EXPERIMENTAL COUNTER-CALLING TO DETERMINE THE FUNCTION OF CALLS FOR VEERIES (*CATHARUS FUSCESCENS)*

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Abstract. The Veery (*Catharus fuscescens*) is a North American thrush with a large and unique repertoire of calls that researchers believe may be used for both inter- and intraspecific communication. To learn more about how veeries use these calls for communication between individuals, I conducted an experimental counter-calling, type-matching playback study in which I was interested to see if the birds would call back a response of the same type to a speaker-played call sequence. I used four of the most common call types (veer, tunnel, squeeze, and whisper) to conduct a playback experiment in which I played these calls to veeries and recorded their vocal responses. My main questions to be explored in this study were (1) Do veeries type-match their calls with a given stimulus? (2) Do veeries show individual use preferences for one call type over another? (3) Does a stimulus whisper call prompt a song response? I analysed these recordings to extract the response data and determined that there is a statistically significant difference between observed and expected data, suggesting that veeries do not use their calls randomly. I also examined the data for patterns, determining that veeries use veer and tunnel calls more often than other types, and that within the four call types, the most call type-matching occurs in veer and tunnel call types. I also examined the song response to whisper calls, inferring that a bird that responds to a whisper call with song frequently may be more aggressive. My initial foray into veery call research is a starting point for other research to determine the function of the various veery calls. The data that I produced may lead to further understanding of veeries and their methods of communication through vocalizations.

INTRODUCTION

Communication is the transfer of information between two individuals of the same or different species, and can occur through many different modes; visual, auditory, olfactory, and physical. All animals employ some means of communication through which they interact with their environment and living things around them. Some animals may use physical interactions when greeting their mate, or leave scent markers to delineate territory. Others may use visual displays such as baring teeth or flicking wingtips (Dilger 1956). However, the one method of communication that most animal species use frequently is auditory communications through vocalizations.

Vocalizations come in many different forms: e.g., the roaring of a lion at dusk to the chirping of young nestlings to let a parent know they are hungry. In all cases, one animal is sending out a message to be heard and understood by a single or multiple listeners. In vocal communications, there is usually information being conveyed by the sounds, and there is a response to the vocalization. In avian species, the most common forms of auditory communication are songs and calls. These vocalizations have distinctly different functions. Calls are simple vocalizations used by both males and females to communicate information such as location, danger, food availability, and nestling needs. Songs are complex vocalizations, usually learned and used primarily by the males of the species for territory maintenance and attracting mates (Marler 1967).

In this study, I focused on the Veery (*Catharus fuscescens*), a passerine songbird that breeds in temperate forests in North America. One of the earliest researchers of the veery, M. Dilger (1956), described vocalizations emitted by the bird and speculated as to their function and purpose in hostile interactions. He mentioned two of the calls emitted by the veery, but did not go into great detail about the frequency or structure of those calls. D.E. Samuel (1972) provided more structural information about the various calls of the veery, as well as spectrograms for a few of the calls and descriptive details of the sound. He also provided speculation as to the aggressive use of these calls in hostile situations, using anecdotal evidence to provide functions to the behaviours he observed. However, Samuel spent most of his time on the songs and conducted little research looking at veery call repertoires.

One area of vocal communication that is well researched in some bird species is song type-matching, which is when two birds respond to each other's songs so that the songs begin match one another. Several songbird species have been shown to have song "repertoires", which means that they have a variable number of different songs to use in territorial and breeding displays (Beecher et al. 1996). Individuals may share the very similar songs, or they may have a slightly different songs but with the same elements, or they may not have any shared songs. When individuals counter-sing with each other they have three potential options; to "type-match" the song of their opponent, to choose a similar song type from their repertoire (repertoire match), or to respond with a completely different song that the other bird does not share; unshared song (Burt et al. 2002). There are varying degrees of dominance that these different options display, however research has indicated that type-matching is a way for individuals to identify themselves to strangers they do not recognize and maintain their territories (Stoddard et al. 1992). Beecher's 1996 study on repertoire and song type-matching hypothesized that song type-matching is a more directed and intentional form of response than repertoire matching to a stimulus song, and therefore could be a more aggressive response type. Call type-matching is similar in that the responding bird can either choose the same call type or a different call type that both birds share. However, Heckscher (2007) provided a different potential reason for call-matching, hypothesizing that calls travel across physical distance better than song, maintaining their structure and identification, suggesting that birds may replace the need for a physical approach with a vocal response.

One type of veery vocalization that seems to be used very differently to most types of calls is the whisper call. Belinsky and Schmidt (2015) recorded and compared the variations in whisper calls and looked at possible functions of these calls. They determined that veeries sometimes use many different types of whisper calls to introduce their songs, where whisper calls are added in advance of the song in agonistic confrontations. This suggests that whisper calls may function in aggressive interactions.

In this study, I examined whether veeries have non-random vocalization responses to call stimuli. Specifically, I asked: (1) Do veeries type-match their calls with a given stimulus? (2) Do veeries show individual use preferences for one call type over another? (3) Does a stimulus whisper call prompt a song response? For this particular study, I focused on four of the main veery call types: veer (A), tunnel (B), squeeze (C) and whisper (D). This study is important because it will give future researchers greater insight into veery calls, as well as some basic understanding of which calls are most common and the possible functions of these calls.

METHODS

This study was conducted in deciduous forests at the Cary Institute of Ecosystem Studies in Dutchess County, New York, U.S.A. Playback trials were conducted in June and July 2015 on the study species Veery, sampled in various locations on the Cary Institute property.

Construction of Playback Exemplar Tracks

For the playback exemplar tracks, I used four types of calls that I mixed together at random, specifically (A) the veer call, (B) the tunnel call, (C) the squeeze call, and (D) the whisper call. I had four different exemplar stimulus sound files for my experiment, two of which were at set intervals of 2 seconds between each call, and two that had random intervals between each call. I found and isolated 3 high quality examples of each of the four call types. Next, I created a random number sequence in Excel between 0.01 and 0.99, which I used to decide the order of the calls in the Exemplar track. I translated the random numbers into the four calls by separating the random numbers into these groupings: A (veer call) was between 0.00 and 0.24, B (tunnel call) was between 0.25 and 0.49, C (squeeze call) was between 0.50 and 0.74, and D (whisper call) was between 0.75 and 0.99. Third, I determined which of the three examples I would use for each call by creating another random number sequence between 1 and 3, which corresponded to the name of each example call for each call type. Fourth, using another random number sequence I generated the time intervals to place between each call. Using numbers between 1 and 3 seconds by 0.5-second intervals. I rounded my raw 3 decimal point values using the following method; I rounded numbers ending in 0.03 up to nearest the 0.5 value, and numbers ending in 0.07 down to the nearest 0.5 value. Using Raven software (Cornell Laboratory of Ornithology, Ithaca, New York, U.S.A.), I cut and pasted the sound files into an exemplar track exactly 10 minutes in length with intervals included. I created an additional sound file with a frog sound at the beginning, followed by five minutes of silence, and another track with just a frog sound. Finally, after adding all four of the completed exemplar tracks and the two frog tracks to iTunes, I created four playlists. Each playlist had a frog at the beginning, silence, then the exemplar track (repeated twice), then a frog sound at the end. I did this for all four exemplar tracks, ending up with 20 minutes of stimulus calling for each trial.

Counter-calling Playback Experiment

The experimental sampling in this study was conducted within the property of the Cary Institute of Ecosystem Studies, New York, USA. 12 out of the 15 playback trials were conducted in the early morning between the hours of 0600 and 1000, with the remaining 3 conducted in the early evening between the hours of 1500 and 1800. To ensure that birds were not sampled more than once I spaced out my sample sites by about ≥200m, a larger area than the average boundary of a veeries' territory, to avoid overlap. When conducting the trials, I attached a small, cordless speaker with an iPod to a tree about 1m off the ground. I then moved about 25m away from the speakers, crouched down and remained still, with only my arm moving to point the speaker in the direction of any veeries. I used a shotgun microphone with windshield to record veery response, and a portable hand-held recorder. The latter was used to narrate any observed behaviour of the veeries that came into range of the trial. After finishing my data collection, I analysed all of the recordings using Raven. I listened to all of the trials, and marked all response calls made by veeries, I then input all of these responses (including no response) into a table of values before combining all data and performing statistical tests.

Statistical Analyses

I performed a chi-squared test of independence to test for significance in my hypothesis of non-random responses to stimulus calls. I first compiled all my results from the various trials and calculated a table of expected values if the null hypothesis were true. Once I had my observed data and expected data, I ran a chi-squared test. I predicted that (1) veeries would show statistical significance of non-random responses by replying to the stimulus call with the same call to show type-matching, (2) some veeries would use one call type more than the others types when responding to the stimulus, and (3) a whisper call on the stimulus track would result in a song response from the veeries.

RESULTS

Observed vs. Expected Data

Before I began my statistical analysis, I compiled all of my data into an Observed Calls table (Table 1) that showed the proportion of each stimulus, response call pairing out of the total collected data. I had a sample size of 15 individual veeries that were sampled which yielded a total 1,070 total response calls out of a total of 6,516 stimulus calls in all of the trials. I calculated a table of Expected Calls table (Table 2), which showed the proportion of each stimulus, response call pairing that one would expect if the null hypothesis of no purpose to veery calls were accepted. I then used these two tables to construct a Chi-squared table (Table 3) from which I found that there was a statistically significant (p-value<0.025) difference between the observed and expected data.

Call Matching

I calculated the average percent of type matching for each call type across all the 15 sample veeries and found that there was an average of 15.5% veer-matching, 9.8% tunnel-matching, 3.4% squeeze-matching, and 2.1% whisper-matching (Figure 2).

Individual Preferences

I calculated the percentage of each call type response for each of the 15 veeries sampled in the study. I calculated the call type out of the total of all four major call types for each individual before calculating the average; veer was the response call 50.3% of the time, tunnel 28.9%, squeeze 9.8%, and whisper 11.1% (Figure 3).

Song Response to Stimulus Whisper

I calculated the percentage of song response to stimulus whisper calls and the average of 10.5% of all stimulus whisper calls returning a song response (Figure 4). There was variability among the all the sampled veeries, however no statistical test was run for this variability.

DISCUSSION

The data supported my hypothesis that veeries do not use calls randomly and that their calls do have some function. I had three main research questions: (1) Do veeries type-match their calls with a given stimulus? (2) Do veeries show individual use preferences for one call type over another? (3) Does a stimulus whisper call prompt a song response?

Studies have shown in the past that veeries use some calls more often than others in agonistic interactions (Samuel 1972), and that some calls are used in agonistic interactions in combination with song (Belinsky et al. 2015). Specifically, Belinsky et al. (2015) pioneered research on the whisper call in veeries, noting that these calls were used more often in agonistic interactions than during normal singing. Prior to this research, there has only been brief mention and descriptions of veery calls and behavioural observations (Dilger 1956; Samuel 1972; Hecksher 2007), and very little research has examined the function of the various veery calls.

In my counter-calling experiment, I gathered veery responses to stimulus calls in order to see how veeries used their call repertoire when counter-calling. The data collected during this experiment did suggest that veeries respond with non-random calls to a stimulus call and this indicates that there may be some function to their calling patterns. While this experiment did not focus on determining the functions of individual call types, it did pave the way for future research to explore individual call function. Veeries used more veer and tunnel response than squeeze and whisper, "veering" in response about 50.3% of the time, using tunnel calls 28.9% of the time, squeeze 9.8%, and whisper 11.1% (Figure 3). The difference in the frequency of use of various call types indicates that there may be some function to the use of a response of a certain call type. Veer calls were used the most often, and may therefore be a general call used to communicate basic information about food or location. The squeeze and whisper calls were used far less often, and so they may have a more specific purpose to their use, such as indicating situations of danger or agonistic situations (Samuel 1972).

Call type-matching was also of interest in the design and execution of this experiment. Type-matching in some species has been seen as a stronger response to territory breaches than non-matching, and the use of type-matching may show a dominant response (Beecher 1996). On average, veeries type-matched veer stimulus 15.5% of the time, tunnel 9.8% of the time, 3.4% squeeze, and 2.1% whisper (Figure 2). While there was weak statistical support for call type-matching, this groundwork could give future researchers a starting point. To gain a better understanding of call matching in future studies, a sample size great than 15 should be gathered.

Some veeries show individual differences in that one bird might use one call frequently, while other birds used all four call types with similar frequency. From anecdotal evidence witnessed during the trials, I could see that the way individual birds reacted to the stimulus calls differed. Some birds took a long time to appear near the speaker and then flew from tree to tree in the vicinity, calling very little, before leaving the area. Others came to investigate immediately after the trial began and then responded for most of the 20 minutes of the trial. Some birds stayed on a single branch of a tree for the entire time they were there, calling frequently, while others flew around a lot, from tree branch to a log on the ground and responded infrequently. From this observed behaviour and the variation in the collected data, we can infer that veeries have differing levels of aggression and dominance, possibly due to the proximity of their nest site or their stage in the breeding season.

I also saw individual variation and preference when I examined my data for whisper calls and song response. Belinsky et. al. (2015) inferred that whisper calls are used in agonistic interactions more often than when in normal, unprovoked interactions. The experiment showed that different veeries responded to whisper calls with song at varying regularity. Some veeries used song to respond to whisper stimulus nearly 20% of the time, while others would respond <5% of the time with song. On average, a whisper stimulus call resulted in song response 10.5% of the time. This could be a way of showing how aggressive or dominant a certain male veery might be when defending his territory and rebuffing an intruder.

The results of the playback experiment lead to speculation about the possible functions of the various calls used by the veery. While there is little statistical significance to the conclusions made using the data, there is anecdotal evidence from the data and observed behavioural data that could lead to further conclusions about call use and function. To gain greater insight into the purpose of veery calls and their use in counter-calling situations this experiment should be repeated with a larger sample size and over a greater area of veery habitat. While the data cannot be used to make definitive claims about call function, this experiment was a key step to understanding veery behaviour.

Research on bird calls in the past has generally been underappreciated and understudied in comparison to song, possibly due to the vocal complexity and interesting structural features associated with song. However, as song bird vocalizations are studied, research to understand call behaviour is becoming more common. While some birds have a relatively limited call repertoire, veeries are the ideal species to study due to their large call repertoire and the variety of vocalizations they make in different situations. This species is also declining, and therefore it is necessary to understand their methods of communication in relation to breeding and territory use to successfully create conservation plans.

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APPENDIX

TABLE 1. The proportion of each observed call type collected from a sample size of 15 veeries and 1,070 total response calls.

		Observed Stimulus Calls (proportion)				**TOTAL**
		Veer	Tunnel	Squeeze	Whisper	
Response Calls	Veer	0.155	0.121	0.098	0.108	**0.43**
	Tunnel	0.073	0.098	0.074	0.055	**0.3**
	Squeeze	0.031	0.036	0.034	0.021	**0.121**
	Whisper	0.017	0.036	0.023	0.021	**0.096**
Total:		**0.276**	**0.291**	**0.229**	**0.205**	
			Total:	**1**		

TABLE 2. The proportion of each expected call type assuming that we accept the null hypothesis of no purpose to veery calls.

		Expected Stimulus Calls (proportion)				**TOTAL**
		Veer	Tunnel	Squeeze	Whisper	
Response Calls	Veer	0.133	0.14	0.111	0.099	**0.483**
	Tunnel	0.083	0.087	0.069	0.061	**0.3**
	Squeeze	0.033	0.035	0.028	0.025	**0.121**
	Whisper	0.027	0.028	0.022	0.02	**0.096**
Total:		**0.276**	**0.291**	**0.229**	**0.205**	
			Total:	**1**		

TABLE 3. The table of Chi-squared values calculated from the Observed and Expected stimulus calls (Figure 1 & Figure 2).

		CHI^2 Table of Values				**TOTAL**
		Veer	Tunnel	Squeeze	Whisper	
Response Calls	Veer	3.862	2.734	1.151	0.980	**8.727**
	Tunnel	1.245	1.467	0.412	0.683	**3.808**
	Squeeze	0.185	0.007	1.414	0.734	**2.340**
	Whisper	3.806	2.171	0.085	0.040	**6.103**
Total:		**9.100**	**6.379**	**3.062**	**2.438**	
			X2 =	**20.978**		

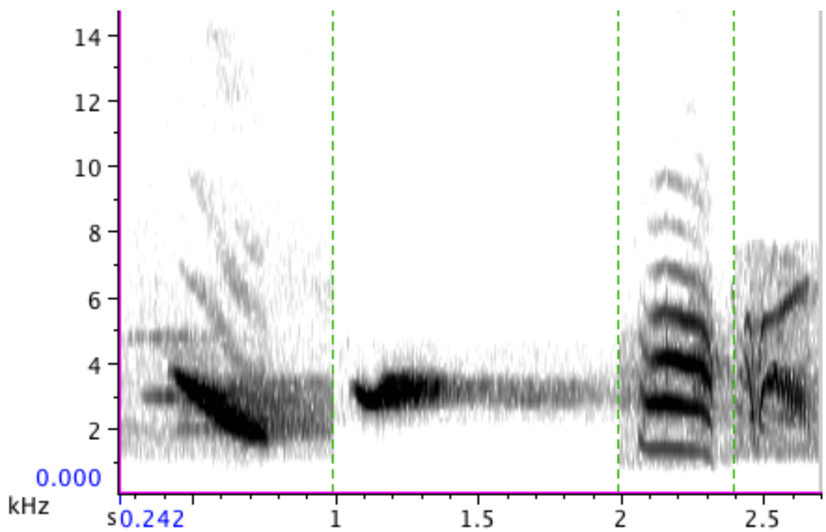

FIGURE 1. Sonogram images of the four call types used in this study. From left to right: veer, tunnel, squeeze, and whisper. These images were produced with Raven Software from previous call recordings taken at the Cary Institute of Ecosystem Studies.

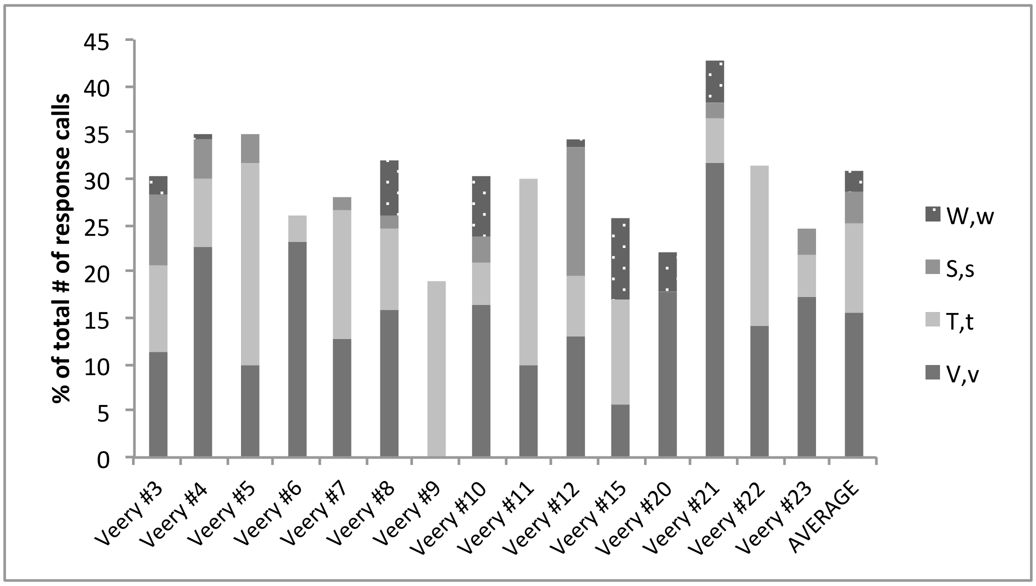

FIGURE 2. All the sample veeries and the percentage of type matching they used for each call-type. The legend tells that W,w represents the Whisper stimulus, whisper response, and the same is true for the other call types. The last column on the right shows the average percentage of type matching for each call type.

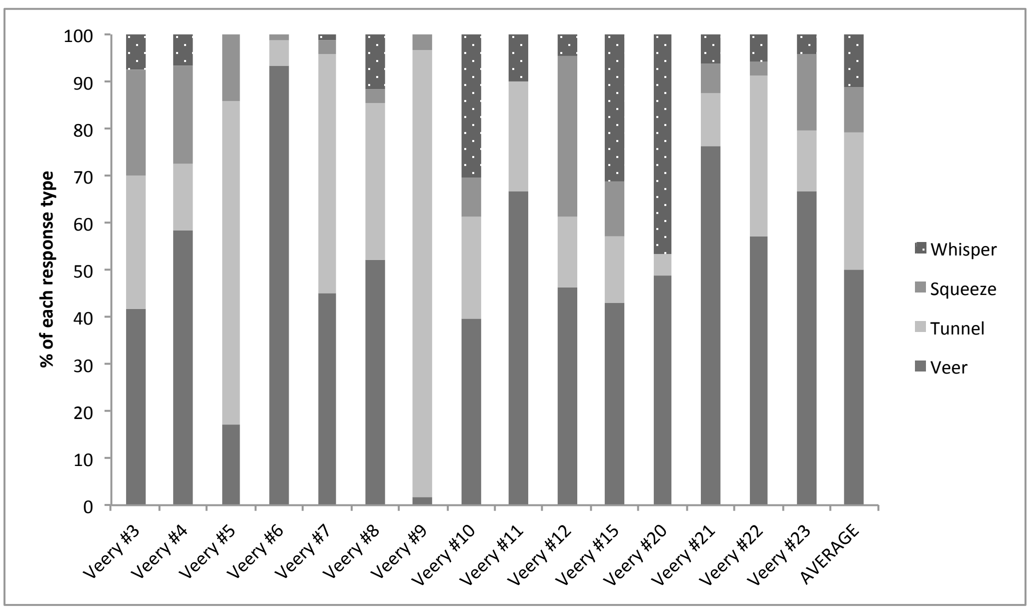

FIGURE 3. The percent call type response for each of the 15 veeries sampled in the study. Each individual had different call preferences and there is variability among individuals. The last column shows the average % of call responses among all veeries in the sample.

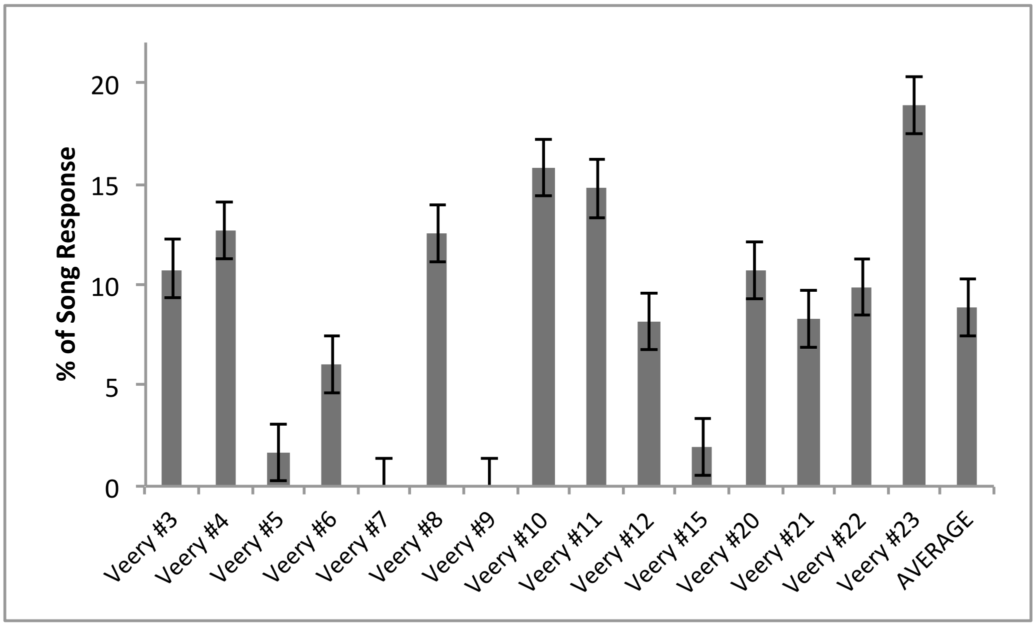

FIGURE 4. Visual representation of the percentage of song response to stimulus whisper calls with error bars. There is some variability between different veeries, however there was an average of 10.5% of all whisper stimulus calls returning a song response.