

The Effect of an Indirect Predator Cue on Veery (*Catharus fuscescens*) Dusk Chorus

by

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## Chapter I

### General Introduction

In a world of uncertainty, organisms either adapt or perish. Consequently, to reduce uncertainty, organisms seek information about their natural environment from a variety of sources (Dall et al. 2005). Vocal communication involves the transfer of signals from sender to receiver. This communication dyad, however, is often exploited by unintentional participants, termed *eavesdroppers* (Peake 2005). Increased knowledge about the state of the environment can in turn mean an adaptive advantage for an eavesdropper. Because the composition of natural environments supports an array of organisms, (i.e., different species filling different niches), the greatest interaction and access to eavesdropping is between heterospecifics. Competition is not necessarily a factor in heterospecific interactions, thereby allowing for the access of newly acquired information without the drain of competition between species (Seppänen et al. 2007). In fact, eavesdropping behavior has been experimentally shown to occur in approximately 70 vertebrate species (Magrath et al. 2015).

One benefit to eavesdropping behavior may include increased knowledge of predatory threats, which directly impacts the fitness of an organism. Under the perceived presence of a direct predator, calls of the Barred Owl (*Strix varia*), Schmidt and Belinsky (2013) demonstrated that male Veeries (*Catharus fuscescens*) modify their dusk chorusing behavior by reducing song rate and chorus timing. The results of this study suggest that during dusk chorus, a high risk of predation is perceived by male Veeries. Previous studies, however, have shown that indirect cues elicit greater changes in

perceived predation risk than do direct cues (van der Veen 2002; Lind et al. 2005; Schmidt et al. 2008).

Here, I explore the extent to which Veery dusk chorusing behavior may be modified in the presence of an indirect predator cue, the “seet” call of the Eastern Tufted Titmouse (*Baeolophus bicolor*; hereafter titmouse). The titmouse is highly vocal, utilizing two distinct alarm calls-- seet and “chick-a-dee” -- encoded with information pertaining to predator class and risk assessment (Hetrick and Sieving 2011). The chick-a-dee call is the dominant mobbing vocalization associated with antipredator behavior (Hailman 1989), consisting of a single “chick” call followed by subsequent “dee” notes (Latimer 1977; Hetrick and Sieving 2011). The number of dee notes is often positively correlated to threat level (Templeton et al. 2005). The chick-a-dee alarm call is easy to localize and often reserved for terrestrial predators (i.e., snakes, mammals) or perched avian predators (Langham et al. 2006; Sieving et al. 2010). In contrast, seet calls are short, high-frequency vocalizations that are difficult to localize. Seet calls often denote the presence of an aerial raptor and/or attack from above-- the response to such a predator being to escape, hide, and/or reduce movement (Templeton and Green 2007; Hetrick and Sieving 2011).

I sought to determine if male Veeries eavesdrop on titmouse alarm calls, indirectly indicating predation risk, and in turn modify (reduce) their dusk chorusing behavior. The potential fitness benefit of eavesdropping behavior is that it collects information from more sources, i.e., individuals - both conspecific and heterospecific, with the latter being potentially more numerous and their information complementary to that provided from conspecifics. Together, these sources provide a more complete



understanding (i.e., habitat quality, food patch quality, predation risk, etc.) of their environment. If such information indicates high ambient risk, Veeries may feel an acute tradeoff between the need to attract a mate while simultaneously putting itself at greater risk to predators.

My study presents valuable insight into anti-predator behavior and dusk chorusing behavior in a passerine. To date, <4% of published work in the field of vocal communication pertains to nocturnal vocalization (La 2011). My study sought to address this, in small part, by further exploring dusk chorusing behaviors in a diurnal passerine.

## Chapter II

### The Effect of an Indirect Predator Cue on Veery (*Catharus fuscescens*) Dusk Chorus

#### Abstract

In passerines, song serves as a vital component of communication, either to solicit a mate or defend a territory. In the presence of a predator, however, vocal communication can be detrimental, making individuals more susceptible to the risk of predation. Singing at dusk, when light levels are diminished, can exacerbate this risk, particularly for a primarily diurnal species. As an adaptive means of assessing risk, organisms can acquire information regarding the surrounding environment, particularly risk, via heterospecific eavesdropping to make informed decisions. Here, I investigated whether a diurnal passerine, the Veery (*Catharus fuscescens*), eavesdropped on indirect predator cues, the set alarm call of the Tufted Titmouse (*Baeolophus bicolor*), at dusk. Using a playback design, three 30-second pulses of barred owl calls were broadcasted over the course of a 25-minute period surrounding sunset (i.e., when dusk chorus vocalizations are maximized), while Veery dusk chorusing behavior was simultaneously recorded. Using paired t-tests, I determined that Veeries did not modify their dusk chorusing behavior in the presence of indirect predatory cues.

#### Introduction

In passerines, male song serves as a vital component of communication, in which they function to advertise a territory to both solicit a mate and defend against conspecifics (Catchpole and Slater 2008). Within these respective contexts, song may advertise the male's quality to a perspective mate (Otter et al. 1997) or his resource-holding potential

(Parker 1974). In addition, song type or other attributes of song within iterative interactions (i.e., counter-singing bouts) between males may provide information regarding aggressiveness and intent to escalate contests. Song, therefore, provides many important benefits to males through social interactions with conspecifics (Catchpole and Slater 2008). In turn, extended singing behavior is costly to perform. Costs include energetic expenditure while singing (Eberhardt 1994; Oberweger and Goller 2001) and missed opportunities to gather food or perform other fitness-enhancing activities (Brown et al. 1994; Brown 1999). Song may also enhance an individual's risk of predation if the bird is distracted, or if song itself provides potential information to predators, such as location (Mougeot and Bretagnolle 2000; Krams 2001; Hale 2004; Peake 2005). Furthermore, activities that require directed attention, as is likely when engaging in counter-singing bouts with rival males, may produce a cost of multitasking (Schmidt and Brown 1996; Kotler et al. 2004; Felts and Schmidt 2010), such that distracted songsters may experience a higher risk of predation. In diurnal species, these costs are likely to be inflated during periods of low light: dawn and dusk.

Dawn and dusk are also the primary times at which many diurnal bird species engage in counter singing. Most attention in the primary literature has focused on the dawn chorus. It has been assumed that dawn chorusing imposes tradeoffs with the ability to forage and thus might be an indicator of a male's resource-holding potential (Parker 1974). However, there are multiple alternative hypotheses for dawn singing, including the quality and distance of sound transmission in the early morning (Brown and Handford 2003). Of the two primary chorusing periods, attention to dusk chorusing has been neglected in favor of dawn chorusing. For instance, La (2011) noted in a recent review

that less than 4% of studies in avian vocalization have focused on nocturnal communication, despite the fact that 30% of North American birds (70% of which are considered diurnal) vocalize at night. In North America, diurnal thrushes (*Catharus* spp.) and wrens (Troglodytidae), and the nocturnal, non-passerine Caprimulgids, are the primary land birds recognized to frequently vocalize at dusk and at night; in Europe this group also includes chats (e.g. the common nightingale, *Luscinia megarhynchos*) (Amrhein et al. 2004). Within the caprimulgids, it has been shown that increased predation risk may be a cost to singing. For instance, Woods and Brigham (2008) demonstrated that Common Poorwills (*Phalaenoptilus nuttallii*) decrease their counter-singing with conspecifics on full moon nights and in the presence of Great Horned Owls (*Bubo virginianus*) (Woods and Brigham 2008). Similar observations have been made for nocturnal seabirds. Mougeot and Bretagnolle (2000) demonstrated that predatory skuas are attracted by the calls of vocalizing seabirds, such as the Blue Petrel (*Halobaena caerulea*), and that petrels in turn reduce their singing in response to experimental playbacks of skua vocalizations.

These studies are examples of what is now referred to as interceptive eavesdropping: “the use of information in signals by individuals other than the primary target” (Peake 2005). Interceptive eavesdroppers may include conspecifics, as in the case of multiple males and females potentially gaining information from the public displays (vocal or visual) between two members of the same or opposite sex. Interceptive eavesdroppers may also include heterospecifics, such as the examples in which predators may locate their prey based on the latter's sexual displays. In turn, prey may intercept signals of their predators to reduce their risk of being depredated.

It has become clear in the past two decades that eavesdropping behavior is ubiquitous: communication that is intended within species may reach unintended audiences (i.e., eavesdroppers) and thus impose a high cost to communication (Hughes et al. 2010; Magrath et al. 2010; Haff and Magrath 2013). The classic example of interceptive eavesdropping in a predator-prey context was conducted on Túngara frogs (*Engystomops pustulosus*). Túngara frogs use an acoustic mating signal, known as the “chuck” call, to attract a mate. Predators of this species, such as the fringe-lipped bat (*Trachops cirrhosus*), in turn utilize these chuck calls to locate their prey, thereby increasing predation events on frogs (Ryan et al. 1981). As this and the other aforementioned studies demonstrate, signals that function in mate choice and selection can impose costs on the signaler. In turn, by eavesdropping on predators, potential prey may modulate their communication to reduce the probability of a predation event. Returning to the Túngara frog example, frogs do indeed reduce their use of chuck calls in the presence of bats, which not only cue in on the calls themselves, but also on the radiation or ripples on the water surface from where the frogs call (Halfwerk et al. 2014).

Schmidt and Belinsky (2013) tested the heterospecific eavesdropper hypothesis on dusk chorusing on the Veery (*Catharus fuuscescens*). The Veery is a diurnal passerine that has both a pronounced dawn and dusk chorus (Samuel 1972; Belinsky et al. 2012; Schmidt and Belinsky 2013). Despite potential predation risk, vocal communication serves an important role in mate attraction. Hence, dusk singing in Veeries represents a fitness tradeoff between mate attraction and heightened exposure to predation risk, particularly under low light conditions. To test this, Schmidt and Belinsky (2013) subjected Veeries to experimental playbacks of Barred Owls (*Strix varia*). The owl

stimulus was limited to three short bursts 15 minutes before sunset, at sunset, and 10 minutes post-sunset. Veeries singing under heightened perceived owl presence demonstrated: (1) reduced song rates post-sunset, (2) reduced singing bouts (a bout being measured as > 18 songs per 3-minute intervals), (3) earlier time of last song and (4) earlier time of last singing bout. The results of this study suggest that during dusk chorus, a higher risk of predation is perceived by male Veeries, consistent with Ryan et al. (1981).

Broadcasting an owl vocalization provides Veeries with a direct cue of owl presence. It should be noted, however, that direct cues of predators may supply additional, inadvertent information. For instance, it has been suggested that hunting predators do not vocalize to avoid giving away their location to prey or cause prey to be more apprehensive and engage in behaviors that make them harder to catch (Schmidt et al. 2008); however, the response by Veeries to the owl playback is not consistent with this hypothesis. Second, many organisms receive indirect cues of risk and/or predator presence. These may include alarm calls of heterospecific prey species.

Birds in the family Paridae (titmice and chickadees) possess a highly complex communication system, involving antipredator vocal behavior (Templeton et al. 2005; Hetrick and Sieving 2011) and aggressive mobbing displays (Contreras and Sieving 2011). These birds are considered *nuclear species*, living as non-migratory year-round residents and providing valuable information for other sympatric forest-dwelling species, often which share common predators (Templeton et al. 2005; Langham et al. 2006; Sieving et al. 2010; Hetrick and Sieving 2011).

The Tufted Titmouse (*Baeolophus bicolor*; hereafter titmouse) is a socially dominant, passive-nuclear species whose presence benefits heterospecifics. In the non-breeding season, the titmouse helps establish wintering flight paths for mixed-flock species (Contreras and Sieving 2011). In the breeding season, sympatric avian species seek out habitat in close proximity to titmice, as the titmice have likely had relatively more time to evaluate the risk of predation in a given habitat patch. Thus, titmouse occupancy serves as an honest signal of predation risk (Mönkkönen and Forsman 2001). Furthermore, the titmouse is highly vocal, utilizing two distinct alarm calls encoded with information pertaining to predator class and risk assessment (Hetrick and Sieving 2011). In the presence of perched raptors or terrestrial predators, titmice vocalize a series of mobbing calls, “chick-a-dee”, to elicit predator inspection and mobbing aggression from peers (Langham et al. 2006). When faced with an aerial predator, however, titmice vocalize using a high frequency “seet” call which signifies an imminent threat, the immediate response being to escape, hide, and/or reduce movement (Templeton and Green 2007), sometimes for extended periods of time (Hetrick and Sieving 2011).

These indirect predator cues serve as vital information to assess the state of one’s environment and their use should directly correlate to an organism’s fitness. Receiving indirect cues, and thereby using this information to make a more informed response, can increase vigilance behavior, consequently reducing risk of predation (Altendorf et al. 2001; Laundré et al. 2001; Kuczynski 2015). In fact, previous studies indicate that indirect cues elicit greater changes in perceived predation risk than did direct cues (van der Veen 2002; Lind et al. 2005; Schmidt et al. 2008).

For my thesis, I implemented a playback experiment designed after Schmidt and Belinsky (2013) to address whether Veery dusk chorusing behavior was altered in the presence of alarm calls of titmice. I hypothesized that given the high risk of predation in diminished light conditions, male Veeries will eavesdrop on the alarm calls of titmice and modify their dusk chorus as an adaptive response. If true, I predict that when exposed to titmouse seet calls, Veeries will: (1) reduced the number of singing bouts post-sunset, (2) reduced total song output post-sunset, and (3) cease singing behavior earlier in the evening compared to control trials.

## **Methods**

### *Study Species*

The Veery (*Catharus fuscescens*) is a ~30 g Neotropical migrant belonging to the family Turdidae. Its name reflects the sound made by one of its calls. Its song, however, is a series of downward spiraling notes, ethereal in nature, sometimes mechanical, and containing both an upper and lower voice, which reflects independent song production from each syrinx (Figure 1). This allows the Veery to strongly harmonize during singing, which may impede localization by predators. Brennan and Jones (2015) demonstrated that Veeries have a repertoire size of 1-6 songs used repetitively or alternatively within a singing bout. Only males of this species sing, with singing behavior intensified during both dawn and dusk. The dusk chorusing behavior in the Veery may be linked to vocal masking from heterospecifics via acoustic competition, as Veeries experience greater vocal masking at dawn than at dusk (Belinsky et al. 2012). Therefore, dusk chorusing may be a more effective period for the Veeries to advertise for mates.



### Study Site

All research was conducted at the Cary Institute of Ecosystem Studies, Millbrook, New York (41°47'01.0" N, 73°43'56.5" W). The Cary property contains approximately 325 ha of secondary, temperate deciduous forest. The predominant hardwood canopy species include red oak (*Quercus rubra*), sugar maple (*Acer saccharum*), and chestnut oak (*Quercus montana*). Various groves of both eastern hemlock (*Tsuga canadensis*) and white pine (*Pinus strobus*) are also dispersed throughout. Several invasive understory species, such as multiflora rose (*Rosa multiflora*), Japanese barberry (*Berberis thunbergii*), and *Lonicera* spp., are abundant throughout the property. These species have become locally important to the Veery, as they provide excellent nesting substrates.

The Cary Institute is home to a diverse array of sympatric passerines: the Ovenbird (*Seiurus aurocapillus*), Wood Thrush (*Hylocichla mustelina*), Gray Catbird (*Dumetella carolinensis*), and the American Robin (*Turdus migratorius*). A commonality exists between predators of the Veery and these other avian species. The Barred Owl (*Strix varia*) represent the primary nocturnal avian predator on site, with typically three breeding pairs observed on site each spring (Schmidt, unpublished data). Barred Owls have been linked to Wood Thrush mortality on site (Schmidt et al. 2008). Other predators, such as the Great Horned Owl (*Bubo virginianus*), Sharp-shinned Hawk (*Accipiter striatus*), and Cooper's Hawk (*Accipiter cooperii*), also breed on site and also represent a potential predation risk to Veeries.

### Experimental Design

My study was conducted during the peak of the Veery breeding season, across 3 consecutive years (May 29-June 24 2013, May 21-July 5 2014, and June 5-June 25

2015). These dates correspond to the period of intense dusk chorusing behavior in Veeries. My study relied on easy access to vocalizing birds in diminishing light conditions; therefore, all data collection was accomplished via easy foot access from roads. Individual Veeries were not identifiable. Thus, it is possible that the same individuals may have been sampled across years. Veeries, however, retain strong site fidelity at this location (personal observation). To minimize risk of recording overlap, recording locations were chosen systematically throughout the property to avoid overlap of individuals and with respect to the previous year's site locations. Plus, on any given recording night, the spacing of recorded trials were  $\geq 400$  m apart to reduced exposure to audio stimuli (previous work by Weary et al. [1991] suggests Veery territory size to be less than 250 m).

Three 30-second periods of audio stimuli were used over the course of a 25-minute period surrounding sunset, i.e., when dusk chorus vocalizations are maximized (Figure 2). To avoid the habituation of individuals to stimuli, audio recordings were held to 30 s short bursts. A paired treatment design was implemented, whereby each individual Veery was exposed to 2 treatments of audio stimuli: (1) gray treefrog chorus (*Hyla versicolor*) and (2) the seet alarm calls of the titmouse. Gray treefrogs are abundant at the field site, non-threatening to Veeries, and vocalize regularly, making them an appropriate audio control for this study. The order in which stimuli were presented was chosen at random, with trials occurring on consecutive evenings, barring any inclement weather, which would prevent accurate recordings of individuals. Recording only occurred on nights without precipitation (i.e., rain), wind speeds  $\leq 10$  mph, and an absence of major disturbance (e.g. July 4<sup>th</sup> fireworks).

Prior to recording, dusk chorusing Veeries were scouted to determine their approximate location. However, birds are mobile animals and as such, selecting an ideal central location in which to record was not always successful for each trial. Therefore, criteria were established to identify a successful recording attempt: (1)  $\geq 25$  Veery songs recorded, (2) Veery song  $\geq 7$  db from the background noise, (3) Veery song displayed an *upper voice* (Figure 1), (4) Veery song  $\leq 50\%$  masked by other background song (i.e., conspecific and heterospecific bird song), and (5) the recording must be void of major disturbance. To evaluate these criteria, I pre-assessed recordings using Raven Pro 1.4 (Bioacoustics Research Program 2011) prior to additional recording attempts. Thus, trial numbers for each individual bird were between 2-4 recordings and were required to be made within a  $\leq 7$ -day period and adhere to the paired study design.

To avoid human influence on Veery behavior, trials were set up  $\geq 25$  minutes prior to sunset. Exemplars were assembled in playlists using iTunes (version 11, Apple Inc.) by adding timed increments of silence surrounding broadcasts of audio stimuli. Three exemplar structures were created (Figure 3). This design and use of the iPod nano *sequential loop* function allowed me to independently run multiple trials each night while preserving accuracy to sunset. Trials ended  $\geq 60$  minutes past sunset, at which time all recording equipment was removed. The rebar stake, which marked microphone recording location, and all flagging tape remained on site until the conclusion of all trials.

To reduce effects of pseudoreplication, I created 5 unique audio exemplars for each treatment. Audio recordings for 3 gray treefrog recordings were obtained from the Macaulay Library at the Cornell Lab of Ornithology, and additional exemplars were used from the study by Schmidt and Belinsky (2013). For gray treefrog files, amplitude was

adjusted to 64 dB SPL ( $\pm 2$  dB), measured at a distance of 1 m, using Raven Pro 1.4 (Bioacoustics Research Program 2011). This was done to avoid distortion of sound quality. For titmouse trials, recordings of 2 titmouse alarm call were obtained from Dr. K.S. Sieving (University of Florida). Three additional titmouse files were personally recorded on May 17<sup>th</sup>-18<sup>th</sup>, 2013 using a mist net and active capture protocol. I used a Telinga parabolic reflector (Telinga Microphones), a Sennheiser MKH 62 microphone (Sennheiser Electronic GMBH & Co.), and Roland R-05 Wave/MP3 recorder to record set alarm calls made during mist net extraction. To simulate a naturally calling titmouse, playback amplitude for all titmouse recordings was adjusted to 72 dB SPL ( $\pm 2$  dB), measured at a distance of 1 m, using Raven Pro 1.4 software (Bioacoustics Research Program 2011).

A passive recording protocol was used like that of Schmidt and Belinsky (2013) to broadcast audio stimuli and record Veery song. Recordings were made using a Sennheiser ME 62 Omnidirectional microphone (with K-6 power module) (Sennheiser Electronic GMBH & Co.) placed 1 m off the ground using rebar stakes and zip ties and connected to a Roland R-05 Wave/MP3 (Roland Corporation) recorder, placed on the ground and set to an input level of 50. I recorded at a sample rate of 44.8 kHz and 24 bits, with gain set to a standardized level. A Yamaha PDX-11 portable speaker (Yamaha Corporation) and iPod nano (Apple Inc.) were placed approximately 25 m away, at a height of 2 m, facing the direction of the microphone (Figure 4). All sound trials were conducted passively and timed accurately according to sunset, using the UV Naval Observatory Master Clock for accuracy. Throughout experimentation, IACUC protocol 13042-04 was stringently followed.

### Analyses

All playback recordings (n=50) were analyzed by 2 trained observers using Raven Pro 1.4 (Bioacoustics Research Program 2011). Program preset values were used with the exception of contrast, which was adjusted to 60 to allow for greater clarity in detecting song morphology. Accuracy between individual assessors was evaluated; when independently assessing the same 5 trials, 98% similarity existed in song identification between individuals. Analysis for each trial considered the criteria for a successful recording. Using the computer software, visual identification of Veery songs on the spectrograph remained the primary method of identification. The flute-like songs of the Veery, however, are thought to be variable between individuals and often detectable by ear (Borror 1964, Samuel 1972). Therefore, when warranted, Veery songs were identified by ear in addition to their visual spectrographs.

Singing behavior, including the total number of songs, time of last song, and number of singing bouts, were assessed by 1-minute increments from sunset (the time of the 2<sup>nd</sup> exemplar) to 55 minutes post-sunset for 25 individual Veeries. This was a deviation from Schmidt and Belinsky (2013), who assessed song rate at 3-minute increments and only to 54 minutes post-sunset, the predetermined that Veeries halt singing behavior. Adjustments were made in my study to account for the fact that 1 Veery (bird T, trial 2) sang 55 minutes post-sunset. For all birds, the last song (negatively correlated with light levels, as the visual ability to discern predators diminishes with light level) was noted as the minute post-sunset in which each individual Veery ceased singing.

Following Schmidt and Belinsky (2013), I defined a singing bout as  $\geq 18$  songs per 3-minute interval. Since my data was organized in 1-minute blocks, however, I quantified a singing bout as each succession of 18 Veery songs within  $\leq 3$  minutes, which allowed for fluidity when analyzing song rates without regards to set intervals. The total time (minutes) spent in singing bouts, time of first bout, and time of last bout were also assessed.

I tested for an exemplar effect among treatment exemplars using a one-way analysis of variance (ANOVA), conducted in R using the statistical package *lme4* (Bates et al. 2015). The results of the ANOVA proved non-significant for gray treefrog trials ( $F_5=0.582$ ,  $P=0.679$ ) and titmouse trials ( $F_5=0.817$ ,  $P=0.529$ ), alike (Figure 5). Therefore, all trials, with respect for treatment, were pooled for analyses.

All data, including differences between treatments, was normally distributed based on the Shapiro-Wilk test. Given the paired design of the experiment, I assessed the three predictions within my hypothesis using two-tailed, paired t-tests with the significance level set to  $\alpha = 0.05$ .

## **Results**

On average, Veeries sang 6% more songs in their control trials than their titmouse alarm call trials ( $103.60 \pm 0.52$  vs.  $91.72 \pm 0.64$ ); however, this difference was not significant ( $t_{24}=1.485$ ,  $P=0.15$ ; Figure 6a). Within the first minute of analysis, immediately following sunset, Veeries exposed to titmouse stimuli sang statistically fewer songs than did control birds ( $t_{24}=2.54$ ,  $P<0.018$ ). A non-significant effect, however was detected following the first minute after exposure to the third exemplar, which

corresponds to 10 minutes post-sunset ( $t_{24}=1.1508$ ,  $P=0.2611$ ). Furthermore, in both treatments, singing behavior was negatively correlated with time (Figure 6b).

Veeries sang their last song 3 minutes later, on average, in control than in titmouse trials; however, this difference was not significant ( $t_{24}=1.724$ ,  $P=0.098$ ; Figure 7). Based on the singing behavior of one individual, bird T, singing continued 21 minutes later during the control trial. Excluding this bird from analysis ( $n = 48$ ), however, singing behavior in titmouse trials continued up to 3 minutes later compared to control trials.

Lastly, statistical significance was not observed in my analyses pertaining to Veery singing bouts. When comparing length of time in which Veeries engaged in extended singing bouts, individuals did, however, spend more time singing in control trials ( $9.28 \text{ minutes} \pm 0.74$  vs.  $7.88 \text{ minutes} \pm 0.83$ ;  $t_{24}= 0.983$ ,  $P=0.335$ ), leading to more total songs in extended singing bouts in control trials ( $75.36 \pm 0.71$  vs.  $63.12 \pm 0.88$ ;  $t_{24}= 1.14$ ,  $P=0.265$ ; Figure 8). Additionally, the commencement of singing bouts occurred ( $4.32 \pm 1.35$  vs.  $4.36 \pm 1.20$ ;  $t_{24}= -0.040$ ,  $P=0.969$ ) minutes post-sunset in control and treatment trials, respectively. Lastly, although not statistically significant, Veeries did ceased singing behavior later in the evening ( $16.12 \pm 0.55$  vs.  $13.68 \pm 0.60$ ;  $t_{24}=1.26$ ,  $P=0.220$ ) in control trials.

## **Discussion**

My study tested the hypothesis that dusk singing in Veeries would decline under higher perceived predation risk as informed by indirect cues of predator presence: titmouse alarm calls. I used the same design as Schmidt and Belinsky (2013) but used titmouse alarm calls rather than Barred Owl calls because titmouse alarm calls are more

general indicators of risk than are owl calls. Many bird (and some mammal) species display heightened perceived predation risk to such calls (Ryan et. al 1981; Maougeot and Bretagnolle 2000; Rainey et. al 2004; Deecke et al. 2005; Randler 2006; Laumann et al. 2007; Schmidt et al. 2008; Emmering and Schmidt 2011; Hetrick and Sieving 2011; Schmidt and Belinsky 2013).

Given the close similarity of the two studies, I predicted that when exposed to titmouse alarm calls, Veeries would exhibit pronounced decreases in dusk chorusing and the number of singing bouts, and would cease singing earlier in the evening, as demonstrated in Schmidt and Belinsky (2013). Contrary to my predictions, during diminishing light conditions post-sunset, Veeries did not significantly modify their singing behavior as a response to titmouse alarm calls. However, my results did exhibit trends that are consistent with several of my predictions (i.e., post-sunset, on average, Veeries exposed to seet calls sang fewer numbers of singing bouts, reduced total song output, and ceased singing behavior earlier in the evening compared to control trials). My conclusions are that Veery dusk chorusing behavior is not significantly influenced by the indirect information regarding predation risk transmitted via titmouse alarm calls.

One unique finding from my research is the short-term response to seet call vocalizations, specifically at sunset. In the first minute of analysis, immediately following sunset, Veeries exposed to titmouse stimuli sang statistically fewer songs than did control birds. This behavior could be the result of a startled response, in that continued exposure to seet calls justified a cause for concern. However, this response occurred after the second exposure to seet calls in the experiment. There is no further difference between treatments after being exposed to the third exemplar, 10 minutes post-sunset. At this



point, following three bouts of titmouse alarm call exposure, it is possible that birds viewed the alarm call as false information, seeing as no predation threat ever materialized.

This study differed from Schmidt and Belinsky (2013) in that indirect alarm calls were used instead of direct predator cues to signify the presence of a predatory threat. Both types of vocalizations signal predator presence and should increase perceived predation risk. The two studies viewed together suggest that Veeries may be more likely to respond to direct information about risk (i.e., owl calls) as compared to indirect information (titmouse alarm calls). Alternatively, owl calls are very specific in regards to the source of risk, where ETTI calls are not. However, if both direct and indirect cues are honest indicators of risk, it remains uncertain why Veeries do not respond to both.

Several hypotheses for the lack of response exist. First, owls are a potent direct source of mortality, whereas information from indirect cues is less certain. Second, there may be a strong cost to reducing dusk chorusing if male song output at dusk is important for advertising male quality and obtaining mates. Finally, Veeries may alter other behaviors, which were not quantified here, such as moving to a less-exposed perch, or reducing the amplitude of their songs.

Finally, my methods of song analysis differed from Schmidt and Belinsky (2013) in that my analyses of audio recordings were more detailed and critical. The previous study identified quantity of Veery song in 3-minute intervals without imposing strict criteria for selection. For my study, I limited my selection of Veery song to specific criteria: (1)  $\geq 25$  Veery songs recorded, (2) Veery song  $\geq 7$  db from the background noise, (3) Veery song displayed an *upper voice* (Figure 1), (4) Veery song  $\leq 50\%$  masked by

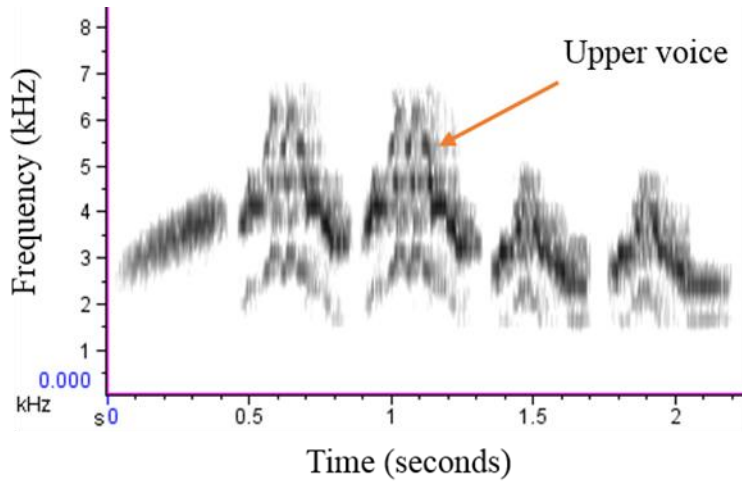
other background song (i.e., conspecific and heterospecific bird song), and (5) the recording must be void of major disturbance. I believed this to be necessary, as counter-singing between males and the presence of background Veery songs (i.e., neighboring males), degraded in quality, were detected on my recordings (a  $\geq 3$ -minute period of singing by non-focal Veeries was detected in 36% of gray treefrog and 24% of titmouse trials). I wanted to avoid counting all Veery songs present on the spectrograph and instead assessed only the target male and his singing. To do this, I needed to account for and adjust selection criteria for background noise and song sound pressure level (measured in dB). I also relied on the visual presence of the *upper voice*, as this Veery morphological feature was key for proper song identification, especially when recording quality was degraded and background noise was present.

My study would have been enhanced by properly identifying individuals performing their dusk chorus. This is relevant, because proper identification may have allowed me to identify at what stage the targeted bird was in his breeding cycle. Veeries tend to have pronounced singing behavior that corresponds to attracting a mate. However, birds also sing to defend and denote territory borders. It is possible that a Veery, feeling particularly threatened by an intruding male(s), may intensify its singing behavior at dusk to deter rivals. Given that the majority of adult Veeries on the property are color-banded, identifying individual birds may have allowed for surveying behaviors at other times of the day to establish nesting status and possibly locate a nesting locale, as to make selecting a recording location more accurate.

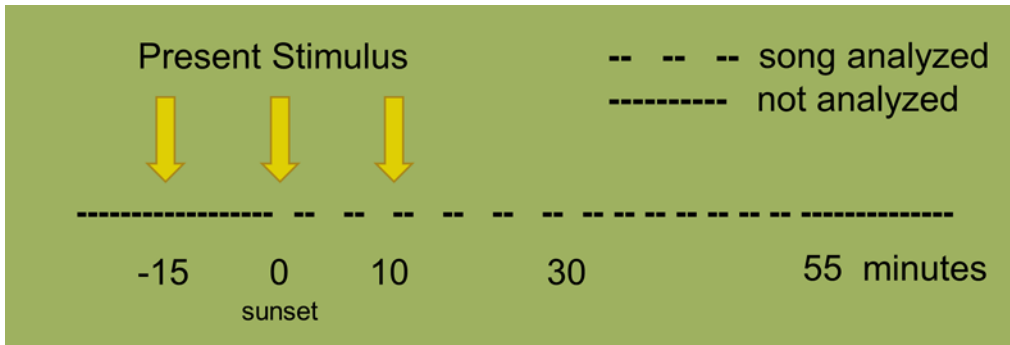
My study presents a valuable perspective as it relates to anti-predator behavior and dusk chorusing in a passerine. Despite lack of statistical findings, my study shows

trends supporting eavesdropping behaviors by male Veeries at dusk and is of value to the understanding of dusk chorus, which is underrepresented in the literature (La 2011).

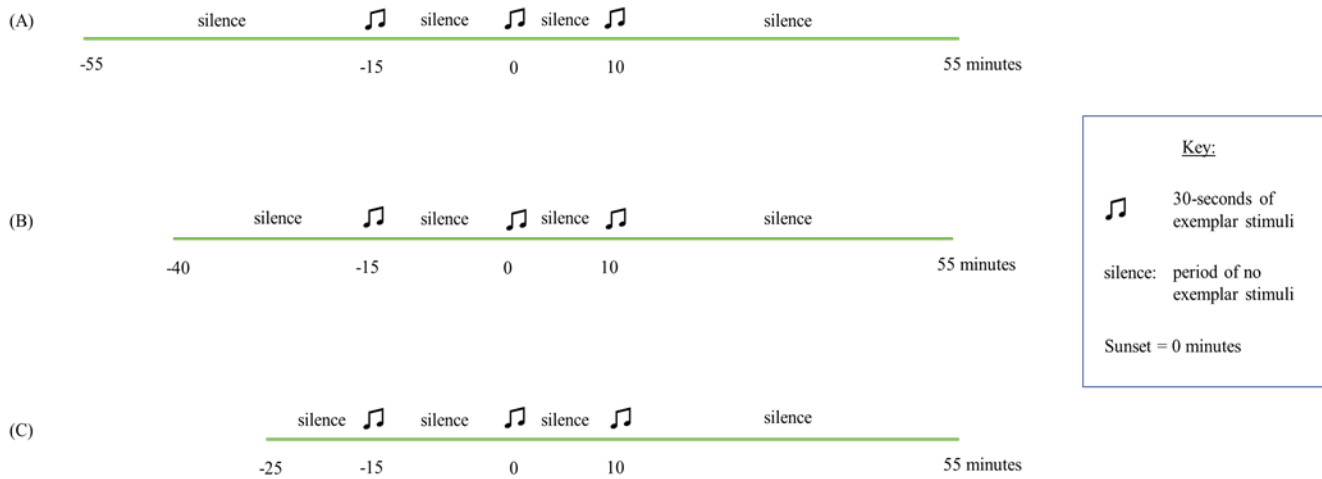
Additional study into dusk chorusing behaviors, both in diurnal and nocturnal birds, in the context of song and physical behaviors is warranted. This study hopes to serve as a stepping-stone for work to come in hopes of demystifying dusk chorusing and anti-predatory behavior in an evolutionary context.



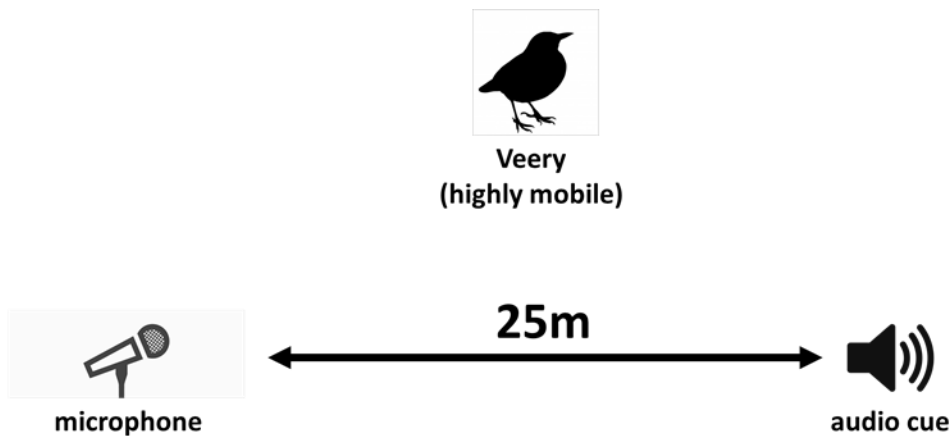
**Figure 1.** Spectrograph of Veery song depicting upper voice within a common song type.



**Figure 2.** Timing of audio stimuli broadcasts surrounding sunset. Three 30-second periods of audio stimuli were used over the course of a 25-minute period surrounding sunset. Analyses of Veery song occurred from sunset to 55 minutes post-sunset.

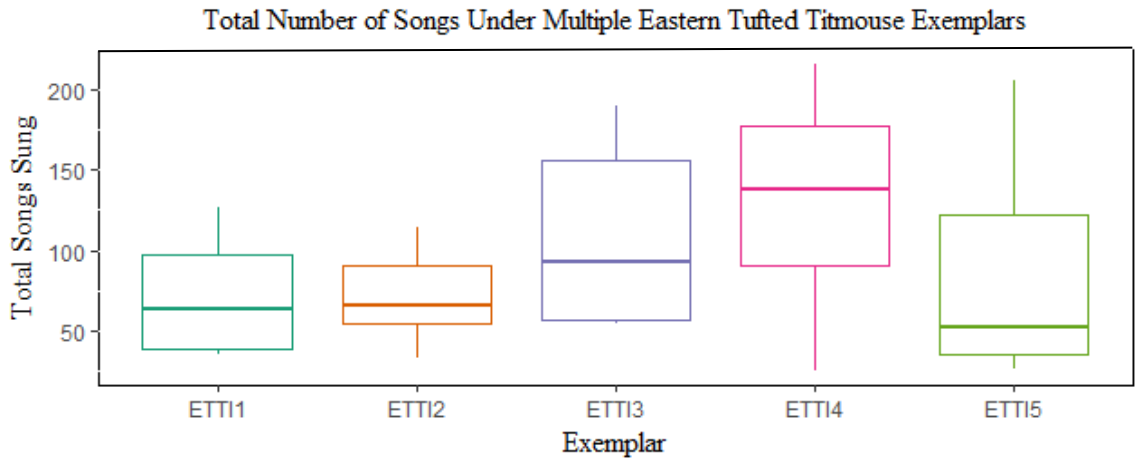


**Figure 3. Structural arrangement of audio exemplars beginning a) 55 minutes prior to sunset, b) 40 minutes prior to sunset, and c) 10 minutes prior to sunset, for respective treatments: gray tree frog and titmouse seet alarm call. Audio bursts were limited to 30 seconds, surrounded by periods of silence on the recordings.**

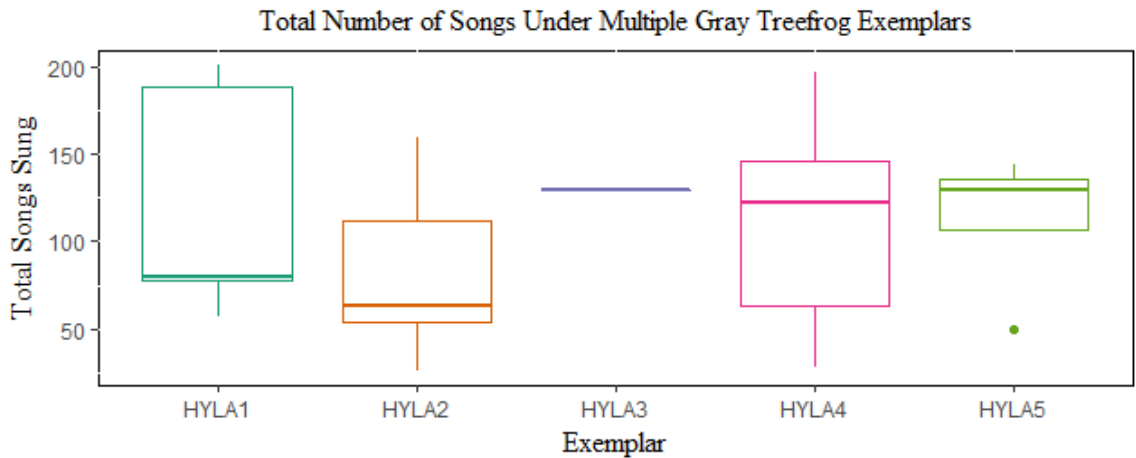


**Figure 4. Experimental passive recording set-up depicting omnidirectional microphone placement and speakers, at a distance of 25 m away. The Veery is mobile throughout the experiment.**

a.

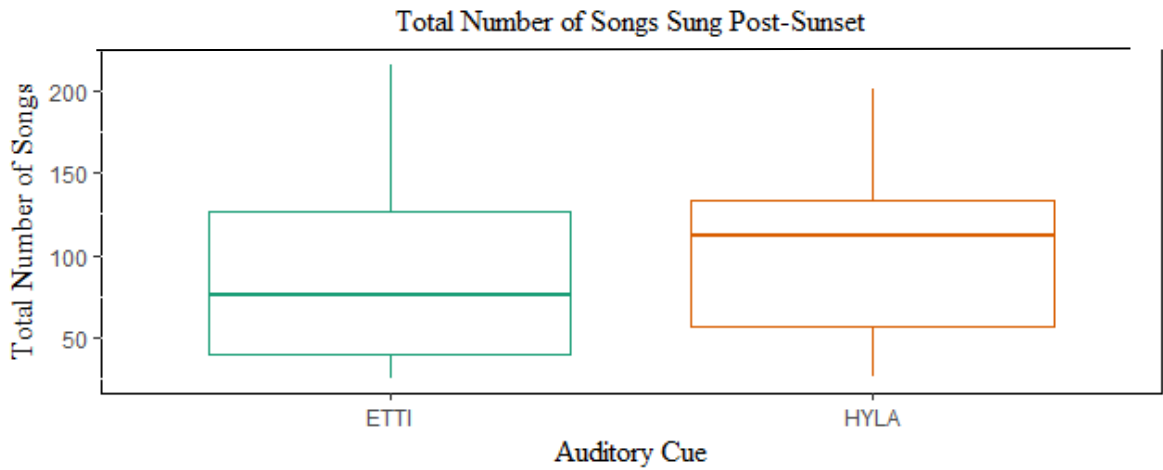


b.

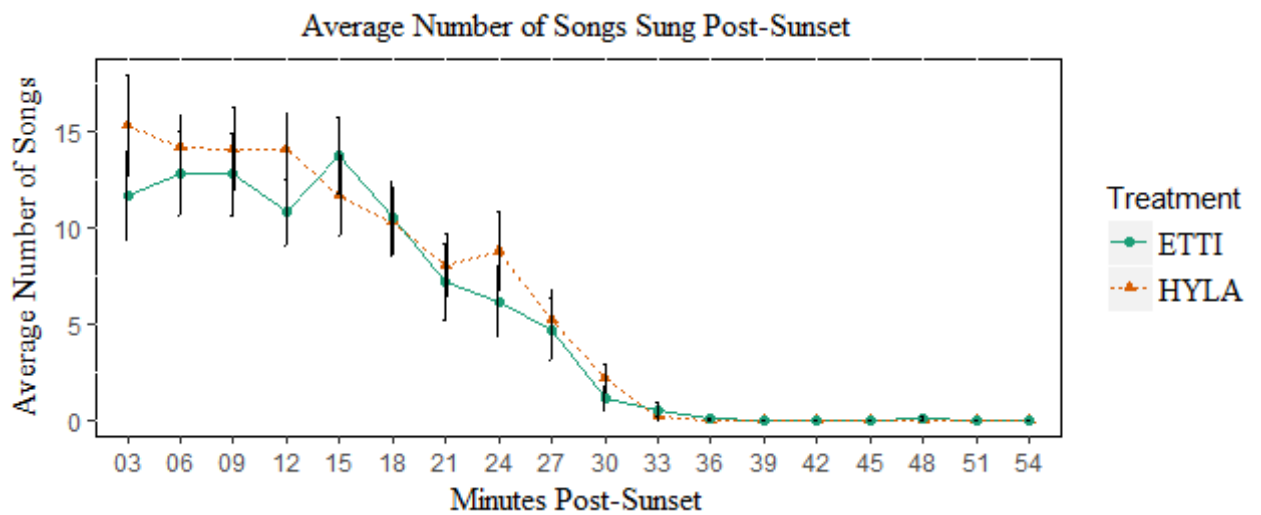


**Figure 5. Exemplar effect: results of one-way ANOVA for total number of songs sung when exposed to: a) 5 individual titmouse (ETTI) set call exemplars, and b) 5 individual gray treefrog (HYLA) exemplars. The term “ETTI” represents the abbreviation for ornithological banding code for titmouse. The term “HYLA” corresponds to the Genus for grey treefrog. The results of a one-way ANOVA proved not significant for gray treefrog trials ( $f_5=0.582$ ,  $p=0.679$ ) and titmouse trials ( $f_5=0.817$ ,  $P=0.529$ ), alike. Therefore, all trials, with respect for treatment, were pooled for the analyses.**

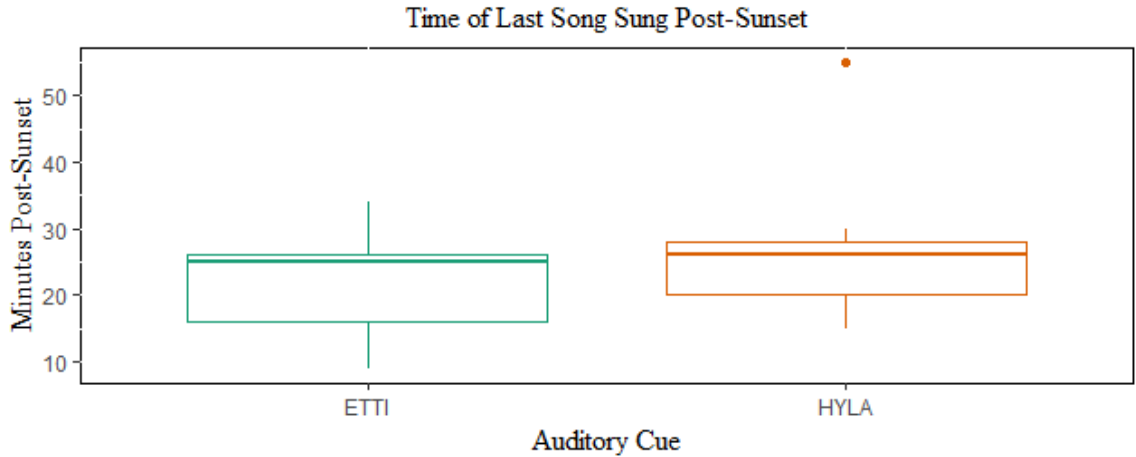
a.



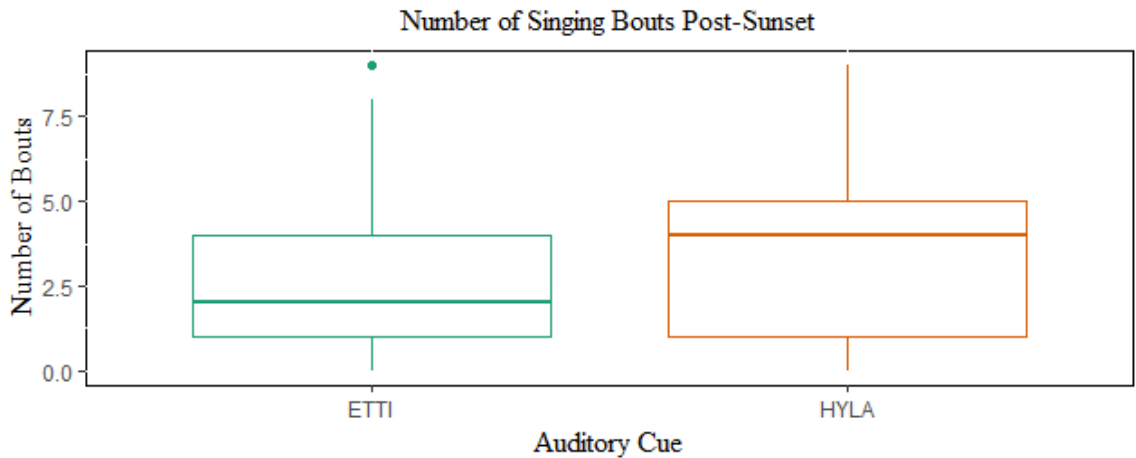
b.



**Figure 6a.** Results of a paired t-test depicting total number of songs recorded when exposed to respective treatment: titmouse (ETTI) *seet* alarm calls or gray treefrog (HYLA) chorus. On average, Veeries sang 6% more songs in their control trial than their titmouse trials ( $103.60 \pm 0.52$  vs.  $91.72 \pm 0.64$ ); however, this difference was not significant ( $t_{24}=1.485$ ,  $P=0.15$ ). **6b.** Average number of Veery songs sung over time, post-sunset, by respective treatment: gray treefrog (HYLA) and titmouse (ETTI) *seet* alarm calls.



**Figure 7. Results of a paired t-test corresponding to the timing of last song for each respective treatment: gray treefrog (HYLA) and titmouse (ETTI) seet alarm calls. Veeries sang their last song 3 minutes later, on average, in control vs. titmouse trials ( $t_{24}=1.724$ ,  $P=0.098$ ).**



**Figure 8. Results of a paired t-test depiction the average total number of songs within Veery singing bouts, respective of treatment: gray treefrog (HYLA) and titmouse (ETTI) seet alarm calls ( $t_{24}= 0.983$ ,  $P=0.335$ ).**



### **Chapter III**

#### **Conclusion**

Avian dusk chorus is an underrepresented facet of avian communication, with nocturnal communication currently representing only 4% of all published literature pertaining to avian communication (La 2010). The dusk chorusing behavior of the Veery has previously been explored. Belinsky et al. (2012) determined that male Veeries experience significantly more vocal masking at dawn chorus than at dusk chorus, thus suggesting the importance of dusk as an opportune time to vocalize to attract a mate. Schmidt and Belinsky (2013) further explored the effects of a direct predator cue, Barred Owl calls, on the dusk chorusing behavior of male Veeries. This study determined that Veeries viewed owl vocalizations, a direct cue, as a credible threat of predation, thereby modifying their dusk chorusing behavior (Schmidt and Belinsky 2013).

My research sought to expand upon this foundation of research into male Veery dusk chorusing by assessing the effect of an indirect cue of predation, alarm calls (seet) of the titmouse, a highly vocal, nuclear species. I analyzed Veery dusk chorusing behavior-- specifically song rate and singing duration-- to establish an assessment of threat in the environment in diminishing light levels post-sunset. My results suggest that titmouse alarm calls did not signify a credible predatory threat from the perspective of the male Veery at dusk. However, trends in favor of the importance of indirect cues were loosely observed.

To reduce uncertainty, organisms acquire information regarding the state of their environment (Dall et al. 2005). Precedent exists to support the combined use of direct and indirect cues to make a more informed decision regarding the spatial environment and

threat of predation (Nersesian et al. 2012). Expanding research into other dusk chorusing behaviors, such as perch level, modification of song amplitude, and correlation to breeding/nest status, will complement what we already know of the Veery dusk chorus. When assessing behavioral effects, it seems prudent to look at the combined effects both indirect and direct predatory cues have on Veery dusk chorusing behavior.

This study represented one approach to assess Veery eavesdropping behavior and the use of indirect predatory cues. My research adds to the current understanding of dusk vocal behavior in the Veery. This study, in small part, seeks to rectify the scarcity of dusk chorus literature in the field of animal communication. It is my hope that my research can be used as a stepping-stone to inspire additional examination into Veery dusk chorusing behaviors.

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