

**Stranger Danger: Interspecific
Vocal Responses of Selected
Diurnal Passerines to Indirect
Predator Alarm Calls**

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ABSTRACT

This study examines how a bird community as a whole and more specifically three common diurnal passerines, the veery (*Catharus fuscescens*), the wood thrush (*Hylocichla mustelina*), and the scarlet tanager (*Piranga olivacea*), respond to indirect predator alarm calls of the eastern tufted titmouse (*Baeolophus bicolor*; ETTI) around dusk, a peak period of bird vocalization. A total of 14 plots were subjected to two 65 min playback-recording trials over 2 consecutive days: an experimental treatment using playbacks of ETTI alarm calls, and a control treatment using “neutral” calls of the gray tree frog (*Hyla versicolor*). In general, the dusk chorus as a whole did not significantly respond to ETTI alarm calls. However, the three focal species each exhibited an increase in calls relative to their song output, which supports the occurrence of heterospecific eavesdropping.

Keywords: avian alarm calls, eastern tufted titmouse (*Baeolophus bicolor*), veery (*Catharus fuscescens*), wood thrush (*Hylocichla mustelina*), scarlet tanager (*Piranga olivacea*), heterospecific eavesdropping, soundscape ecology

1. INTRODUCTION

Sound is a dynamic, information-rich component of landscapes. Collectively, sounds create a “soundscape” filled with various types of environmental and social information. The interactions between organisms and the surrounding soundscape are the focus of soundscape ecology (Pijanowski et al. 2011). The founders of this branch of ecology, Pijanowski et al. (2011), describe it as the intersection of geologic, biologic, and anthropocentric sound in a landscape across space and time. More specifically, soundscape ecology examines how the dynamics of these collective sounds affect intra- and interspecific communication systems, species life-history patterns, and population and community dynamics.

Biologic or biophonic sound (i.e., vocalizations of organisms) is an important source of information and communication, especially among birds. Most birds have 5 to 14 distinct vocalizations of different acoustical structure and related function. Birds sing to communicate territorial ownership, attract mates, and broadcast personal characteristics; they call to warn of potential dangers or ward off intruders (Gill 2007). Generally, birds have two “peak” times for singing: dawn and dusk. It is not fully understood why birds tend to vocalize during dawn and dusk. Some research has indicated that the dawn chorus may help male birds exchange information about their social standing (McGregor 2005). Hutchinson (2001) and McNamara et al. (1987) proposed that the dawn chorus may be a byproduct of excess overnight energy reserves and/or low-light levels, which make feeding more energy-intensive and relatively unprofitable. Schmidt and Belinsky (2013) expanded on the latter hypothesis, suggesting that the relatively low-light environment at dawn may decrease visibility of vocalizing birds, thereby reducing the risk of predation.

Even less is known about the function of the avian dusk chorus and how avian communities perceive, use, and share information during this time of the day. Studies investigating nocturnal vocalizations comprise less than 4% of the literature on avian vocalization (La 2011). Hypotheses similar

to those for the dawn chorus have been put forward to explain why birds sing around dusk, such as decreased visibility at low light levels (e.g. McGregor 2005). Schmidt and Belinsky (2013) hypothesized that eavesdropping on vocal signals by other species may help birds exploit potential food resources or avoid danger by nesting in areas where (predator) alarm calls are uncommon (Dall et al. 2005).

Indirect predator alarm calls, such as alarm calls of the eastern tufted titmouse (*Baeolophus bicolor*- hereafter referred to as ETTI), communicate important messages, which can affect both immediate survival and overall fitness. As a species that tends to forage in mixed-species flocks, ETTI often sounds distinctive alarm calls and other vocalizations signaling imminent danger (Leavesley & Magrath 2005; Contreras and Sieving 2011). Besides warning group members of danger, ETTI alarm calls may attract others to aid a threatened individual, or confuse a predator or perceived threat (Branch & Freeberg 2012). Alarm calls may also inform predators that they have been detected and induce them to abort their mission (Hetrick 2006). Some studies have suggested that these calls may even communicate size and relative severity of the threat (Courter & Ritchison 2010). Because the ETTI can convey so many different types of information through its alarm calls, it (along with other highly vigilant and social species of the family *Paridae*) is considered a "community informant" (Contreras & Sieving 2011). While ETTI alarm calls are thought to be directed to conspecifics, they may also be acquired and used as informational cues by numerous heterospecifics (Contreras & Sieving 2011; Gill & Bierema 2013). The use of such indirect social information by individuals of different species to assess the quality of environmental parameters in a given habitat is referred to as heterospecific eavesdropping (Valone 2007; Dall et al. 2005).

In this study I examine potential heterospecific eavesdropping behavior by avian dusk chorus species in an eastern deciduous mixed oak forest community by investigating how broadcasting public information by a community informant at dusk modifies singing and calling vocalizations. When exposed to an informant's alarm calls, avian dusk chorus species are likely to decrease their song output to avoid

attracting predators or signaling the relative location of a possible nest, offspring, and kin/mate. In addition, they may increase their call output in order to warn mates, offspring, and kin of impending danger. Here I focus in particular on the response of three common, diurnal, dusk-vocalizing, passerine species: the veery (*Catharus fuscescens*), the wood thrush (*Hylocichla mustelina*) and the scarlet tanager (*Piranga olivacea*). All three focal species are vulnerable to a wide array of predators (Bevier et al. 2005; Schmidt, unpublished data). Thus, it would be to their advantage to eavesdrop on community informants such as the eastern tufted titmouse, a common species in eastern deciduous mixed oak forests (Grubb & Pravasudov 1994; Contreras & Sieving 2011). However, since the nesting ecology of the three focal species is quite different, the response of these species to a possible threat may vary as well. Veeries, which nest close to or on the forest floor (≤ 1.5 m above ground level; Bevier et al. 2005), are more at risk of predation by ground predators and more likely to show a strong response to potential danger. The wood thrush nests in the middle canopy (average nest height is 2.3 m, most nests are typically ≤ 6.5 m above ground level; Evans et al. 2011); it has less to fear from ground predators, which would warrant a more moderate response. The scarlet tanager occupies nests in the upper canopy (≥ 10 m above ground level; Mowbray 1999), where aerial predation becomes a greater threat. Here reduced activity would be more beneficial to avoid detection.

Thus, I hypothesize that when exposed to ETTI alarm calls, (1) avian dusk chorus species will eavesdrop on the community informant to obtain important predation risk information, (2) avian dusk chorus species will respond to the signaled threat by reducing their song output and increasing call output, and (3) ground nesting birds, such as the veery, will exhibit a greater increase in calling behavior than species that nest higher off of the ground such as the wood thrush and scarlet tanager. To test these hypotheses I designed a playback-recording experiment using playbacks of ETTI alarm calls in the experimental treatment and playbacks of the common, low-risk dusk call of the gray tree frog (*Hyla*

versicolor), to which the dusk chorus is not expected to react (Emmering & Schmidt 2011), in the control treatment.

Specifically, my objectives are (1) to determine the basic composition of the avian dusk chorus (species list, species presence/absence, and species contribution to dusk chorus song total), (2) to establish whether the avian community reduces the amount and distribution of song vocalizations in response to alarm calls (total number of songs in control treatment versus experimental treatment, and the distribution of the number of songs per plot over recording time for both treatments), and (3) to establish whether the three focal species change the amount and distribution of song and call vocalizations in response to alarm calls (total number of songs as well as calls in control treatment versus experimental treatment, and the distribution of the number of songs and calls per plot over recording time in both treatments, for each species separately). This study is part of long-term research on the singing behavior of veeries conducted by Dr. Kenneth Smith (Texas Tech University) and Dr. Kara Belinsky (Arcadia University) in cooperation with the Cary Institute of Ecosystem Studies, New York.

2. METHODS

2.1. Study Area

The study was conducted at the Cary Institute of Ecosystem Studies in Dutchess County, southeastern New York, USA (41° 50' N, 73° 45' W) (Figure 1). The Cary Institute is located in the Hudson Valley, which is a physiographic section of the larger Ridge-and-Valley province in the eastern temperate forest ecological region (Fenneman 1921; Fenneman & Johnson 1946). The Hudson Valley is characterized by a moderate to mildly humid climate, relatively dense and diverse forest cover, and a high density of human inhabitants (see Appendix 1). The Cary Institute property encompasses approximately 325 ha of mixed oak forest largely composed of second-growth oaks (*Quercus rubra* and

Q. prinus) and maples (*Acer* spp.) in the overstory. Oaks, sugar maple (*Acer saccharum*), American hophornbeam (*Ostrya virginiana*), and American hornbeam (*Carpinus caroliniana*) are the most common trees found in the understory and maple-leaved viburnum (*Viburnum acerifolium*), witch-hazel (*Hamamelis virginiana*), and *Vaccinium* spp. are common shrubs (Schmidt & Belinsky 2013; Schmidt & Ostfeld 2008). Limited-access roads, paths, trails, and ephemeral wetlands are found throughout the property (Belinsky et al. 2012). Common birds include the veery, wood thrush, scarlet tanager, ovenbird (*Seiurus aurocapilla*), American robin (*Turdus migratorius*), gray catbird (*Dumetella carolinensis*), red-eyed vireo (*Vireo olivaceus*), and eastern bluebird (*Sialia sialis*; Belinsky et al. 2012). A detailed description of the study area is provided by Belinsky et al. (2012).

2.2. Plot Selection

For this study, I selected 14 plots within the campus of the Cary Institute (Figure 1). Since this experiment was part of a larger study on veeries, the selection process focused on areas where veeries were regularly observed or heard singing at dusk at least 2 days prior to a playback-recording trial. Because veeries tend to sing in a specific location of their territory for 5-7 days (Schmidt and Belinsky 2013), the selected plots were likely to contain an active veery nesting site. I exposed each plot to two playback trials: an experimental treatment, using playback calls of the eastern tufted titmouse, and a control treatment, using playback calls of the gray tree frog. The two playback trials were carried out over 2 consecutive days, or at most within 4 days of each other in case of inclement weather (defined as wind speeds >10km/h and/or moderate to heavy precipitation; Schmidt & Belinsky 2013). The order of the stimuli was randomly assigned. In spite of precautions, weather conditions may have influenced the results of some recordings that were located next to a stream (e.g. plot G); high runoff after a storm may have masked songs and calls of birds near a recording station (Figure 1). Plots were spaced at least 300 m apart to minimize the chance of sampling the same bird community (Schmidt & Belinsky 2013).

2.3. Playback and Recording Protocol

Each playback-recording trial started 20 min before and ended 45 min after sunset (i.e. “dusk”). The trials were conducted from 19 May to 6 July, 2013. I followed the protocol established by Schmidt and Belinsky (2013). Before the start of a trial, I attached a Sennheiser ME 62 omnidirectional microphone (Sennheiser, Wedemark Wennebostel, Germany) with K-6 power module to a metal rebar post 1 m above the ground. The microphone was connected to a Roland R-05 Wave/MP3 recorder (Roland, Los Angeles, CA), which was housed in a waterproof plastic box. I recorded all sound files as WAV files at a sampling rate of 44.8 kHz and 24 bit. All playback calls were loaded on Apple iPod shuffles (Apple, Cupertino, CA), which were connected to a Yamaha PDX-11 portable amplified speaker (Yamaha, Buena Park, CA) attached to a tree or branch ≥ 2 m above ground level. The speaker was positioned 25 m away from and facing the microphone. Playback amplitude was approximately 73 dB SPL measured at 1 m in distance from the speaker. As the experimental treatment playback call, I used the high “seet” vocalization of the eastern tufted titmouse, also known as “high zee,” “high see,” “aerial predator,” or “attack call,” a signal of potential danger (Hetrick & Sieving 2011). To mimic intraspecific heterogeneity in vocalizations, I made use of recordings of 5 different, individual eastern tufted titmice (5 exemplars), one of which was randomly chosen for each trial. All playback exemplars were adjusted to the same amplitude using Raven Pro 1.4 software. Playback calls of the exemplar were broadcast three times during a recording trial for a period of 1 minute: 15 min before sunset, at sunset, and 10 min after sunset.

After equipment setup, I waited until 25 min before sunset to start the iPod. I used a test tone to ensure that the system was operational. For each recording trial, I documented pertinent information including date (Julian day), plot name, plot location, trial number, name of exemplar playback used, recorder used, recorder start time, and playback start time. The first 10 min of the playback were silent to allow for time to quietly vacate the area and minimize disturbance resulting from equipment setup. I

returned to collect the recording and playback equipment 60 min after sunset, so as not to interfere with the normal singing behavior of the dusk chorus, in particular the veery, which has been reported to sing until 54 min after sunset (Schmidt & Belinsky 2013). This study was conducted in compliance with the ethical standards of animal care and use at Texas Tech University.

2.4. Song and Call Analysis

The recordings were transferred to an external hard drive and labeled based on plot location and treatment (e.g. plot location A that received the control treatment, was labeled as AC). I used RavenPro 1.4 (Bioacoustics Research Program 2011) to visualize the sound files in the form of a spectrogram and recorded the number of songs for each one minute interval of recording time. For the three focal species I was able to determine the number of songs as well as the number of calls; calls for other species of the dusk chorus could not be determined. I began collecting data from each sound file 5 min before the first (exemplar) playback to obtain baseline data of song and call vocalizations prior to treatment and stopped at the end of the “dusk” period, 45 minutes after sunset. I identified the songs and calls based on descriptions from Sibley (2003), resources from the Cornell Lab of Ornithology, including the Macaulay Library (2013), and Birds of North America (Appendix 2; Appendix 3; Appendix 4; Appendix 5; Appendix 6). I also used recordings of veery calls made at the Cary Institute to identify calls for this particular species (Schmidt, unpublished data).

2.5. Statistical Analyses

Descriptive Analyses—To describe the avian dusk chorus community composition and determine their overall vocal response to the treatments, I created a dusk chorus species list based on occurrence (i.e. presence/absence) of (vocalizing) species across plots and treatments. I also calculated the percent of total dusk chorus song output that each species contributed.

Multivariate Community Analyses—To investigate whether the dusk chorus species composition exhibits obvious groupings, I used two different forms of ordination, multivariate techniques that arrange sites along axes based on species' composition and abundance (Jongman et al. 1987). I performed a Two-Way-Indicator Species Analysis (TWINSpan) based on the species composition of the dusk chorus and the number of songs reported for each species by plot and treatment (i.e. trial). Species and trials are simultaneously ranked along a dominant gradient: trials across the top and species down the left side (Coker and Coker 1992; McCune et al. 2002; Table 1). The default pseudospecies cut levels were used.

I also performed a Principal Component Analysis (PCA) on the same data. A PCA orthogonal-linear transformation projects the data into a new coordinate system such that the greatest variance is expressed along the first coordinate (the first principal component), the second greatest variance along the second coordinate, and so on. Sample plots that are placed close together in a multi-dimensional space are more similar than those farther spaced apart. I used PC-ORD to conduct both PCA and TWINSpan analyses (McCune and Mefford 2011).

I used both multivariate tests to evaluate whether the trials for a specific plot were more similar to each other than to those of other plots. The TWINSpan results generally grouped the two trials of a specific plot for the dusk chorus as a whole close together, so that a matched pair approach appears acceptable in further analyses (Table 1). The PCA showed analogous results and in addition revealed a clustering of (paired) trials in the center of the diagram, indicating that the plots are similar enough for use as replicates in the experiment (Figure 2).

Univariate Analyses—I used the chi-square test of independence and matched pair analyses to test the hypotheses that species of the dusk chorus respond to the experimental treatment by changing their song and/or call output. I first examined the distribution (histogram and box-plot) and the normal probability plot of the differences between the treatments for each plot; I also conducted a Shapiro-Wilk test for normality on the same data. If the data were approximately normally distributed, I used a

matched pair t-test to test for significance between the two treatments. In most instances, the data were markedly skewed, sometimes with outliers, in which case I employed a non-parametric matched pair analysis (Wilcoxon paired sample test).

I examined differences in distribution of total number of songs for control and experimental treatments over recording time using the non-parametric Kolmogorov-Smirnov (K-S) test. The K-S test is an appropriate test when the data have not met either the assumption of normality or the assumption of equal variances, as was the case in this study. The tests were conducted on a plot by plot basis for the entire dusk chorus and for each of the focal species separately, using 5-min and 1-min time intervals. All univariate tests were conducted using SAS version 9.2. (Statistical Analysis System 2011).

Finally, song and call output may change over time, introducing an additional source of variation that can mask treatment effects. For the dusk chorus as a whole the scatterplots of the number of songs versus time (Julian day) showed at most a very weak positive linear association for the control as well as the experimental treatment (Figure 3, Figure 4). Thus, correction for a possible time effect does not seem to be necessary. However, for some of the focal species stronger trends were noted; it may be beneficial to standardize these results with respect to time, such as in an analysis of variance with time as a covariate (ANCOVA). This is outside the scope of the present study.

Other sources of variation that could confound or mask possible treatment effects include variation in space and variation stemming from the execution of playback experiments (Appendix 7). Playback experiments inherently cause a certain amount of disturbance, but by subjecting the control trial to the same kind of disturbance, the variation due to execution should be comparable among trials. Habitat changes over the study area can affect species composition and vocalization behavior, eliminating any observable treatment effect. No attempt has been made to specifically address this source of variation.

3. RESULTS

3.1. Avian Dusk Chorus Composition

Over the course of this study I recorded more than 20,000 songs produced by 32 different species (Table 2). The veery and the wood thrush dominated the avian dusk chorus; they were present in $\geq 80\%$ of the plots and together contributed over 70% of the avian dusk chorus song total (Table 3; Figure 5; Figure 6). Five other common species, the ovenbird, gray catbird, eastern wood pewee (*Contopus virens*), eastern towhee (*Pipilo erythrophthalmus*), and scarlet tanager, were responsible for another 16% of the dusk chorus song total, whereas the last 10% of recorded songs were made up by the remaining 25 species of dusk chorus participants. As expected, species occurrence has a (moderately) strong positive linear association with percent contribution to the dusk chorus (Pearson correlation coefficient $r_p = 0.69$).

3.2. Effect of Eastern Tufted Titmouse Alarm Calls on Focal Species Vocalizations

In the control treatment, the number of songs in relation to the number of calls recorded for the same species (the song-to-call ratio) is roughly the same for the veery and the scarlet tanager (4:3 and 1:1, respectively; Table 4; Figure 7). However, wood thrush vocalizations have a much higher song-to-call ratio; 6 songs were recorded for every 1 call. I used a chi-square test of independence to investigate if the distribution of vocalizations is affected by treatment, using the null hypothesis that the two treatments (control and experimental) are independent. For all three focal species the test statistic is highly significant (Table 4), indicating a strong association between treatment and type of vocalization. The residuals suggest a relative shift from songs to calls in the experimental versus the control treatment for all three species. For the veery and scarlet tanager the residuals do not indicate large deviations, but the values switch signs indicative of a relative decrease in one category in favor of

another. For the wood thrush, the residuals point to fewer than expected calls in the control treatment and more than expected calls in the experimental treatment.

3.3. Effect of Eastern Tufted Titmouse Alarm Calls on Avian Dusk Chorus and Focal Species Song Output

The distribution of the dusk chorus song output is not indicative of a strong response to ETTI alarm calls (Table 5; Figure 8). The medians of the two treatments are relatively close and their ranges overlap considerably, although there is much more variation in the control than in the experimental treatment data set. A similar trend can be observed for the veery and wood thrush separately (Table 6; Figure 9). The wide range in the veery and wood thrush data reveals substantial variation in singing behavior among the plots. The total song output of the scarlet tanager is small in comparison to that of the veery or wood thrush and shows a marked reduction under the experimental treatment (Table 6; Figure 9).

When the differences between the treatments were tested using the Wilcoxon paired sample test (or, where appropriate, the matched-pair t-test) on the same data sets, neither the dusk chorus as a whole, nor the veery, or the wood thrush show a statistically significant response in singing behavior to ETTI alarm calls (Table 7). Only the song output for the scarlet tanager is significantly lower in the experimental treatment, but it should be noted that the sample size for this species is very small ($N = 9$, W -value = 8, $p \leq 0.05$; Table 7).

In addition, I generally found no significant differences when I compared the distribution of the number of songs over recording time for the control treatment versus the experimental treatment of each plot, either for the entire dusk chorus or for any of the focal species separately, based on the 5-min interval K-S tests (Appendix 8). In one plot (G) significantly more songs of the dusk chorus were recorded for the control treatment than for the experimental treatment ($N = 14$, D -statistic = 0.57, $p = 0.02$; Appendix 8). At the finer 1-min interval, the K-S tests showed significant differences in distributions in a number of plots for song output of the entire avian dusk chorus as well as the focal species separately

(Table 8). However, the trends were not consistent. For instance, for the dusk chorus as a whole, the distribution of songs in the experimental trial was significantly lower than that in the control trial in 4 plots, but in 3 other plots the relationship was reversed, with the remaining plots showing no significant effect (Table 8).

3.4. Effect of Eastern Tufted Titmouse Alarm Calls on Focal Species Call Output

Of the three focal species, only the veery shows a marked and statistically significant increase in calling behavior when exposed to ETTI alarm calls ($N = 14$, W -value = 10, $p \leq 0.05$; Table 9; Table 7; Figure 10). The number of calls for the wood thrush also seems to increase (t -statistic = 1.87, $p = 0.04$; Table 7), but the effect is less pronounced because of the generally low call output of the wood thrush. For the scarlet tanager there is no evidence to suggest any change in calling behavior in response to ETTI alarm calls (Table 7; Table 9).

Again, I found no significant differences between the distributions of the number of calls over (recording) time for the control and experimental treatments based on the 5-min interval K-S tests for each plot for any of the three focal species (Appendix 9). The 1-min interval K-S tests revealed significant differences in distribution of the number of calls in 4 out of 14 plots for the veery only, but the results are inconsistent and do not support an overall increase in calling behavior for this species (Table 10).

4. DISCUSSION

Veeries contributed most songs to the dusk chorus, about 40% of the total number of songs documented during this study. This was not especially surprising since plots were selected based on the presence of a singing male veery and veeries are an abundantly vocalizing species (Belinsky et al. 2012). The wood thrush was the second largest contributor to the dusk chorus, producing about 34% of the

total number of songs. These findings support other studies that noted a high volume of song output for Turdidae species (Samuel 1972; Weary et al. 1986), which may be related to the tendency of species in this family to have overlapping territories (Weary et al. 1986). In addition, veeries may favor dusk chorus singing due to high acoustic competition at dawn (Belinsky et al. 2012), which would provide a further explanation for their prevalence in the dusk chorus. Species that commonly compete with veeries by masking veery songs, such as the ovenbird and gray catbird (Belinsky et al. 2012), were present in more than 80% of the plots, but contributed very little to the dusk chorus song total (about 2-3%). Thus, it seems that veeries (and possibly the wood thrush) do not experience high levels of acoustic competition around dusk, allowing for more unhindered intra- and interspecific communication.

I found that the dusk chorus as a whole did not significantly or consistently reduce song output in response to the experimental treatment (Table 7). This does not mean that eavesdropping did not occur. The veery and the wood thrush, which together comprised about 75% of the dusk chorus song output, did not markedly modify their singing behavior, and a small reduction in the number of songs by one species, as was found for the scarlet tanager, could have been cancelled by a slight increase in another.

It is also possible that the alarm signal used did not trigger a change in singing behavior substantial enough to be detected. The high “seet” call of the tufted titmouse is indicative of aerial predators, which are commonly less active at dusk. Around sunset and into the night, a greater threat is posed by owls, such as the barred owl (*Strix varia*), which have been reported in the study area (Schmidt et al. 2013). Whereas an overflying hawk may elicit a “freeze” response (Marler & Slabbekoorn 2004, Hetrick & Sieving 2011), many birds aggressively “mob” an -often stationary- owl accompanied by a very different alarm call. For example, the mobbing calls of the eastern tufted titmouse are a series of harsh “dee” notes (Schmidt et al. 2010). Therefore, the high “seet” call may not be perceived as a relevant threat at dusk. Moreover, no eastern tufted titmice were observed in the study area and no ETTI songs or calls

were recorded during this study, so dusk chorus species may have been reluctant to react to an unfamiliar or unexpected informant. In hindsight, the high “seet” call may not have been the most appropriate playback call to detect heterospecific eavesdropping in the dusk chorus.

Although the occurrence of heterospecific eavesdropping based on changes in song vocalizations could not be established for all species combined, there is compelling evidence that each of the three focal species separately did demonstrate a specific response to ETTI calls. The results are broadly in agreement my hypothesis: all three species reduced their song output relative to their call output (Table 4; Table 7). For the veery this relative shift from songs to calls was achieved by a significant increase in the number of calls, whereas the scarlet tanager displayed a significant decrease in the number of songs. The wood thrush exhibited a disproportionately greater increase in calls than songs after exposure to ETTI calls.

As hypothesized, nesting ecology seems to influence call output: about 5 times as many total calls were recorded for the ground-nesting veery than for the wood thrush, and fewer still were produced by the scarlet tanager (Table 4). After exposure to ETTI calls, the total call output by the veery increased by 77%; the comparatively low total call output of the wood thrush showed an increase of about 60% and the total call output of the scarlet tanager showed no change. Thus, it seems that ground nesting birds call more and exhibit a greater increase in calling behavior than those nesting at greater height above the ground or in the upper canopy, but each species’ response to an indirect predator alarm call may be more complex than these results suggests.

The veery produced a high volume of vocalizations comprised of an equal number of songs and calls, which suggests it is a constant and vigilant participant of the dusk chorus, as was found by others (Hetrick & Sieving 2011). After exposure to ETTI alarm calls the veery responded by raising its state of alertness and producing more calls: it perceived the signal, then reinforced it and so acted as a (secondary) community informant (Table 7). In the absence of species such as the eastern tufted

titmouse or other highly vigilant Paridae, the veery, with its impressive repertoire of 7 known calls, may very well function as a primary community informant, as the present study and other authors seem to suggest (Hetrick & Sieving 2011; Samuel 1972).

The wood thrush showed the same strong vocalization behavior around dusk, but with a much higher song to call ratio (Table 4). While a solid contributor to the dusk chorus, it appeared not nearly as vigilant as the veery. Since it nests higher above the ground, it is less vulnerable to predation and therefore has less need to be continuously on the lookout for potential danger. It also produced a much more measured response to eastern tufted titmouse calls. That it reacted at all suggests that it did take notice and used eavesdropping to evaluate its surroundings.

The song to call ratio of the scarlet tanager was similar to that of the veery, but -in contrast to the veery- it was not a very strong dusk chorus contributor (Table 4). In the upper canopy where the scarlet tanager builds its nest, potential danger comes mainly from above in the form of aerial predators. In this context the high “seet” call used as playback is especially alarming, since it represents the general alert for exactly this form of danger (Hetrick & Sieving 2011). An attack from above can escalate very quickly, so by (immediately) reducing its song output the scarlet tanager would make itself less conspicuous. A strong response is even more crucial in light of its vivid morphology (Journey et al. 2013). Like the wood thrush, the scarlet tanager is listening in on other, more vigilant species such as the veery to assess the risk of “stranger danger.”

5. CONSERVATION MANAGEMENT IMPLICATIONS

Since vocalizations play such a critical role in the life of birds, anything that affects the production or perception of auditory signals can have a major impact on bird communities. Currently, many soundscape ecology related studies are examining the effect of anthropogenic noise pollution on avian

communication systems. In the present study I found that noise pollution from cars on the highway near the study area were audible on almost every sound recording and often masked bird songs and calls. In fact, noise pollution is the single most important factor impacting forested habitat beyond 50 meters from the road (Slabbekoorn & Ripmeester 2008).

The long term effects of noise pollution are as yet unknown, but some studies have already reported changes in singing behavior and spacing of territories, which appeared to be directly related to the level of noise experienced (McLaughlin & Kunc 2013). With increasing urbanization some species may be driven out of suburban and urban areas altogether, thereby removing their auditory signals as well. The cascading effects of loss of information on a community as a whole, with all its interdependent relationships, is unclear. Pijanowski et al. (2011) hypothesize that in more heavily disturbed habitats with incomplete species assemblages, coordination between interspecific vocalizations will be severely curtailed, negatively affecting survival and ultimately species fitness (Tuomainen & Candolin 2011). Thus, even when habitat requirements are fulfilled, noise pollution can lead loss of species diversity and homogenization of bird communities over broad geographical areas (Slabbekoorn & Ripmeester 2008).

This has important implications for habitat management, especially with respect to birds. Conservation efforts will be more effective when sources of noise pollution are taken into consideration, for instance in the selection of a location or the establishment of boundaries for a preserve or conservation area. Other management practices that may reduce the effects of noise pollution include the creation of buffer zones and (earthen) sound walls. Concern for the preservation of the soundscape should be part of the management objectives from the inception of a conservation effort.

Finally, a playback experiment in of itself can be a source of unintended disturbance, since it deliberately manipulates the soundscape of a community. Therefore, playback experiments should be conducted with restraint. The experimental design should carefully balance the insight gained by

conducting the experiment and the stress placed on the community, especially when alarm calls are used as playback.

6. CONCLUSION

While the dusk chorus as a whole did not significantly or consistently reduce song output, the three focal species did exhibit a decrease in song output relative to their call output in response to indirect predator alarm calls of the eastern tufted titmouse. The veery produced a greater call output while maintaining the same number of song vocalizations. The wood thrush showed a small, disproportionately greater increase in calls than songs, and the scarlet tanager reduced its song output while maintaining its call vocalizations. The veery was highly vigilant and acted as a (secondary) community informant. As a ground nesting species, it engaged more frequently in calling behavior than the wood thrush or the scarlet tanager, which nest higher above the ground. Thus, all three species seemed to be listening in on the dusk chorus, but each responded to the perceived alarm call consistent with their nesting ecology.

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Table 1

A TWINSpan two-way ordered table for the avian dusk chorus community using total song data for each species per plot (A-P) and treatment (C- Control, E-Experimental). The 0/1 numbering at the bottom and on right specify classifications of the trials and species; letters across the top specify trial and the 4-letter codes along the left specify species.

	E E K K P M M P	F F D D I L O O C I L C G A A G B B J J	
	C E C E C E C E	C E E C E E C E C C C E E C E C E C E C	
	1 1 2 2 2 2 2	1 1 1 2 2 2 1 2 1 1 1 1	
	9 0 9 0 8 3 4 7	1 2 7 8 6 2 5 6 5 5 1 6 4 1 2 3 3 4 7 8	
31 HOWR	- - - - - 3 -	- - - - - - - - - - - - - - - - -	1 1 1 1 1
30 MODO	- - - - - 3 3	- - - - - - - - - - - - - - - - -	1 1 1 1 1
29 FISP	- - - 4 5 4 - 4	- - - - - - - - - - - - - - - - -	1 1 1 1 1
32 CAWR	- - - 5 - - -	- - - - - - - - - - - - - - - - -	1 1 1 1 0
28 INBU	- - 2 - - - -	- - - - - - - - - - - - - - - - -	1 1 1 1 0
22 COYE	5 5 5 4 4 - 5 -	- - - - - - - - - - - - - - - - -	1 1 1 1 0
23 SOSP	5 5 4 - 4 5 1 3	- - - - - - - - - - - - - - - - -	1 1 1 0
24 YTVI	4 2 - - - - -	- - - - - - - - - - - - - - - - -	1 1 0
21 RWBL	5 5 - - - 3 - -	4 3 - - - - - - - - - - - - - - -	1 1 0
20 AMGO	2 - - - - 2 - -	- - 3 - - - - - - - - - - - - - -	1 0 1
19 BWWA	- 2 - - - - -	- - 1 - - - - - - - - - - - - - -	1 0 1
18 AMRE	5 5 2 1 - - - -	4 4 - - - - - 2 - - 5 - - - - - -	1 0 0
15 BAWW	3 - - - - 3 4 3	5 1 5 5 - - - - 1 2 - - - - - - -	1 0 0
12 AMRO	5 4 - - - 4 - -	- 5 - - 4 3 - 3 - - - - - - - - -	1 0 0
10 RBGR	4 - - - - 5 5 -	4 2 - - 2 - - - 5 3 5 5 5 - - - - -	0 1 1
14 EATO	4 - 5 5 5 3 - 2	3 1 5 5 5 - 4 - 5 5 5 - - 2 5 - - - -	0 1 0
7 GRCA	5 5 5 5 5 5 5 5	5 4 5 5 5 5 4 5 5 5 5 5 - 3 2 2 - - -	0 1 0
4 WOTH	- 5 5 5 5 5 5 5	5 5 5 5 5 5 5 5 5 5 5 5 5 5 1 5 5 5 5	0 1 0
1 VEER	5 5 5 5 5 5 5 5	5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5	0 1 0
2 OVEN	1 1 3 3 1 3 3 2	5 5 5 5 5 4 5 5 4 5 4 5 5 4 3 2 - 2 5 5	0 0 1 1
27 BAOW	- - - - - - - -	- - - - 3 - - - - - - - - - - - - 4	0 0 1 0 1
6 SCTA	- - 4 - - - -	5 5 - - 2 - 3 - 3 5 - 3 4 5 4 4 5 5 5 5	0 0 1 0 1
5 EWPE	- - - - - 2 - -	3 - 4 5 2 5 - 2 5 - 5 5 2 4 3 - 5 5 5 5	0 0 1 0 1
17 PIWO	- - - - - - - -	- - - - - - - 1 - - - - - - - - - 2	0 0 1 0 0
11 EAPH	- - - - - - - -	- - - - - - - - 2 - - - - - - - 3 -	0 0 1 0 0
9 GCFL	- - - - - - - -	3 2 - - - - - - - - - - - 2 - 5 5 - -	0 0 1 0 0
3 REVI	- - - - - - - -	- - - - - - - - 2 - 5 - 4 5 - 5 - - -	0 0 1 0 0
26 EWPW	- - - - - - - -	2 - - - - - - - - - - - - - - - - -	0 0 0 1
25 CHSP	- - - - - - - -	4 1 - - - - - - - - - - - - - - - -	0 0 0 1
16 YEWA	- - - - - - - -	- - - - - - - 1 - - - - - - - - - -	0 0 0 1
8 LOWA	- - - - - - - -	3 - - - - - - - - - - - - - - - - -	0 0 0 1
13 NOCA	- 3 - - - - - -	- - - - 4 5 1 - 5 3 - 1 - - - - - - -	0 0 0 0
	0 0 0 0 0 0 0 0	1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	
	0 0 1 1 1 1 1 1	0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1	
	0 0 0 1 1 1	0 0 1 1 1 1 1 1 1 1 1 1 0 0 0 0 0 0 1 1	
		0 0 0 0 0 0 1 1 1 1 1 0 0 0 1 1	
		0 0 1 1 1 1 0 0 0 1 1	

Table 2

Dusk chorus species composition (4-letter species abbreviations) for each of the 14 plots (A-P) by treatment (C-Control and E-Experimental) and day of trial (Julian Day). Numbers in the table represent total number of songs recorded per trial per species.

Plot ID	AC	AE	BE	BC	CC	CE	DE	DC	EC	EE	FC	FE	GC	GE	IC	IE	JE	JC	KC	KE	LC	LE	ME	MC	OC	OE	PE	PC	Total
Julian Day	149	150	149	150	154	155	154	155	156	160	163	165	162	163	168	170	170	171	171	172	172	175	175	177	183	184	183	187	
VEER	131	153	93	134	180	327	336	331	177	242	285	251	55	117	693	561	499	270	47	39	408	586	213	143	467	502	209	447	7896
OVEN	12	8	0	2	16	28	22	21	1	1	41	60	4	27	51	27	21	28	5	9	12	14	5	8	35	31	4	1	494
REVI	15	50	29	0	0	89	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	186
WOTH	280	428	427	527	245	315	396	231	0	230	154	195	1	191	312	327	304	93	394	247	219	51	76	277	130	204	214	412	6880
EWPE	12	9	55	243	65	26	19	30	0	0	6	0	0	3	0	2	115	89	0	0	24	21	2	0	0	2	0	0	723
SCTA	36	17	23	63	5	6	0	0	0	0	51	99	18	16	96	2	38	105	11	0	0	0	0	0	6	0	0	0	592
GRCA	9	4	0	0	22	20	35	28	42	37	41	11	3	0	30	26	0	0	22	21	21	37	24	27	11	30	25	31	557
LOWA	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
GCFL	0	3	25	85	0	0	0	0	0	0	6	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	121
RBGR	0	0	0	0	45	103	0	0	12	0	14	4	0	55	5	2	0	0	0	0	0	26	0	70	60	0	0	0	396
EAPH	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	5	0	0	0	0	0	0	0	0	0	0	0	7
AMRO	0	0	0	0	0	0	0	0	20	17	0	32	0	0	0	14	0	0	0	0	0	5	12	0	0	9	0	0	109
NOCA	0	0	0	0	25	1	0	0	0	7	0	0	0	0	5	16	0	0	0	0	0	24	0	0	1	0	0	0	79
EATO	2	41	0	0	30	0	151	116	11	0	5	1	0	0	64	64	0	0	93	30	123	0	5	0	15	0	4	37	792
BAWW	0	0	0	0	1	0	26	28	5	0	20	1	0	0	2	0	0	0	0	0	0	0	5	15	0	0	5	0	108
YEWA	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
PIWO	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	5
AMRE	0	0	0	0	3	41	0	0	113	179	15	13	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	367
BWWA	0	0	0	0	0	0	1	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
AMGO	0	0	0	0	0	0	5	0	4	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	13
RWBL	0	0	0	0	0	0	0	0	40	21	11	8	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	86
COYE	0	0	0	0	0	0	0	0	47	80	0	0	0	0	0	0	0	0	30	16	0	0	0	20	0	0	0	14	207
SOSP	0	0	0	0	0	0	0	0	91	74	0	0	0	0	0	0	0	0	10	0	0	0	28	1	0	0	7	12	223
YTVI	0	0	0	0	0	0	0	0	14	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16
CHSP	0	0	0	0	0	0	0	0	0	0	19	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20
EWPW	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
BAOW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	13	0	0	0	0	0	0	0	0	0	0	21
INBU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2
FISP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0	0	17	0	0	0	13	29	72
MODD	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	7	0	16
HOWR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	0	9
CAWR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	22
Total	646	863	801	1204	793	1111	1145	940	733	1053	841	843	243	572	1431	1219	1152	773	787	548	1005	913	642	746	848	962	671	1192	20034

Table 3

Occurrence of avian dusk chorus species (percent of number of plots present divided by total number of plots), total number of songs per species as percent of total number of dusk chorus songs, and total number of songs per species for all trials.

Species code*	Percent occurrence in plots	Percent of dusk chorus songs	Total songs
VEER	100.00	39.41	7,896
WOTH	96.43	34.34	6,880
OVEN	96.43	2.47	494
GRCA	82.14	2.78	557
EWPE	60.71	3.61	723
EATO	60.71	3.9	792
SCTA	57.14	2.95	592
RBGR	39.29	1.98	396
BAWW	35.71	0.54	108
AMRE	28.57	1.83	367
AMRO	25.00	0.54	109
NOCA	25.00	0.39	79
SOSP	25.00	1.11	223
COYE	21.43	1.03	207
REVI	17.86	0.93	186
GCFL	17.86	0.60	121
RWBL	17.86	0.43	86
FISP	14.29	0.36	72
AMGO	10.71	0.06	13
EAPH	7.14	0.03	7
PIWO	7.14	0.02	5
BWWA	7.14	0.02	4
YTVI	7.14	0.08	16
CHSP	7.14	0.10	20
BAOW	7.14	0.10	21
MODO	7.14	0.08	16
LOWA	3.57	0.03	7
YEWA	3.57	< 0.01	1
EWPW	3.57	0.01	3
INBU	3.57	0.01	2
HOWR	3.57	0.04	9
CAWR	3.57	0.11	22
Total		100.00	20,034

*Species codes and Latin binomials are found in Appendix 10.

Table 4

Total number of vocalizations by treatment and chi-square test of independence results for each of the three focal species. Numbers in parentheses are expected values.

Treatment	Songs		Calls		X ² statistic	p-value
	Control	Experimental	Control	Experimental		
Veery	3,768 (3316)	4,128 (4579)	2,705 (3157)	4,811 (4359)	217.6	3.15 x 10 ⁻⁴⁹
Wood thrush	3,275 (3156)	3,605 (3724)	531 (650)	887 (768)	48.8	2.8 x 10 ⁻¹²
Scarlet tanager	391 (347)	201 (245)	364 (408)	332 (288)	24.9	5.9 x 10 ⁻⁷
Total	7,434	7,934	3,600	6,030		

Table 5

Distribution of the number of songs per plot for the dusk chorus as a whole by treatment.

Statistic	Control	Experimental
Min	81	376
Q₁	583.25	529
Median	652	725.5
Q₃	821	940.25
Max	1263	1049
IQR	237.75	411.25
Upper Outliers	1	0
Lower Outliers	1	0

Table 6

Distribution of the number of songs per plot for the three focal species by treatment.

Statistics	VEER Control	VEER Experimental	WOTH Control	WOTH Experimental	SCTA Control	SCTA Experimental
Min	47	39	0	51	5	0
Q₁	134	153	130	195	8.5	1
Median	225	246.5	238	238.5	36	16
Q₃	408	499	312	327	79.5	30.5
Max	693	586	527	428	105	99
IQR	274	346	182	132	71	29.5
Upper Outliers	0	0	0	0	0	1
Lower Outliers	0	0	0	0	0	0

Table 7

Matched-pair test results of the number of vocalizations per plot for the dusk chorus as a whole (songs only) and the focal species (songs and calls) separately. Statistically significant values are in bold.

Dusk chorus song totals			
<i>Statistical test</i>	<i>Sample size (N)</i>	<i>Test statistic</i>	<i>p-value</i>
Wilcoxon paired-sample test	13	40 (W-value)	> 0.05
Matched-pair t-test	14	-0.28 (t-statistic)	0.60
Veery song totals			
<i>Statistical test</i>	<i>Sample size (N)</i>	<i>Test statistic</i>	<i>P-value</i>
Wilcoxon paired-sample test	14	36 (W-value)	> 0.05
Matched-pair t-test	14	-0.79 (t-statistic)	0.78
Wood thrush song totals			
<i>Statistical test</i>	<i>Sample size (N)</i>	<i>Test statistic</i>	<i>P-value</i>
Wilcoxon paired-sample test	14	43 (W-value)	> 0.05
Matched-pair t-test	14	-0.55 (t-statistic)	0.70
Scarlet tanager song totals			
<i>Statistical test</i>	<i>Sample size (N)</i>	<i>Test statistic</i>	<i>P-value</i>
Wilcoxon paired-sample test	9	8 (W-value)	≤ 0.05
Matched-pair t-test	9	1.43 (t-statistic)	0.09
Veery call totals			
<i>Statistical test</i>	<i>Sample size (N)</i>	<i>Test statistic</i>	<i>P-value</i>
Wilcoxon paired-sample test	14	10 (W-value)	≤ 0.05
Matched-pair t-test	N/A	N/A	N/A
Wood thrush call totals			
<i>Statistical test</i>	<i>Sample size (N)</i>	<i>Test statistic</i>	<i>P-value</i>
Wilcoxon paired-sample test	14	30 (W-value)	> 0.05
Matched-pair t-test	14	1.87 (t-statistic)	0.04
Scarlet tanager call totals			
<i>Statistical test</i>	<i>Sample size (N)</i>	<i>Test statistic</i>	<i>P-value</i>
Wilcoxon paired-sample test	10	24.5 (W-value)	> 0.05
Matched-pair t-test	10	0.62 (t-statistic)	0.33

Table 8

K-S tests to determine differences in the distribution of songs over recording time between control and experimental treatments per plot (A-P) for the three focal species and entire dusk chorus, summarized at 1-min (n=65) intervals. Statistically significant values are in bold.

Paired plots	Veery		Wood thrush		Scarlet tanager		All dusk chorus species	
	D	p-value	D	p-value	D	p-value	D	p-value
A	0.06	1.00	0.26	0.02	0.06	1.00	0.23	0.06
B	0.11	0.85	0.11	0.85	0.12	0.71	0.35	< 0.01
C	0.29	< 0.01	0.17	0.31	0.03	1.00	0.20	0.15
D	0.09	0.94	0.20	0.15	0.00	1.00	0.20	0.15
E	0.15	0.43	0.32	< 0.01*	0.00	1.00	0.32	< 0.01
F	0.11	0.85	0.09	0.94	0.18	0.22	0.06	1.00
G	0.22	0.10	0.31	< 0.01*	0.03	1.00	0.42	< 0.01
I	0.20	0.15	0.09	0.94	0.35	< 0.01*	0.25	0.04*
J	0.35	< 0.01*	0.35	< 0.01*	0.29	< 0.01	0.32	< 0.01*
K	0.06	1.00	0.20	0.15	0.11	0.85	0.26	0.02*
L	0.32	< 0.01	0.29	< 0.01*	0.00	1.00	0.09	0.94
M	0.15	0.43	0.31	< 0.01	0.00	1.00	0.14	0.56
O	0.15	0.43	0.11	0.85	0.08	0.99	0.17	0.31
P	0.31	< 0.01	0.25	0.04	0.00	1.00	0.32	< 0.01

Note: * denotes a plot in which there were statistically more songs in the experimental treatment than control treatment.

Table 9

Distribution of the number of calls per plot for the three focal species by treatment.

Statistic	VEER Control	VEER Experimental	WOTH Control	WOTH Experimental	SCTA Control	SCTA Experimental
Min	29	40	0	0	0	0
Q₁	151	160	15	14	4	8
Median	169	245.5	35.5	48	36.5	25
Q₃	250	393	47	73	69	68
Max	492	1181	106	233	79	78
IQR	99	233	32	59	65	60
Upper Outliers	1	2	2	1	0	0
Lower Outliers	0	0	0	0	0	0

Table 10

K-S tests to determine differences in the distribution of calls over recording time between control and experimental treatments per plot (A-P) for the three focal species, summarized at 1-min (n=65) intervals. Statistically significant values are in bold.

Paired plots	Veery		Wood thrush		Scarlet tanager	
	D	p-value	D	p-value	D	p-value
A	0.06	1.00	0.09	0.94	0.11	0.85
B	0.14	0.56	0.15	0.43	0.12	0.71
C	0.09	0.94	0.08	0.99	0.08	0.99
D	0.08	0.99	0.05	1.00	0.08	0.99
E	0.11	0.85	0.05	1.00	0.00	1.00
F	0.11	0.85	0.09	0.94	0.20	0.15
G	0.06	1.00	0.02	1.00	0.03	1.00
I	0.17	0.31	0.08	0.99	0.12	0.71
J	0.18	0.22	0.08	0.99	0.09	0.94
K	0.25	0.04*	0.22	0.10	0.09	0.94
L	0.20	0.15	0.03	1.00	0.02	1.00
M	0.25	0.04	0.08	0.99	0.00	1.00
O	0.49	< 0.01*	0.05	1.00	0.00	1.00
P	0.37	< 0.01	0.03	1.00	0.00	1.00

Note: * denotes a plot in which there were statistically more calls in the control treatment than experimental treatment.

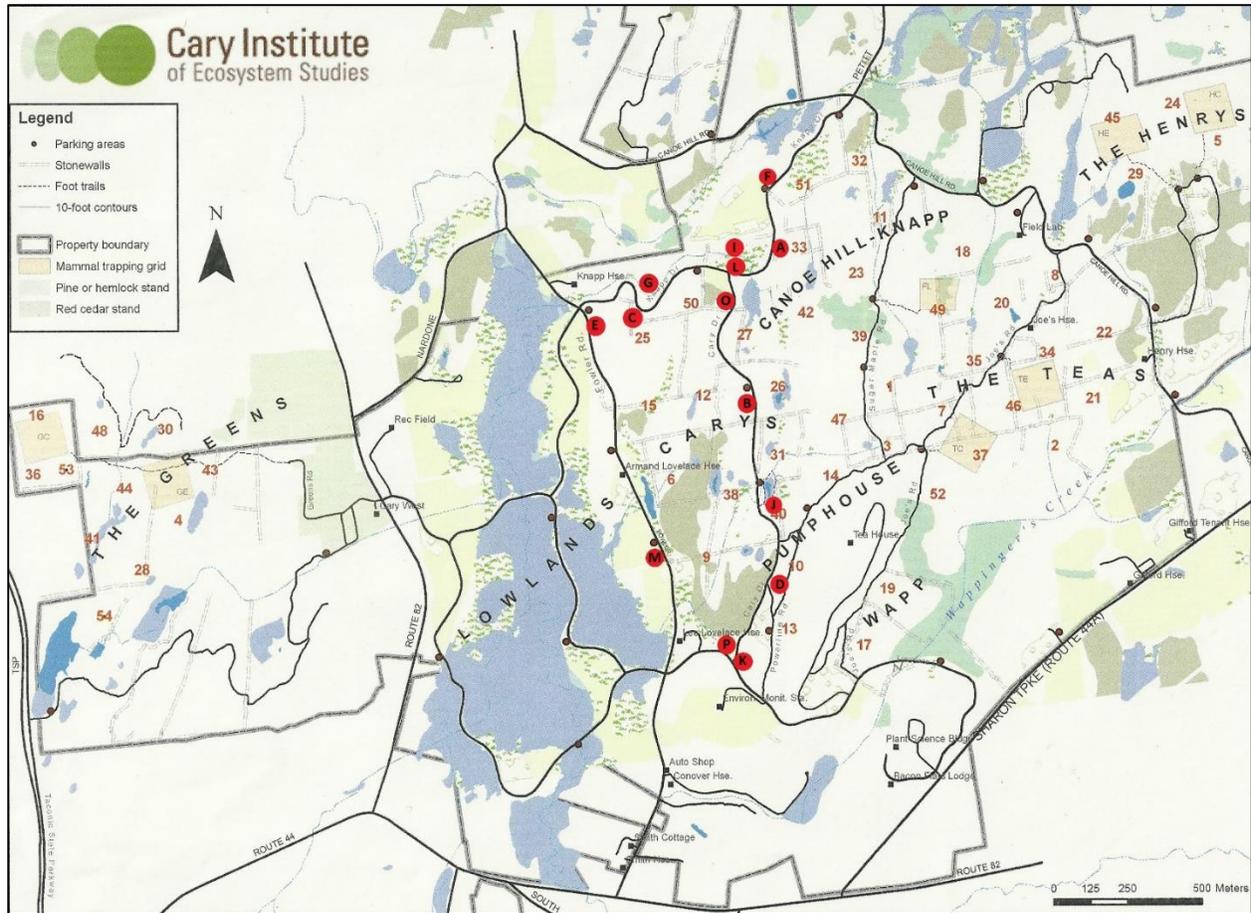


Figure 1
Location of the study area and the sample plots at the Cary Institute of Ecosystem Studies, New York.

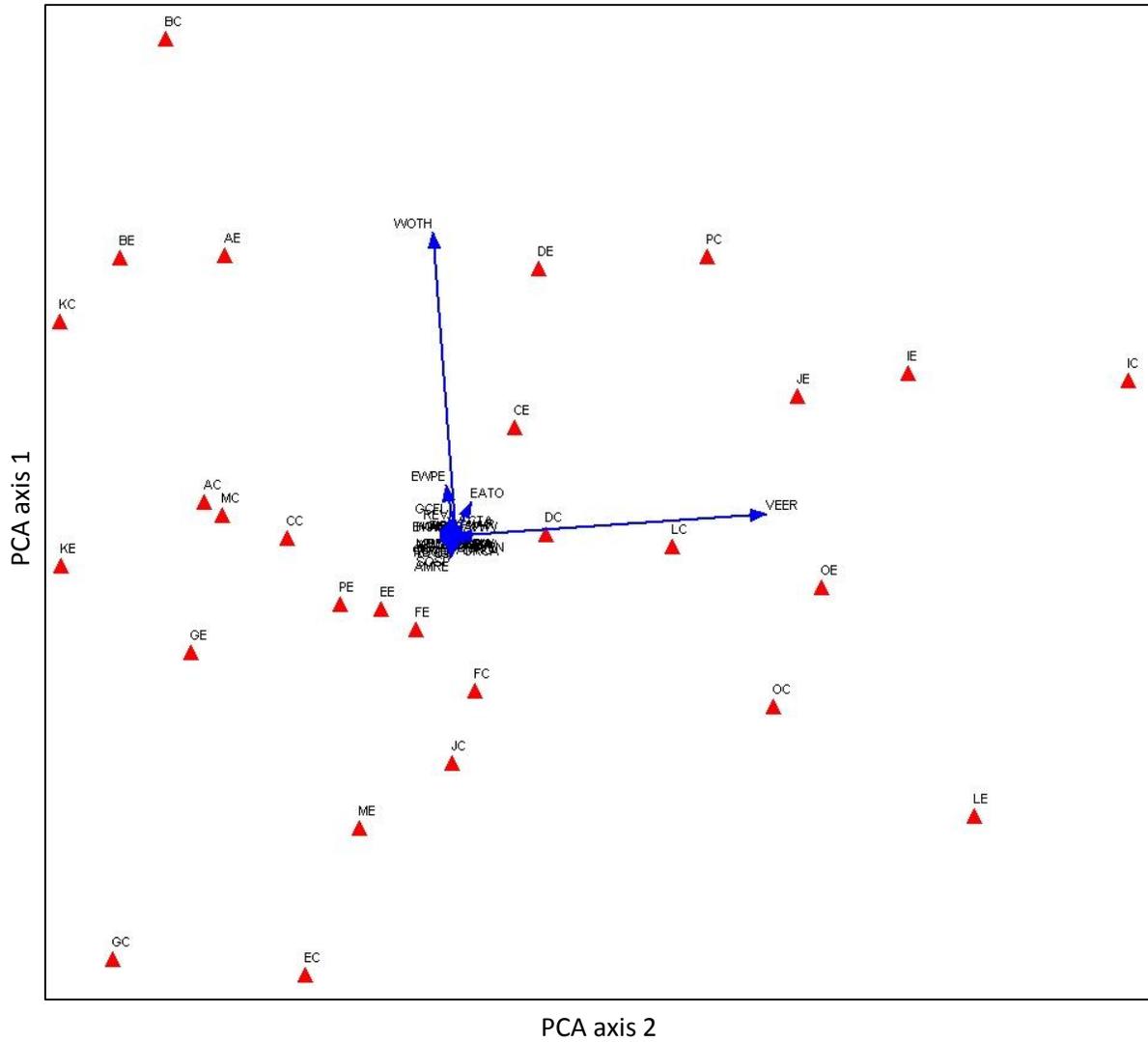
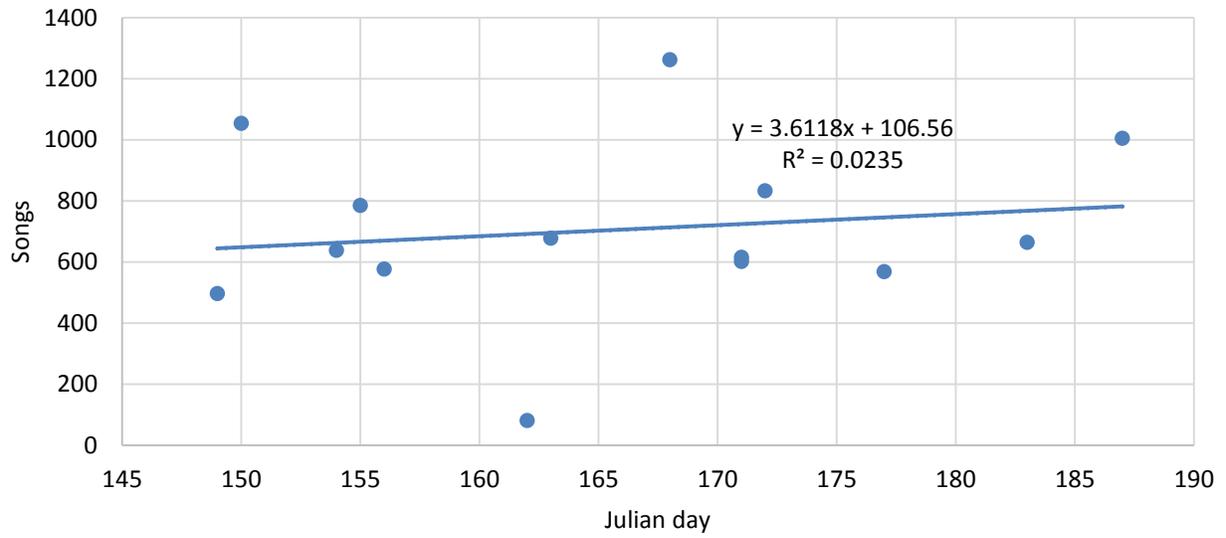
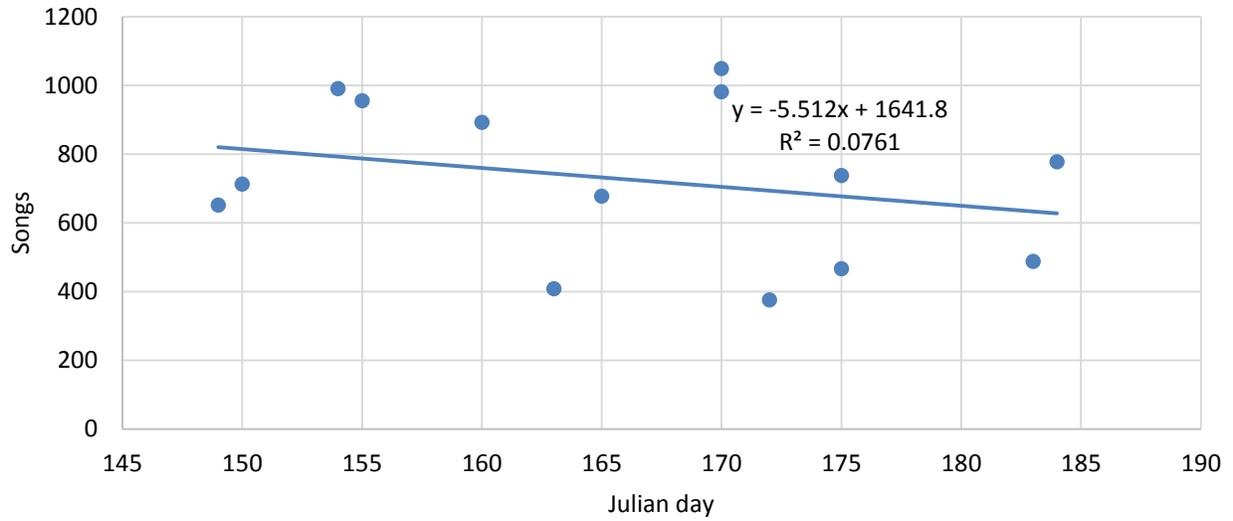


Figure 2
Principal component analysis of the avian dusk chorus based on community composition and total number of songs for each species per trial.

**Figure 3**

Linear relationship between the number of songs in control treatments versus Julian day for the entire dusk chorus.

**Figure 4**

Linear relationship between the number of songs in experimental treatments versus Julian day for the entire dusk chorus.

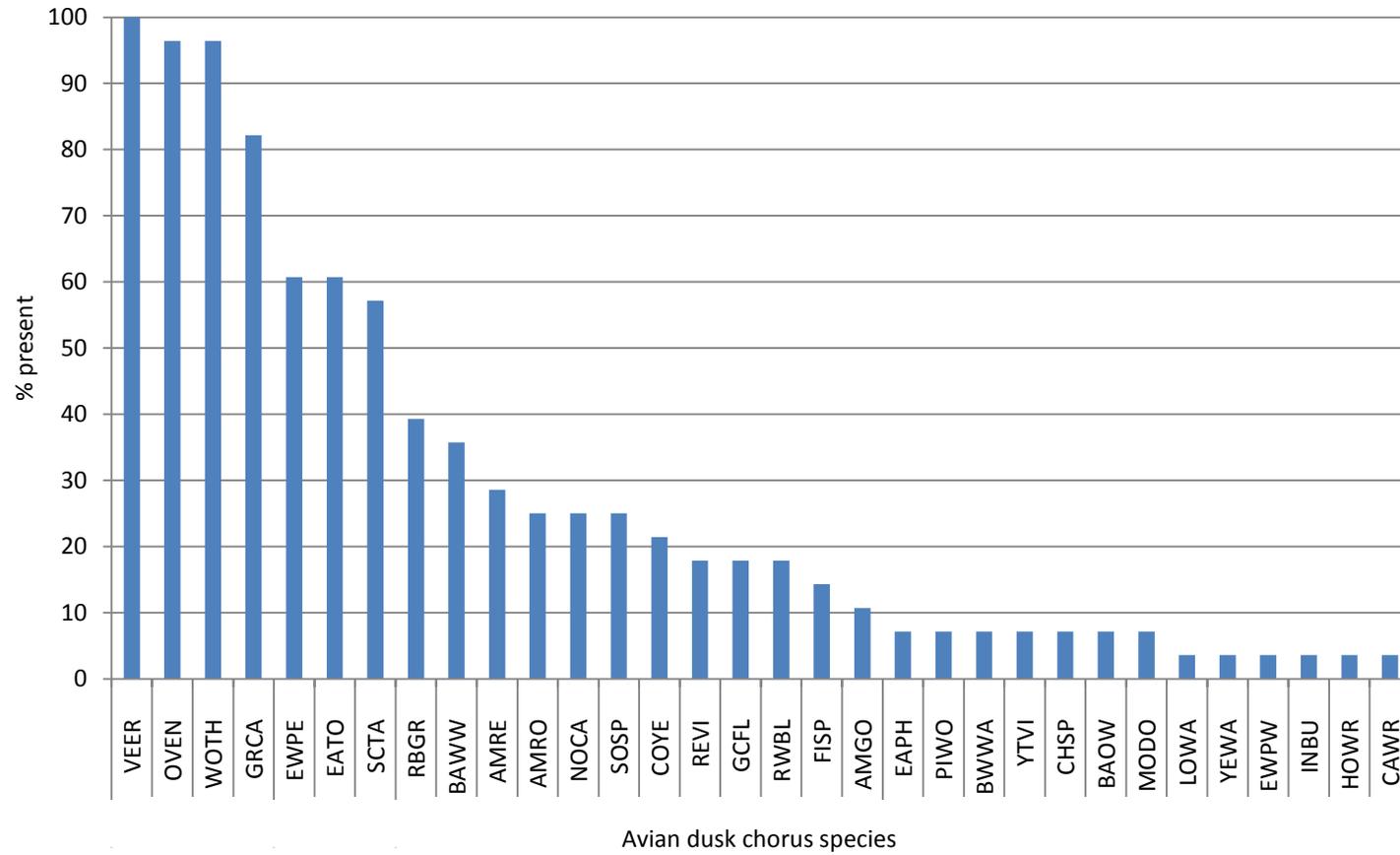


Figure 5
Occurrence of avian dusk chorus species (percent of number of plots present over total number of plots) based on recorded songs.

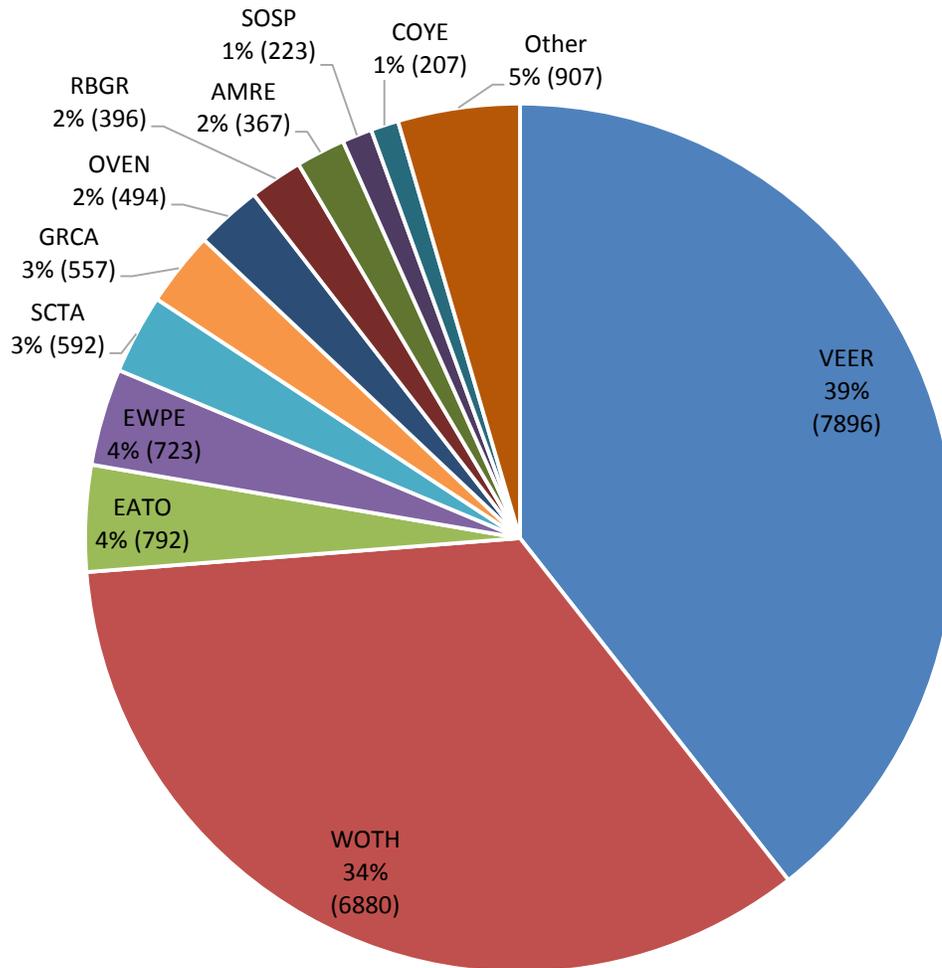


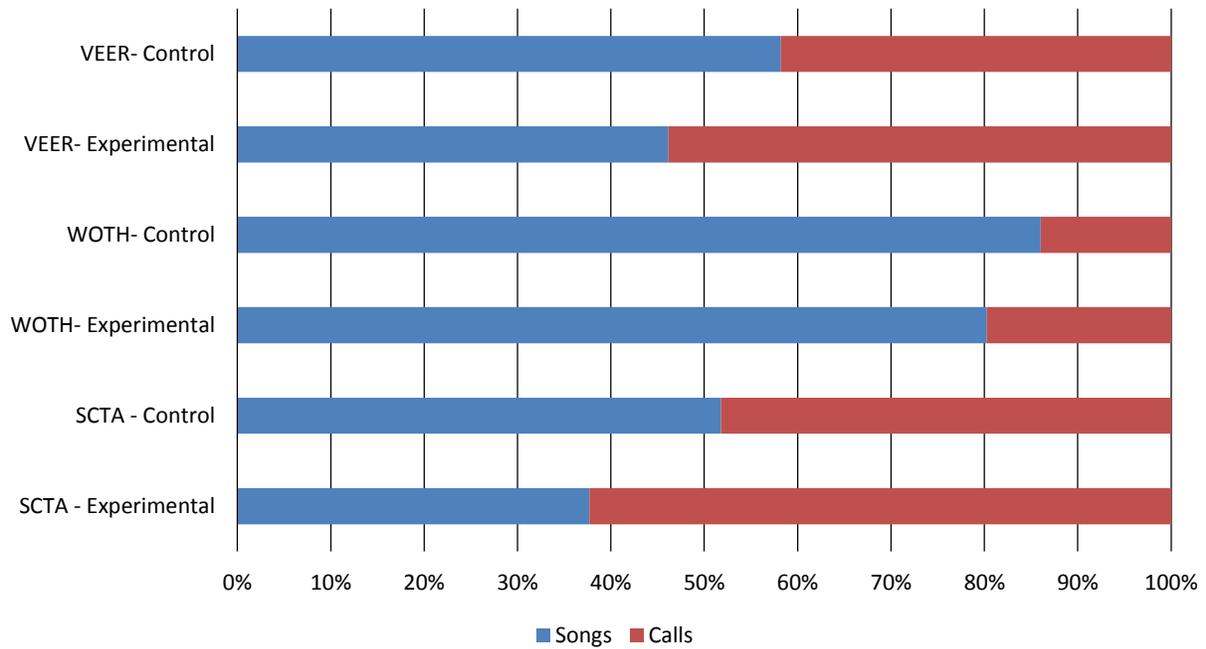
Figure 6

Percent contribution to the dusk chorus based on total number of songs by species for all trials. Data are from Table 3.

Note: Numbers in parenthesis signify song total for each species. "Other" represents 21 species that contribute < 1% to the dusk chorus song total. These species include (in decreasing amount contributed to dusk chorus): REVI, GCFL, AMRO, BAWW, RWBL, NOCA, FISP, CAWR, BAOW, CHSP, YTVI, MODO, AMGO, HOWR, EAPH, LOWA, PIWO, BWWA, EWPW, INBU, and YEWA.

Figure 7

Song to call ratio expressed as percent of total songs and calls by treatment for each of the three focal species.



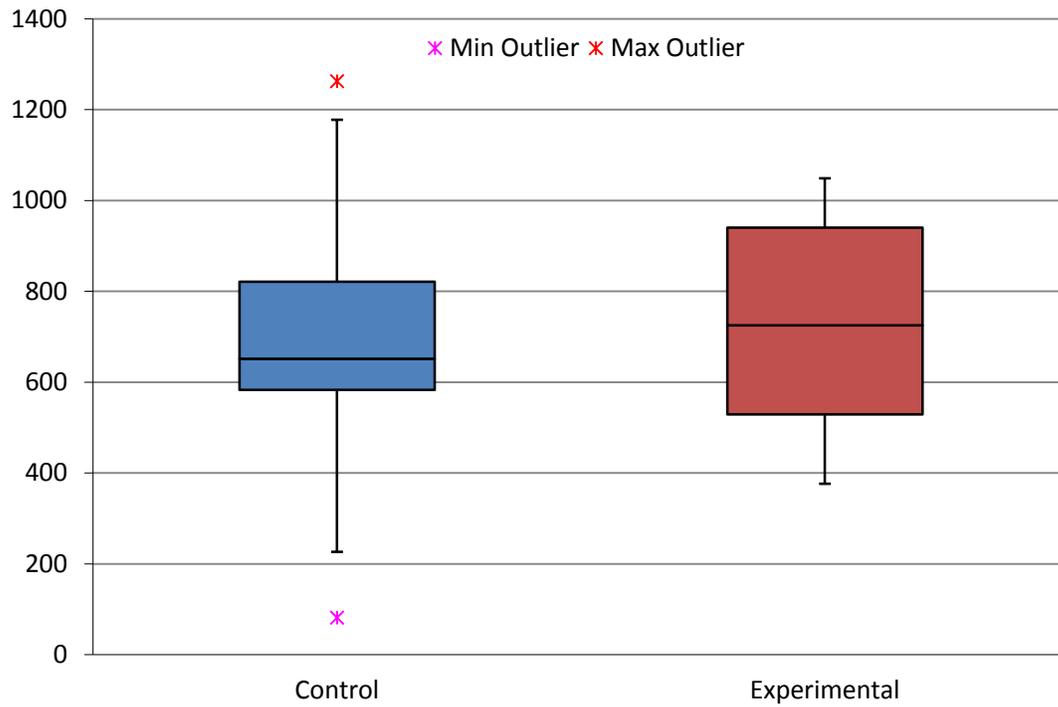
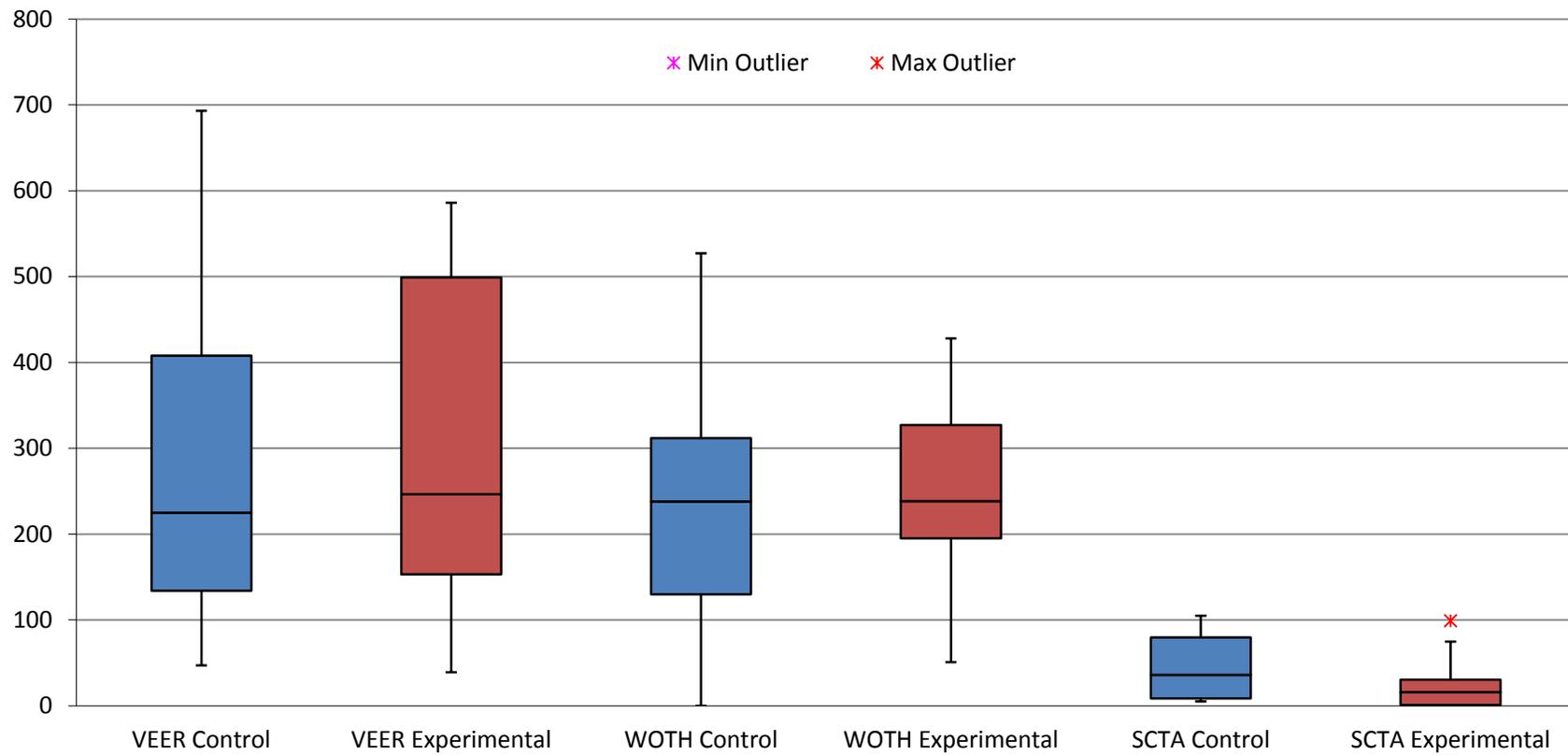
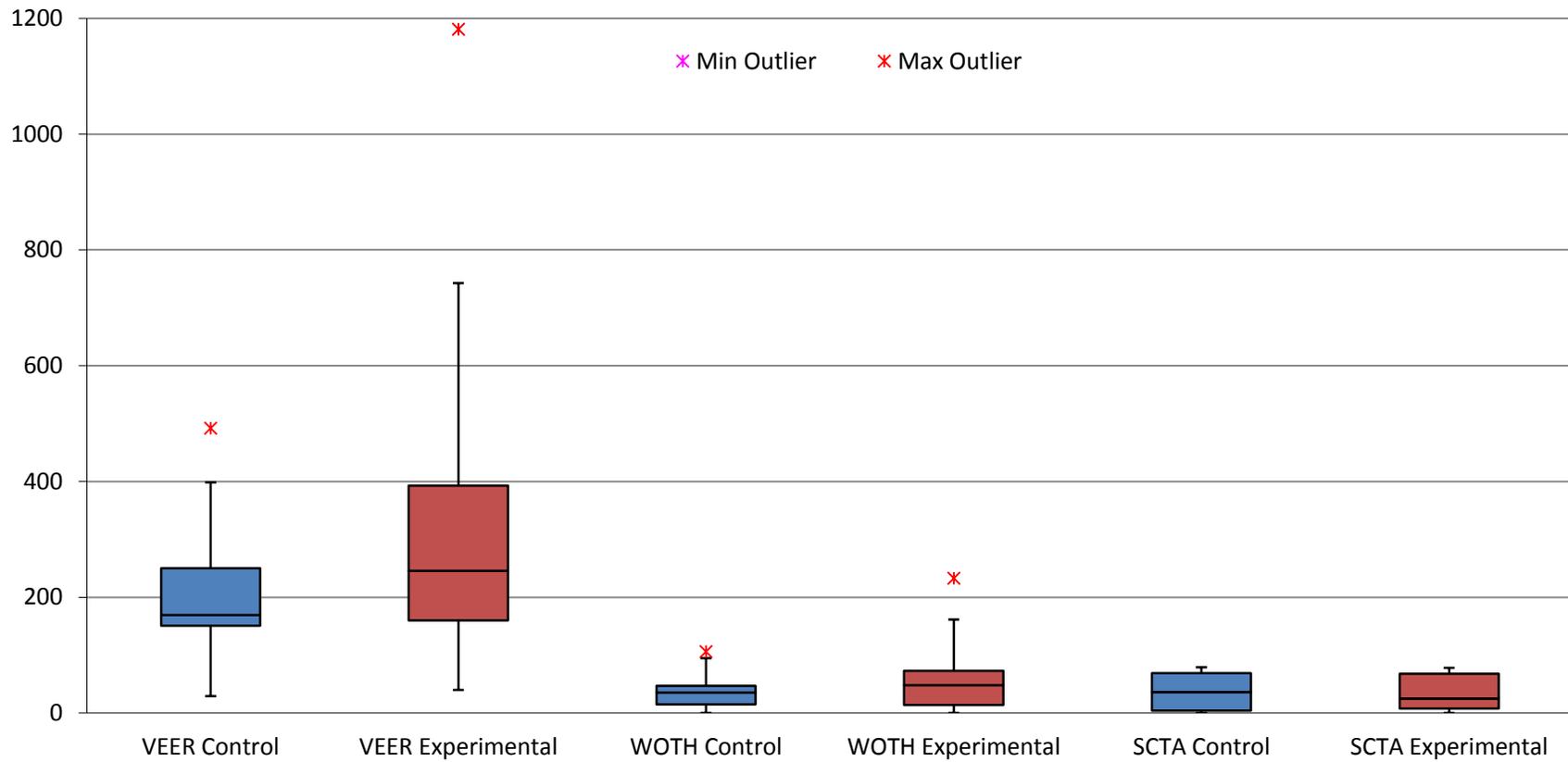


Figure 8
Boxplots of the number of songs per plot for the dusk chorus as a whole by treatment.

**Figure 9**

Boxplots of the number of songs per plot for the veery (VEER), wood thrush (WOTH), and scarlet tanager (SCTA) by treatment

**Figure 10**

Boxplots of the number of calls per plot for the veery (VEER), wood thrush (WOTH), and scarlet tanager (SCTA) by treatment.

Appendix 1

Description of basic abiotic and biotic factors of the eastern temperate forest ecological region.

A variety of geologic materials and landforms are present throughout this ecological region. Younger age sedimentary coastal plains in the south and east contrast to the older, folded and faulted sedimentary, metamorphic and igneous rocks of the Appalachian Mountains that reach elevations over 2,000 m. A mixed limestone-dolomite terrain of plains and hills dominate much of the central part of the region, with other sedimentary rock found on the plateau and plains in the north and west. Glacially derived materials and landforms and areas of glacial lake deposits shape the landscape in the north. Soils are mostly leached, being nutrient-poor to calcium-rich. Surface waters are characterized by an abundance of perennial streams, small areas with high densities of lakes, a diversity of wetland communities and a rich array of maritime ecosystems. The climate is generally warm, humid and temperate, although there is a latitudinal gradient from cool, continental temperatures to those that are subtropical. Summers are hot and humid, and winters are mild to cool. The average daily minimum temperature in winter is -12°C in the north and 4°C in the south. Average daily maximum summer temperatures are 27°C to 32°C . Precipitation amounts of 1,000-1,500mm per year are relatively evenly distributed throughout the year, with most areas having either a summer or spring maximum. Eastern temperate forests form a dense canopy consisting mostly of tall broadleaf, deciduous trees, and needle-leaf conifers. These forests have a diversity of tree, shrub, vine, and herb layers. While various species of oaks, hickories, maples, and pines are common, other wide-ranging tree species included ashes, elms, black cherry, yellow poplar, sweet gum, basswood, hackberry, common persimmon, eastern red cedar, and flowering dogwood. A key tree species, the American chestnut was virtually eliminated from the eastern temperate forests in the first half of the twentieth century by an introduced fungus. This region also contains a great diversity of species within several groups of animals. Mammals of the region include the white-footed mouse, gray squirrel, eastern chipmunk, raccoon, porcupine, gray fox, bobcat, white-tailed deer, and black bear. The region has an extremely diverse population of birds, fish, reptiles, and amphibians.

Note: Modified from Commission for Environmental Cooperation. 1997. Ecological regions of North America: Toward a common perspective. Retrieved March 20, 2014 from http://www.cec.org/storage/42/3484_eco-eng_en.pdf.

Appendix 2

Identification criteria for avian dusk chorus species songs and focal species calls.

Avian dusk chorus species song criteria

- *Veery*: a smooth, rolling spiral *vr di vrreed vreed vreer vreer* (= 1 song).
- *Wood thrush*: The wood thrush's easily recognized, flute-like *ee-oh-lay* is actually only the middle phrase of a three-part song. Combining those with 1–3 variants of the low, soft notes of the introductory phrase and 6–12 variants of the final higher-pitched complex trill, a male can easily sing over 50 distinct songs. However, since the *ee-oh-lay* is easily recognized, each *ee-oh-lay* (= 1) is counted as 1 song.
- *Ovenbird*: a series of explosive, two-syllable phrases increasing in volume *chertee chertee cherTEE cherTEE CHERTEE CHERTEE CHERTEE* (= 1).
- *Gray catbird*: male gray catbirds sing a long, halting series of short notes; one whole song can last many minutes. Sounds include whistles, squeaks, gurgles, whines, and nasal tones. Because of their long songs, 1 song was defined as 1 gray catbird singing for at least 1 minute (e.g. singing for one minute = 1). If the catbird was heard in the following minute again or after that, another tally mark would be given. In other words, the gray catbird column will only have 1 tally in it per minute unless other gray catbirds are heard singing.
- *Eastern wood-pewee*: song a plaintive, clear, slurred, whistled *PEEaweee* or *peeyooo*, often alternated with *peedidip*. Also a down-slurred *wee-ur*. Each phrase (e.g. *PEEawee* = 1) is counted as 1 song.
- *Eastern towhee*: a loud *drink-your-tea!* lasting about 1 second. Each *drink-your-tea* is counted as 1 song (= 1).
- *Scarlet tanager*: the song is usually composed of 4-7 figures/phrases or a burry series of 4–5 chirruping phrases with a hurried quality. Each series of phrases is counted as 1 song (= 1).
- *Rose-breasted grosbeak*: rich, sweetly whistled song. The song can last 6 seconds and consist of 20 notes or syllables. One series of syllables is counted as 1 song (= 1).
- *Black-and-white warbler*: song a series of very high, two-syllable phrases, resembling the sound of a squeaky wheel; *wee-see-wee-see-wee-see*. Each series of phrases is counted as 1 song (= 1).
- *American redstart*: a series of 2–11 thin, high-pitched notes, sometimes ending with an accented phrase; *tsee tsee tsee tsee tzirr* or *tseeta tseeta tseeta tseet* or *tseeo tseeo tseeo tseeo* often alternates two song variations. Each series of phrases is counted as 1 song.
- *American robin*: a string of 10 or so clear whistles assembled from a few often-repeated syllables, and often described as *cheerily, cheer up, cheer up, cheerily, cheer up*. Each series of whistles is counted as 1 song (= 1).
- *Northern cardinal*: the song is a loud string of clear down-slurred or two-parted whistles, often speeding up and ending in a slow trill. The songs typically last 2 to 3 seconds. Syllables can sound like the bird is singing *cheer, cheer, cheer* or *birdie, birdie, birdie*. Each series of whistles is counted as 1 song (= 1).
- *Song sparrow*: a loud, clanking song of 2–6 phrases that typically starts with abrupt, well-spaced notes and finishes with a buzz or trill; *seet seet seet to zleeeeeee tipo zeet zeet*. Each series of phrases is counted as 1 song.
- *Common yellowthroat*: a distinctive *witchety-witchety-witchety* song, about 2 seconds long. Each *witchety-witchety-witchety* is counted as 1 song (= 1).
- *Red-eyed vireo*: these songs have one or more syllables, each syllable consisting of one or more abrupt musical slurs. The songs of a Red-eyed Vireo consist of one or more short syllables (termed "elements" by Lemon 1971), each syllable containing one or more slurs. The slurs in a

syllable are usually connected; slurs separated by more than 0.01 s were considered to be in separate syllables. The syllables of a song are usually only a few hundredths of a second apart; syllables more than 0.3 s apart were considered separate songs. According to Sibley, song is a series of simple, hurried, whistled phrases sounding like “here-I-am, in-the-tree, look-up, at-the-top...” Each phrase (e.g. “here-I-am” = 1) is counted as 1 song (= 1).

- *Great-crested flycatcher*: Song a series of clear, strong alternated phrases *quitta* and *queeto* (or an upward slurred *whee-ep* followed by a downward-slurred *whee-er*). 1 song is defined as a *whee-ep* followed by a *whee-er* (= 1). All other sounds are considered calls.
- *Red-winged blackbird*: song is a distinctive *conk-la-ree*; 1-second song starts with an abrupt note that turns into a musical trill. Each *conk-la-ree* is counted as 1 song (= 1).
- *Field sparrow*: song an accelerating series of soft sweet whistles *teew teew tew tewtewtewtetetetetitetitititi*. Each series of whistles is counted as 1 song (= 1).
- *American goldfinch*: song of high sweet phrases toWEE toWEE toWEEto tweer tweer tweer ti ti ti ti. Each series of phrases is counted as 1 song (= 1).
- *Eastern phoebe*: raspy, two-parted song that gives them their name: *fee-bee*. Each *fee-bee* is counted as 1 song (= 1).
- *Pileated woodpecker*: a high, clear, series of piping calls that lasts several seconds. Each series is counted as 1 song (= 1).
- *Blue-winged warbler*: raspy *bee-buzz*. Each *bee-buzz* is counted as 1 song (= 1).
- *Yellow-throated vireo*: song a series of short burry phrases with a soft slurred pitch changes *rreeyoo, reeyooee, three-eight*. Each series of phrases is counted as 1 song (= 1).
- *Chipping sparrow*: song a simple mechanical trill, usually longer and more rattling than that of similar species. Each trill is counted as one song (= 1).
- *Barred owl*: very distinctive "Who cooks for you?" Each phrase is counted as 1 song (= 1).
- *Mourning dove*: song a mournful hooting *ooAAH cooo coo coo*. Each phrase is counted as 1 song (= 1).
- *Louisiana waterthrush*: begins with two or three clear slurred *seeew* notes followed by a series of jumbled descending chips and chirps (= 1). Or, by another way, a down-slurred *chewy-chewy-twitter-chew* (= 1).
- *Yellow warbler*: song consists of sweet, high, clear, sharply slurred notes *swee swee swee ti ti ti swee*. Each series of notes is counted as 1 song (= 1).
- *Eastern whip-poor-will*: song a loud, clear, whistled *WHIP puwiv WEEW*. Each *WHIP puwiv WEEW* is counted as 1 song (= 1).
- *Indigo bunting*: song is a high, sharp, urgent warble with most phrases repeated *ti ti whee whee zerre zerre*. Each series of phrases is counted as 1 song (= 1).
- *House wren*: song a rapid bubbling series of trills and rattles, rolling and descending. Each series of trills and rattles is counted as 1 song (= 1).
- *Carolina wren*: song is a rich rolling chant of three- or four- syllable phrases *pidaro pidaro pidaro* or *TWEEpudo TWEEpudo TWEEP*. Each phrase is counted as 1 song (= 1).

Focal species call criteria

Veery:

- *harsh chatter call*: a rapid series or chatter of severe, harsh-quality vocalizations.
- *anxious/ack call*: a quick, down-slurred, anxious-quality vocalization.
- *buerr call*: a short, soft, low-pitched vocalization that rise in pitch at the end of the note.
- *tunnel call*: a high, two-pitched, ethereal-quality vocalization.
- *whisper/trill call*: a quiet, rapid trill vocalization.

- *veer call*: a characteristic, short, down-slurred vocalization.

Wood thrush:

- *first level call*: series of 3-6 rapidly delivered, low-frequency (ca. 1–2 kHz) notes rendered as *bup bup, tut tut, or cheuh-huh, or whip-whip-whip*.
- *second-level calls*: about 3-5 notes, louder and higher in frequency than first level call, expressed as *pit, pip, whit, or whip-whip-whip*. May escalate to even higher frequency and faster delivery in relation to degree of agitation.

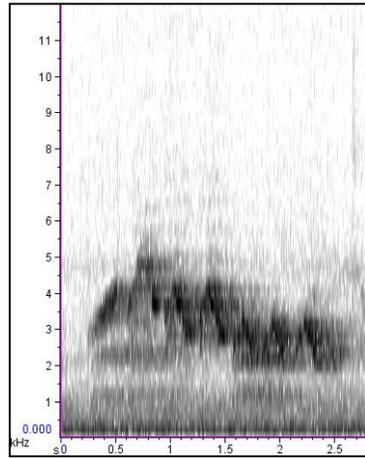
Scarlet tanager:

- simple, 2-note call denoted by a *chik* call quickly followed by a slightly lower-pitched, burry call note; phoneticized in literature as *chip-churr, chic-burr, chuck-ur, or chip-bird*.

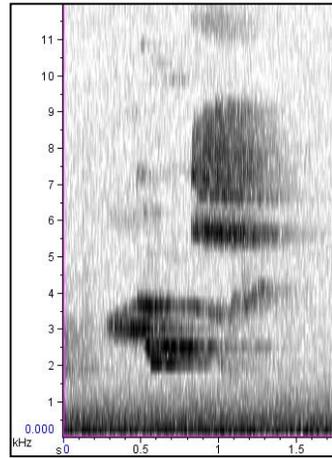
Note: Modified from *Cornell Lab of Ornithology*. 2013. Macaulay Library Web Site. Retrieved November 3, 2013, from <http://macaulaylibrary.org/> and Sibley, D. A. 2003. *The Sibley field guide to birds of Eastern North America*. New York: Alfred A. Knopf.

Appendix 3

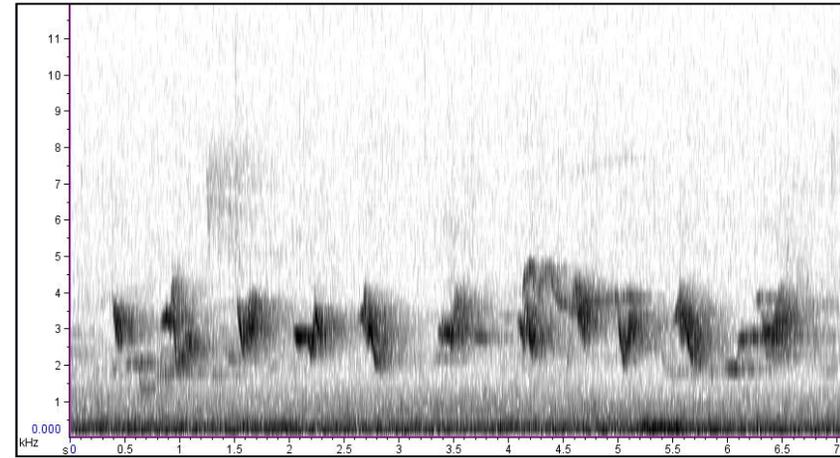
Spectrograms of focal species' songs.



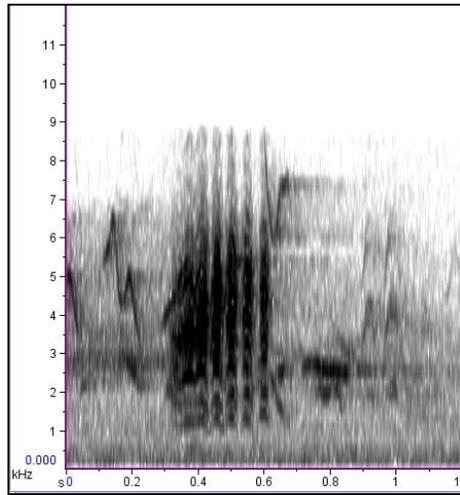
Veery (*Catharus fuscescens*) song



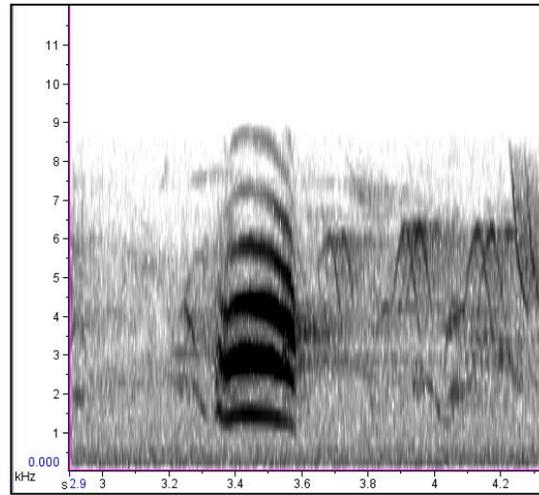
Wood thrush (*Hylocichla mustelina*) song



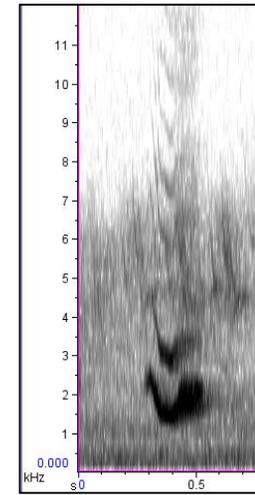
Scarlet tanager (*Piranga olivacea*) song

Appendix 4Spectrograms of veery (*Catharus fuscescens*) calls.

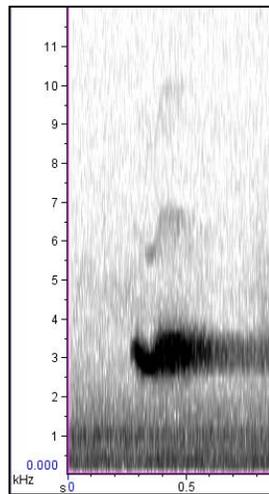
Harsh "chatter" call



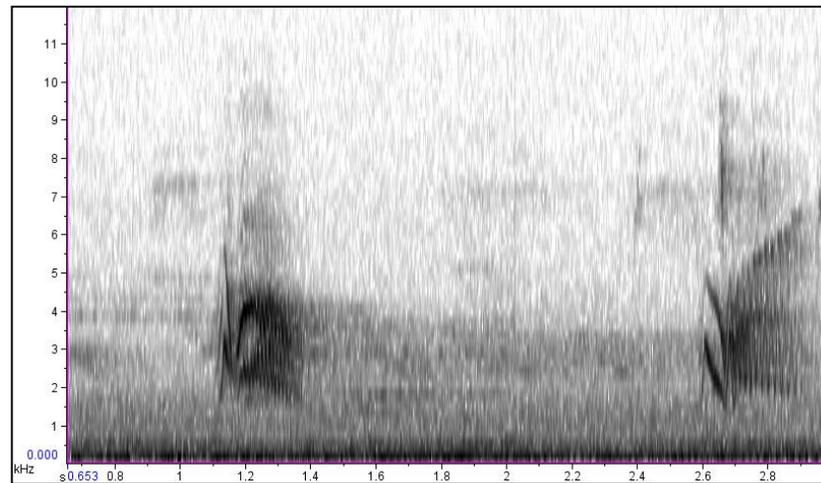
"Anxious"/"ack" call



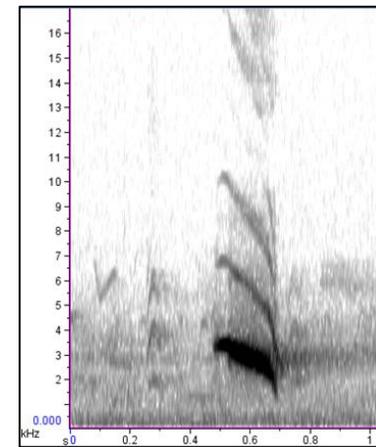
"Buerr" call



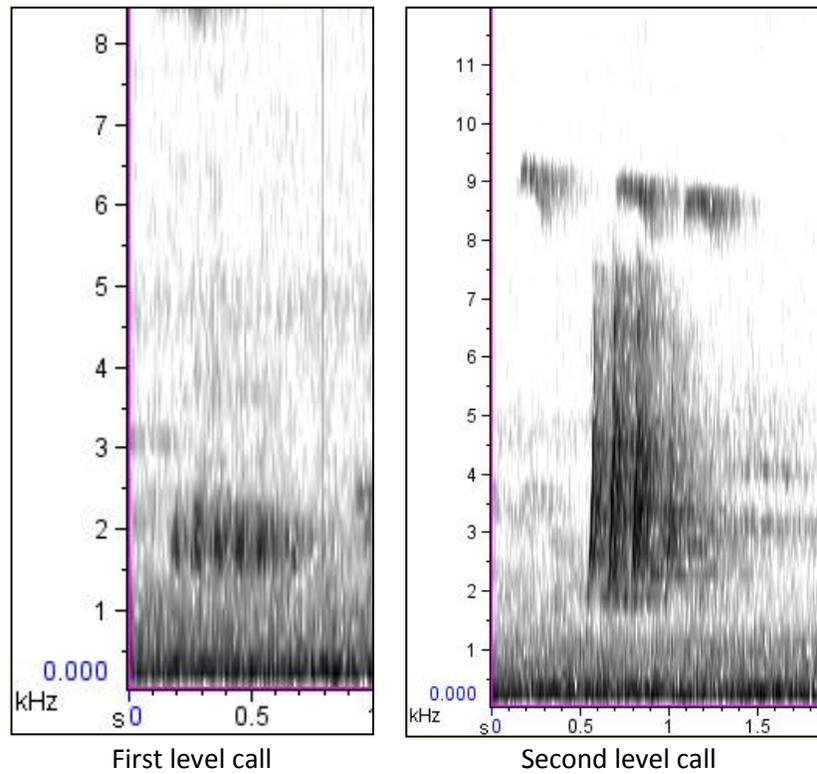
"Tunnel" call



"Whisper"/"trill" call

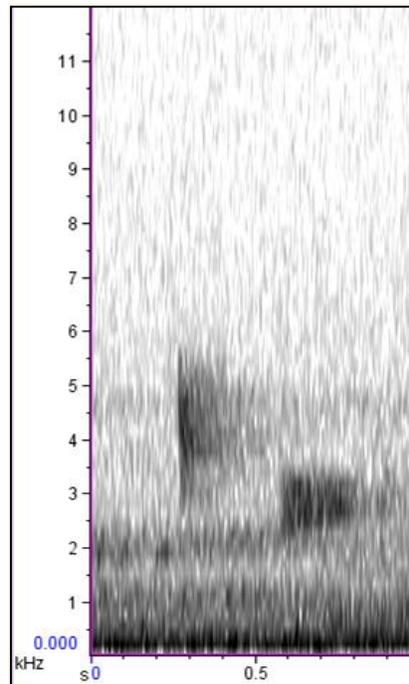


"Veer" call

Appendix 5Spectrograms of wood thrush (*Hylocichla mustelina*) calls.

Appendix 6

Spectrogram of scarlet tanager (*Piranga olivacea*) call.



“Chik-burr” call

Appendix 7

List of potentially confounding variables affecting the execution of playback experiments.

Experimental set-up and sounds

Background Noise
Distortion
Degradation
Sound level
Sound per unit time
Total amount of sound
Playback equipment
Observer bias

Experimental subjects

Location in territory
Distance from speaker
Stage of breeding cycle
Motivation
Other behavior
Neighboring subjects
Predators

Environmental conditions

Time of year
Time of day
Weather
Vegetation
Background noise
Position of speaker

Note: Modified from McGregor et al. 1992 in Catchpole, C. K., and P. J. B. Slater. 1995. Bird song: Biological themes and variations. New York: Cambridge University Press.

Appendix 8

K-S tests to determine differences in the distribution of songs over recording time between control and experimental treatments per plot (A-P) for the three focal species and entire dusk chorus, summarized at 5-min (n=14) intervals. Statistically significant values are in bold.

Paired plot	Veery		Wood thrush		Scarlet tanager		Dusk chorus	
	D	p-value	D	p-value	D	p-value	D	p-value
A	0.21	0.90	0.29	0.62	0.21	0.90	0.29	0.62
B	0.14	1.00	0.14	1.00	0.21	0.90	0.36	0.33
C	0.36	0.33	0.21	0.90	0.21	0.90	0.29	0.62
D	0.14	1.00	0.29	0.62	0.14	1.00	0.36	0.33
E	0.29	0.62	0.36	0.33	0.00	1.00	0.36	0.33
F	0.14	1.00	0.14	1.00	0.29	0.62	0.21	0.90
G	0.29	0.62	0.43	0.15	0.14	1.00	0.57	0.02
I	0.29	0.62	0.14	1.00	0.21	0.90	0.21	0.90
J	0.43	0.15	0.50	0.06	0.21	0.90	0.43	0.15
K	0.07	1.00	0.29	0.62	0.14	1.00	0.43	0.15
L	0.50	0.06	0.36	0.33	0.07	1.00	0.21	0.90
M	0.29	0.62	0.36	0.33	0.00	1.00	0.14	1.00
O	0.21	0.90	0.21	0.90	0.00	1.00	0.14	1.00
P	0.43	0.15	0.29	0.62	0.00	1.00	0.36	0.33

Appendix 9

K-S tests to determine differences in the distribution of calls over recording time between control and experimental treatments per plot (A-P) for the three focal species, summarized at 5-min (n=14) intervals. Statistically significant values are in bold.

Paired plot	Veery		Wood thrush		Scarlet tanager	
	D	p-value	D	p-value	D	p-value
A	0.14	1.00	0.14	1.00	0.21	0.90
B	0.21	0.90	0.29	0.62	0.21	0.90
C	0.14	1.00	0.14	1.00	0.21	0.90
D	0.14	1.00	0.14	1.00	0.14	1.00
E	0.29	0.62	0.14	1.00	0.00	1.00
F	0.21	0.90	0.07	1.00	0.29	0.62
G	0.21	0.90	0.07	1.00	0.14	1.00
I	0.21	0.90	0.14	1.00	0.21	0.90
J	0.21	0.90	0.21	0.90	0.21	0.90
K	0.29	0.62	0.36	0.33	0.14	1.00
L	0.43	0.15	0.07	1.00	0.07	1.00
M	0.36	0.33	0.14	1.00	0.00	1.00
O	0.71	< 0.01*	0.14	1.00	0.00	1.00
P	0.57	0.02*	0.14	1.00	0.00	1.00

Note: * denotes plot in which there were statistically more calls in control treatment than experimental treatment.

Appendix 10

Four letter codes, common names, and Latin binomials of avian species referenced in this study.

Species Code	Species Common Name	Species Latin Binomial Name
VEER	Veery	<i>Catharus fuscescens</i>
WOTH	Wood thrush	<i>Hylocichla mustelina</i>
OVEN	Ovenbird	<i>Seiurus aurocapillus</i>
GRCA	Gray catbird	<i>Dumetella carolinensis</i>
EWPE	Eastern wood-pewee	<i>Contopus virens</i>
EATO	Eastern towhee	<i>Pipilo erythrophthalmus</i>
SCTA	Scarlet tanager	<i>Piranga olivacea</i>
RBGR	Rose-breasted grosbeak	<i>Pheucticus ludovicianus</i>
BAWW	Black-and-white warbler	<i>Mniotilta varia</i>
AMRE	American redstart	<i>Setophaga ruticilla</i>
AMRO	American robin	<i>Turdus migratorius</i>
NOCA	Northern cardinal	<i>Cardinalis cardinalis</i>
SOSP	Song sparrow	<i>Melospiza melodia</i>
COYE	Common yellowthroat	<i>Geothlypis trichas</i>
REVI	Red-eyed vireo	<i>Vireo olivaceus</i>
GCFL	Great-crested flycatcher	<i>Myiarchus crinitus</i>
RWBL	Red-winged blackbird	<i>Agelaius phoeniceus</i>
FISP	Field sparrow	<i>Spizella pusilla</i>
AMGO	American goldfinch	<i>Spinus tristis</i>
EAPH	Eastern phoebe	<i>Sayornis phoebe</i>
PIWO	Pileated woodpecker	<i>Dryocopus pileatus</i>
BWWA	Blue-winged warbler	<i>Vermivora cyanoptera</i>
YTVI	Yellow-throated vireo	<i>Vireo flavifrons</i>
CHSP	Chipping sparrow	<i>Spizella passerina</i>
BAOW	Barred owl	<i>Strix varia</i>
MODO	Mourning dove	<i>Zenaida macroura</i>
LOWA	Louisiana waterthrush	<i>Parkesia motacilla</i>
YEWA	Yellow warbler	<i>Dendroica petechia</i>
EWPW	Eastern whip-poor-will	<i>Caprimulgus vociferus</i>
INBU	Indigo bunting	<i>Passerina cyanea</i>
HOWR	House wren	<i>Troglodytes aedon</i>
CAWR	Carolina wren	<i>Thryothorus ludovicianus</i>