furthermore, from a purely observational standpoint, these whisper calls are often easily detectable by a human listener at distances greater than 5-10m from the bird.

On the other hand, over the course of its journey from the sender to the receiver, a sound may be distorted by any number of environmental factors. Media such as the ground and woodland vegetation absorb a certain amount of sound energy, resulting in decreased amplitude of acoustic signals. These losses are greater for higher frequency sounds and increase with the distance a sound wave must travel (Bradbury & Vehrencamp 1998). Whisper calls could thus conceivably parallel soft song not because of the absolute amplitude when the signal leaves the sender's bill, but because distortion of the higher frequency components of these vocalizations is minimized when sender and receiver are in close proximity.

Another possibility is that whisper calls may be performance signals or a "classic handicap" type of strategic signal. The structure of these vocalizations is extremely complex, spanning a wide range of frequencies in a short period of time, somewhat similar to the trilling of banded wrens, nightingales, and certain sparrow species (see again Fig. 3). Researchers have found that low frequency sounds are produced by one side of the syrinx, while high frequencies are produced by the other. Vocalizations with such rapid modulations in frequency are comparatively difficult to achieve, and thus should be subject to high performance constraints (Podos & Mosley 2009).

In contrast, no intro songs merely involve the omission of the simplest note in the veery's song and should not be as physically difficult to produce. (Replacing the introductory note with a whisper call, however, could reasonably be considered more taxing because it involves switching immediately from an already complex whisper call to phrases two and three of the typical song.)

Although veeries appear to possess only one or two "normal" song types, variable addition or deletion of the aforementioned vocal elements may serve to significantly increase an individual's repertoire size. A number of researchers have found that in song sparrows and several other species, rapid switching of song types or song variants may serve as an aggressive signal (Searcy et al. 2006). In veeries, the ability to insert or remove vocal components may increase variety in an otherwise small repertoire of songs. Larger repertoires can function as index signals, potentially indicating that the sender enjoyed relatively good nutrition during brain and motor development, and/or possesses high genetic quality (Podos & Mosley 2009).

METHODS

Site Description

The playback experiment took place on the grounds of the Cary Institute of Ecosystem Studies in Dutchess County, New York, USA. Oaks and maples are the predominant tree species in veery habitat on the Institute's 778 hectares (www.caryinstitute.org). Trials were conducted between June 6 and July 3, 2012, from 06:00 until 10:00.

Construction of Stimuli

Our methods in this experiment were similar to those employed during the 2010 trials. A different one-minute recording of unaltered, natural veery song recorded on the Cary grounds in 2009 or 2010 served as a control playback in each trial. Each control track contained an average of ten songs, and no calls of any kind. We reused the control tracks and the corresponding whisper call treatment stimuli, containing three whisper calls each, from the 2010 experiment. Using the Cornell Lab of Ornithology's Raven Pro 1.4 software, we randomly inserted an additional three unused whisper calls between songs. We also removed the introductory note from six randomly chosen songs in each treatment stimulus using Raven's filter tool. Each final treatment stimulus thus contained six whisper calls and six no-intro songs. All tracks were loaded onto an Apple iPod Shuffle, which was connected to the speaker via an AV cable for use in the field.

Mounted veery

During this experiment we used a remote-controlled robotic model made from a taxidermied male veery. The robot was placed on a tripod approximately 1.5m off the ground and as close as possible to the speaker in order to create a more realistic stimulus and allow territorial birds a target on which to focus their attentions. The robot is able to flick its wings and bob up and down, movements that approximate hypothesized aggressive signals in *Catharus* thrush species (Dilger 1956). In the 2009 experiment, Dr. Belinsky et al. found no significant difference in vocalizations or behavior in the trials that featured robotic movements versus those where the mount was stationary. Therefore, we do not believe that use of the robot introduced a confounding variable, but rather created a more realistic simulation of a territorial intrusion.

In a 2008 paper, Laidre and Vehrencamp argue that providing a mount, particularly an interactive one, during playback experiments allows territorial males to attack and thus is useful for distinguishing between escalating and de-escalating signals. They state that in many species, signaling is bimodal or multimodal, meaning it contains more than one component; for example, visual displays given in conjunction with vocal signals. Furthermore, these researchers posit that oftentimes a gradual escalation is common and that interactive models create a more realistic simulation of this process (2008). By employing the robotic bird in our trials, we simulated this behavior pattern more realistically and accounted for the possibility that birds respond more readily to a multimodal signaling system.

Field trials

During each trial, we identified the territory of a singing male veery on the Cary Institute grounds and set up the speaker close enough to be heard by the bird but a sufficient distance away to avoid scaring him off with our movements. Each trial utilized a different playback set (a control stimulus plus its corresponding treatment stimulus) so that no stimuli were repeated from one bird to the next. In addition, we conducted each trial at a different site to avoid testing the same veery more than once.

We attached the speaker to a small tree, approximately 1.5 – 2m high, and placed the robot on a tripod directly next to the speaker. The robot was hidden by a square of camouflage cloth attached to a string, which could be pulled from a distance to reveal the mount at the beginning of the control period. We then sat 15 meters from the speaker, from which distance we could operate the equipment and observe the focal male's behavior toward the speaker and mount while minimizing disturbance to him.

Following the same format as the 2010 experiment, we began each trial with a four-minute period of silence (pre-playback), during which we recorded any songs and calls the focal male veery made prior to playback. The robotic mount was camouflaged throughout this portion of the trial. Next we started the one-minute control playback, simultaneously revealing the mount but keeping it stationary. This was followed by one minute of silence, a repeat of the control stimulus, and another minute of silence. At this point, we began the one-minute treatment playback, followed by one minute of silence, then a repeat of both treatment stimulus and silence. While the treatment stimulus was playing, one observer (KLB) operated the robot at random intervals to further mimic territorial intrusion by a rival bird. We continued to record any vocalizations and behaviors of the focal male for during a post-playback period of eight minutes following the treatment playback, keeping the robot stationary during this time.

During each period, the first observer (KLB) narrated the focal bird's vocalizations and approximate distance from the speaker, as well as other behaviors (such as flights, bill wiping, or preening) when the bird was visible. The second observer (CEN) operated the microphone, recorder, and iPod.

RESULTS

We assessed veery responses during each period (pre-playback, control playback, treatment playback, and post-playback). Each period was four minutes long, with the exception of post-playback, which was eight; we therefore halved the number of vocalizations and other behaviors observed during post-playback in order to accurately compare the data across periods.

As with the 2009 and 2010 playback experiments, most of the male veeries in our experiments did respond strongly to playback, though several individuals that we heard singing prior to the experiment fell silent as we set up and did not resume vocalizing of any sort. These trials were aborted, and we subsequently moved on to a different location. Altogether, we conducted 31 trials during which we recorded vocalizations by the focal male. Four of these tracks proved too difficult to analyze due to background noise (wind, power tools, nearby streams), or contained too much interference from neighboring male(s) countersinging to reliably distinguish the songs of the focal bird.

Of the 27 tracks that we used for analysis, we assessed five response variables: number of whisper calls, number of no-intro songs, number of songs where a whisper call replaced the introductory note, and time spent within 5m and within 10m of the speaker and mount. One of these variables—songs where a whisper call replaced the intro note—was not included in our final analyses, as we did not observe enough separate instances during our trials. However, it is a vocalization that we have observed during natural veery singing bouts, particularly during countersinging by rival males, and therefore may merit attention in future experiments.

Because the data were not normally distributed, we used a Wilcoxon/Kruskal-Wallis nonparametric signed-rank test to analyze the differences in means between periods (see Fig. 4). In order to adjust for making multiple correlations within the same data set, we used Bonferroni's correction for all significance tests. The mean number of no intro songs uttered during each control period ($\bar{x}$ =1.70370 ± 0.3654) and treatment period ($\bar{x}$ =1.74074 ± 0.3617) were significantly higher than during the pre- and post-playback periods ($\bar{x}$ =0.03704 ± 0.2788 and $\bar{x}$ = 0.12963 ± 0.2320, respectively; p> χ^2 = <0.0001). The mean number of whisper calls uttered during the control period ($\bar{x}$ =1.37037 ± 0.3387) and the treatment period ($\bar{x}$ =1.51852 ± 0.3617) were likewise significantly higher than the means during the pre-playback ($\bar{x}$ =0.22222 ± 0.2630) and post-playback ($\bar{x}$ =0.18519 ± 0.3027) periods (p> χ^2 = 0.0006). The mean number of partial songs was higher during control playback ($\bar{x}$ =0.259259 ± 0.0371), treatment playback ($\bar{x}$ =0.259259 ± 0.0198), and post-playback ($\bar{x}$ =0.203704 ± 0.0191) than during pre-playback ($\bar{x}$ =0.037037 ± 0.0073), but not significantly different overall across the periods (p> χ^2 = 0.2725).

Proximity to the speaker and/or mount is frequently used as a measure of aggressive intent during behavior studies; a bird that moves closer to his opponent obviously makes himself more vulnerable to attack and therefore should not approach closely unless his aggression level, or willingness to engage in a fight, is relatively high. We therefore examined correlations between each of the hypothesized aggressive vocalizations and the bird's time spent within close proximity (5 or 10m) of the speaker. To do so, we used a Kendall's Tau b nonparametric test for detecting correlations in non-normally distributed data (see Table 1.)

Although no birds physically attacked the mount, the amount of time spent within 5m and within 10m of the speaker was positively correlated with both the mean number of no-intro songs and mean number of whisper calls given. Across all four periods, the number of no intro songs was positively correlated with proximity to the speaker (b=0.3476, p>|Tau b| =<0.0001 for time spent within 5m of the speaker and b=0.5559, p>|Tau b| =<0.0001 for time spent within 10m of the speaker.) Mean number of whisper calls was more weakly correlated with time spent within 5m of the speaker (b=0.2457, p>|Tau b| =0.0043) but stronger for time spent within 10m (b=0.3637, p>|Tau b| = <0.0001).

DISCUSSION

As in the 2010 experiment, focal birds responded similarly to both the unmanipulated control playback and the "high-aggression" treatment playback. On average, they uttered more whisper calls and no intro songs during both playback periods in comparison to pre- and post-playback. However, there was no significant difference between the control and treatment playbacks in either the number of whisper calls or the number of no intro songs performed.

We found that the mean number of no intro songs was positively correlated with the amount of time spent within 5m and 10m of the speaker. Mean number of whisper calls was also correlated with proximity to the speaker, though more strongly for time spent within 10m than for time spent within 5m. Since proximity to the speaker and/or mount is a commonly used measure of aggression in behavior studies (Searcy et al. 2006; Searcy & Beecher 2007), these results suggest that whisper calls and songs missing the introductory note do serve as aggressive signals rather than de-escalating ones.

A number of factors may help explain the birds' similar responses to control and treatment stimuli. As humans, we are limited in how realistic a territorial threat we can simulate. Veeries may well use other behavioral signals, either separately or together with vocalizations, to communicate aggressive intent. For example, most of the birds that we observed singing in close proximity did so from several meters above the speaker and mount; rarely did the focal males sing from the ground level or same height as the mount. We measured proximity in two dimensions, but the height from which a bird vocalizes may project a stronger or weaker signal and therefore may be involved in signaling aggression as well. Although we used a remote-controlled interactive model, playback itself was not interactive and therefore may not have accurately represented natural veery behavior (see Langemann et al. 2000). Additionally, our robotic mount obviously could not hop from perch to perch or ascend to a higher branch, so such potential signals were also missing from our simulation due to technological limitations.

As described in the introduction, sounds may experience considerable distortion as they travel from the sender and are picked up by the receiver. The physics of sound propagation may thus result in distortion, both during the recording of vocalizations for playback and during the playback itself. Since higher frequency sounds experience greater distortion, our recordings of whisper calls for use in the treatment stimuli could conceivably have resulted in the loss of critical information that veeries use for evaluating threats from rivals. This distortion would not have occurred to such an extent in the no intro songs, as we simply used the Raven software to erase introductory notes of normal songs (which are also lower in frequency than whisper calls to begin with.)

By first presenting birds with a control playback (a lower aggression signal) followed by a "hyper-aggressive" treatment playback, we attempted to simulate the pattern of escalation that can occur in agonistic contests. We had hoped that operating the robot during the treatment period would serve to enhance this simulation and allow us to observe a differential response. Despite our efforts, none of the veeries in the 2009, 2010, or 2012 experiments physically attacked the mount during playback trials, though on several occasions individuals were observed flying or swooping low over it.

Dilger (1956) described eliciting attacks using playback techniques and a papier-mâché mount, but our results have indicated that it's relatively difficult to provoke attack behavior in this species. Veeries do not seem to respond as readily to the conventional methods used for evaluating aggressive behavior in sparrows and warblers, which appear to be inherently more pugnacious (Searcy et al. 2005; Hof & Hazlett 2010; Akcay et al. 2011; Anderson et al. 2012). However, Searcy and Beecher clarify that predicting outright attack isn't necessary to classify a signal as aggressive; it must simply predict some type of escalating behavior that would eventually lead to attack (2009). To that end, future experiments could assess the predictive criterion by determining whether the hypothesized aggressive signal predicts a less extreme escalation, such as close approach to the speaker.

Veeries, and perhaps other thrush species, clearly exhibit different aggressive behavioral patterns than the more thoroughly studied sparrow and warbler species. When evaluating aggressive signals in this species via playback experiments, one cannot assume that they will respond in the same fashion as other avian genera. Further observational studies may prove beneficial in identifying other potential aggressive signals and how they are used together in agonistic contexts with the two vocalizations we have described.

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APPENDIX

Table 1. Kendall's Tau b nonparametric correlations between whisper calls, no intro songs, and proximity to the speaker across all four periods.

Correlations Across All Periods		
Response Variables	*Kendall's Tau b*	*Prob>|Tau b|*
Whisper Calls x Time <5m	0.2457	0.0043
Whisper Calls x Time <10m	0.3637	<0.0001
No Intro Songs x Time <5m	0.3476	<0.0001
No Intro Songs x Time <10m	0.5559	<0.0001

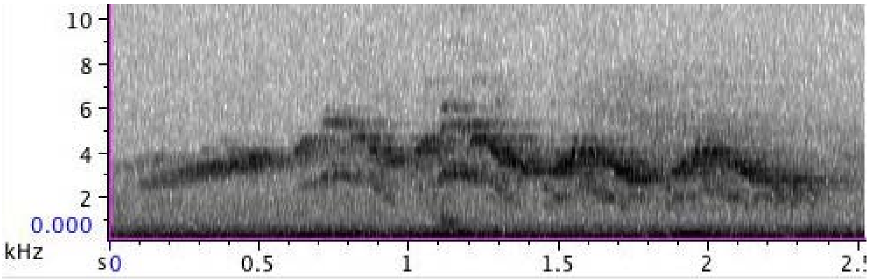

Figure 1. Typical veery song, exhibiting three distinct "phrases".

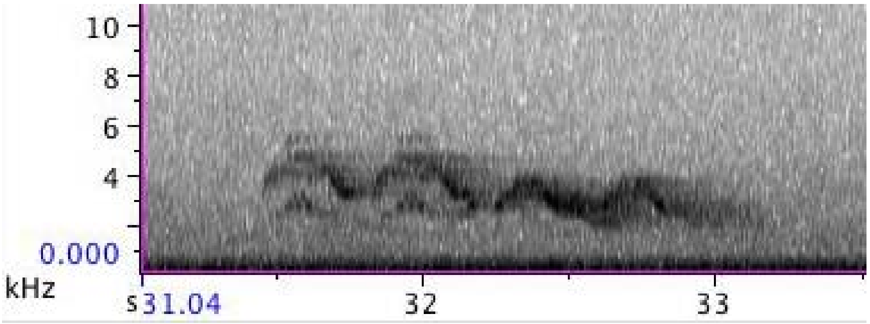

Figure 2. "No intro" song, lacking the typical first phrase or introductory note.

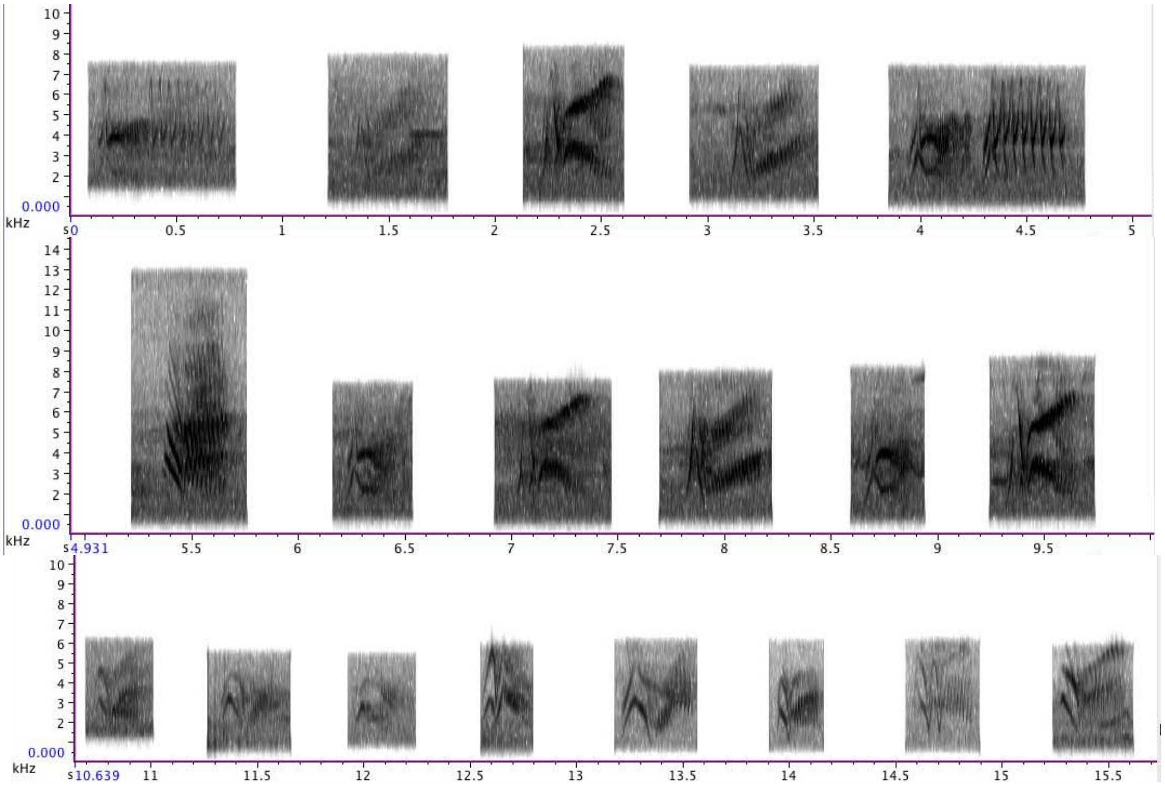

Figure 3. A sampling of whisper calls recorded on the Cary Institute grounds, showing the wide variety of forms and frequency ranges these vocalizations can span.

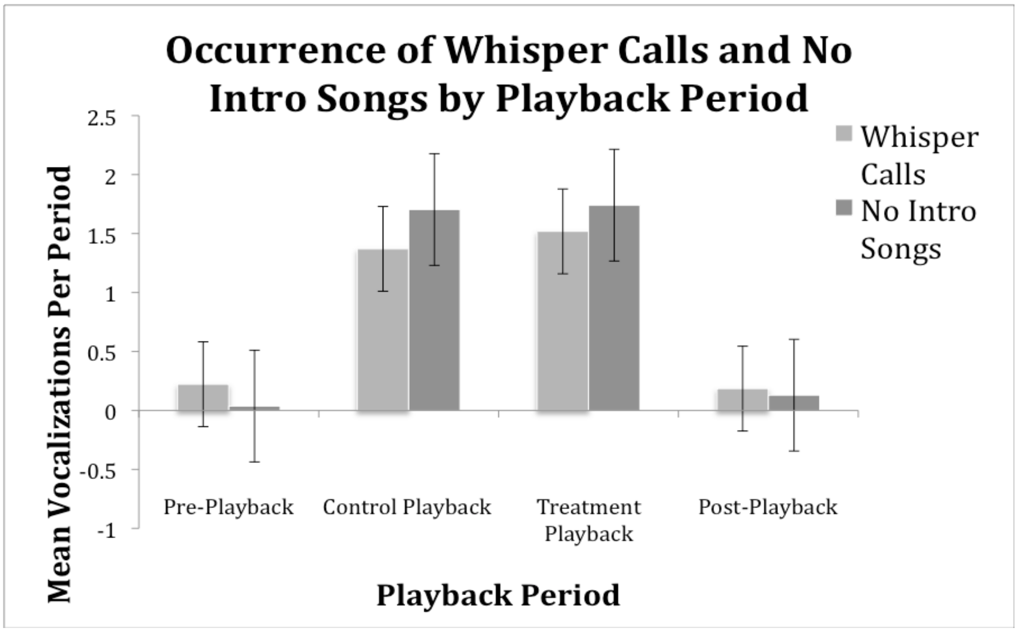

Figure 4. Mean number of hypothesized aggressive vocalizations per playback period (Wilcoxon/Kruksal-Wallis nonparametric signed-rank test.)