

INVESTIGATING VOCAL PLASTICITY IN SONG SPARROWS (MELOSPIZIA  
MELODIA) AS A MECHANISM TO AVOID MASKING NOISE IN URBAN  
ENVIRONMENTS

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partial fulfillment of the requirements for the degree of Master of Biology.

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## TABLE OF CONTENTS

ACKNOWLEDGEMENTS .....	ii
LIST OF TABLES .....	iv
LIST OF FIGURES .....	v
ABSTRACT.....	vi
INTRODUCTION .....	1
METHODS .....	8
<b>Study Area:</b> .....	8
<b>Playback Experiment:</b> .....	9
<b>Sound Analysis:</b> .....	12
<b>Behavioral Analysis:</b> .....	13
<b>Statistical Analysis:</b> .....	14
RESULTS .....	17
<b>Minimum frequency:</b> .....	17
<b>Maximum Frequency:</b> .....	19
<b>Frequency bandwidth:</b> .....	20
<b>Song duration:</b> .....	21
<b>Ambient Noise:</b> .....	23
<b>Behavioral Response to Treatment:</b> .....	23
<b>Song Type Change:</b> .....	24
<b>Immediate Minimum Frequency Change Between <i>Before</i> and <i>During</i> Songs:</b> .....	24
DISCUSSION.....	29
<b>Effects of Ambient Noise</b> .....	30
<b>Song Duration</b> .....	32
<b>Behavioral Response</b> .....	33
<b>Immediate Vocal Response</b> .....	34
<b>Trade-Offs: Detectability</b> .....	36
<b>Trade-off: Female Perception</b> .....	38
<b>Trade-off: Male Perception</b> .....	40
<b>Conclusion</b> .....	42
REFERENCES .....	46

LIST OF TABLES

Table 1. Summary of *a posteriori* comparisons for low frequency.....17  
Table 2. Summary of *a posteriori* comparisons for high frequency.....19  
Table 3. Summary of *a posteriori* comparisons for bandwidth.....20  
Table 4. Summary of *a posteriori* comparisons for song length .....22  
Table 5. Immediate behavioral response to treatment noise.....24  
Table 6. Observed occurrence of the first song type change .....24  
Table 7. Immediate change in low frequency between treatments.....25  
Table 8. Strategies to increase minimum frequency .....26

## LIST OF FIGURES

Figure 1. Waveform and sonograms playback stimuli example .....	15
Figure 2. Sonograms of playback stimuli example .....	16
Figure 3a. Low frequency box-and-whisker plot.....	18
Figure 3b. Individual males' change in minimum frequency .....	18
Figure 4. High frequency box-and-whisker plot.....	19
Figure 5. Bandwidth box-and-whisker plot .....	21
Figure 6. Song length box-and-whisker plot.....	22
Figure 7. Ambient noise and minimum frequency correlation .....	23
Figure 8. Changed song type low frequency box-and-whisker plot .....	27
Figure 9. Same song type low frequency box-and-whisker plot .....	28

## ABSTRACT

### INVESTIGATING VOCAL PLASTICITY IN SONG SPARROWS (*MELOSPIZIA MELODIA*) AS A MECHANISM TO AVOID MASKING NOISE IN URBAN ENVIRONMENTS

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Animals that successfully colonize urban areas must be tolerant of anthropogenic disturbance including noise. Chronic anthropogenic noise may be difficult for animals that use acoustic signals to overcome if it disrupts communication. Most anthropogenic noise is below 1.5 kHz but can spread into higher frequency ranges overlapping with acoustic signals used in animal communication. Songbird species are common urban colonizers that use acoustic signals that are critical for reproductive success. To avoid the masking effects of loud anthropogenic noise, many songbird species that occupy noisy urban areas have been observed to use songs and calls with higher minimum frequencies compared to rural counterparts. Precise mechanisms for the observed frequency shifts are not well understood but can be accomplished through natural selection, cultural selection, and vocal plasticity. In this study, I test whether male song sparrows (*Melospiza melodia*) can use vocal plasticity to avoid masking noise when exposed to experimental noise. Song sparrows that occupy noisy urban habitats are observed to have songs with an increased minimum frequency when compared to song sparrows in quieter areas. However, it is unclear how urban song sparrows can increase minimum frequency because song sparrows do not naturally use frequency shifting during singing but rather use a repertoire of crystallized songs with fixed frequency characteristics. I tested the response of 46 males on the

campus of Western Carolina University with two experimental noise treatments. Noise treatments differ in whether the frequency of the noise overlaps with song sparrow songs (2.5-4.0 kHz, masking) or does not overlap (0.5-1.5 kHz, non-masking). All males were exposed to both treatments but on different days. During trials, I recorded singing before, during and after each treatment. I used Raven Pro to measure minimum and maximum frequency, frequency bandwidth, and song length for up to 10 songs from each period of the trials and calculated means to use in statistical analysis. I found an increase in minimum frequency for songs during the masking noise but not during non-masking noise. There was no difference in maximum frequency between treatments, thus bandwidth was significantly narrower during the masking treatment. I found no significant difference in how males changed perches, song types or variants in response to either noise treatment. However, I found that when males switched to a new song type or variant when the noise started, that they switched to a type or variant that significantly increased the minimum frequency during masking noise. My results suggest that male song sparrows use vocal plasticity to immediately avoid the negative effects of masking noise. My results do not rule out the possibility of cultural or natural selection on frequency shifts observed in urban song sparrows. However, vocal plasticity is a flexible strategy that may allow adopters to both increase detectability in masking noise but also minimize the potential negative impacts of frequency adjustments on song function. Future studies should focus on how vocal plasticity in song sparrows impacts detectability and discrimination of song in anthropogenic noise.

## INTRODUCTION

Urbanization can pose new challenges on wildlife such as increased intraspecific competition, habitat destruction, and introduction of invasive species (Bruitjes & Radford, 2013; Brunton, Clemente, & Burnett, 2020; Crowe, 1979; Shochat, Warren, Faeth, McIntyre, & Hope, 2006). However, some species have successfully adapted to urban landscapes and take advantage of access to resources such as more predictable food sources, decreased interspecific competition, and lower levels of predation (Bókony, Seress, Nagy, Lendvai, & Liker, 2012; McKinney, 2008; Shochat, 2004). Successful adaptation of urbanized habitat requires tolerance of anthropogenic disturbance (Barber, Crooks, & Fristrup, 2010; Francis, Ortega, & Cruz, 2011). However, noise is a feature of anthropogenic disturbance that can be difficult to overcome for animals that depend on acoustic communication. Most of the energy in anthropogenic noise is below 1400 Hz, however, it can mask signals of higher frequencies because of upwards spread of energy at increasing amplitude (Lohr, Wright, & Dooling, 2003). At these frequencies, anthropogenic noise will likely overlap with acoustic signals used in animal communication (Brumm & Slabbekoorn, 2005; Hu & Cardoso, 2009, 2010; Kirsten M. Parris & Schneider, 2009; Patricelli & Blickley, 2006; Potvin, Parris, & Mulder, 2011; Warren, Katti, Ermann, & Brazel, 2006). Animals that colonize urban areas often also rely on acoustic signals for communication during mating (Montague, Danek-Gontard, & Kunc, 2013), in parent-offspring contexts (McIntyre, Leonard, & Horn, 2014), and to alert conspecifics to impending threats (McMullen, Schmidt, & Kunc, 2014; Shannon et al., 2016a). If the frequencies in acoustic signals overlap with those in the noise, all or part of the acoustic signal can be masked, which disrupts communication (Lohr et al., 2003; Montague et al., 2013; Pohl, Leadbeater, Slabbekoorn, Klump, & Langemann, 2012). Thus, the presence of noise in urbanized habitats



that interferes with acoustic communication can negatively impact survival and reproduction for urban colonizers if they cannot overcome the challenge of communicating in a noisy environment (Damsky & Gall, 2017; Kight & Swaddle, 2011). In this study, I investigate the impacts of urban noise on acoustic signals used in mating and territory defense.

Acoustic signals in animals are commonly used in the context of mating (Andersson & Iwasa, 1996; Searcy & Nowicki, 2010). Natural and sexual selection favors acoustic signals used in mating that are effective even in the presence of noise (Wiley, 2006) and thus we expect urban noise to influence the structure or form of acoustic signals. Animals that use acoustic communication in mating have adapted to urban environments by modifying acoustic signals to avoid or reduce the negative effects of anthropogenic noise on communication using a variety of strategies (Brumm, 2006; Hu & Cardoso, 2010; LaZerte, Slabbekoorn, & Otter, 2017; Slabbekoorn & den Boer-Visser, 2006). For example, frogs have been observed to increase the frequency of their calls in an area with loud traffic noise to avoid the lower frequencies of masking noise (Kristen M. Parris, Velik-Lord, & North, 2009). Another strategy is to completely avoid masking from urban noise as shown by European robins (*Erithacus rubecula*), who were observed to sing in the evening, to avoid loud anthropogenic noise during the daytime (Fuller, Warren, & Gaston, 2007). Nightingales (*Luscinia megarhynchos*), employed yet another strategy, increasing the amplitude of their song to be heard above anthropogenic noise (Brumm & Todt, 2002).

A common strategy utilized by songbirds living in noisy urban areas is to raise/change the frequencies of their songs or parts of song to avoid low frequency masking noise (Halfwerk & Slabbekoorn, 2009; Hu & Cardoso, 2009; McMullen et al., 2014; Kristen M. Parris & Schneider, 2009; Rundstrom & Creanza, 2021). Birds that live in noisy areas will improve

signal reception by producing songs with higher minimum frequencies when compared to birds living in quieter areas (Brumm, 2006; Hu & Cardoso, 2010; Slabbekoorn & den Boer-Visser, 2006; Wood & Yezerinac, 2006). Ideally, by singing songs with higher minimum frequencies, songbirds will avoid the negative effects of masking (Dowling, Luther, & Marra, 2012; Kirsten M. Parris & Schneider, 2009; Slabbekoorn & Peet, 2003). Several different studies across passerine species have suggested that songbirds who colonize urban areas avoid the masking effects of noise by producing songs with higher minimum frequency (Horn, Leonard, Ratcliffe, Shackleton, & Weisman, 1992; Pohl et al., 2012; Potvin et al., 2011; Slabbekoorn, 2018; Wood & Yezerinac, 2006). Use of songs that naturally have higher frequency may explain the success of certain species of passerines in urbanized environments (Slabbekoorn & den Boer-Visser, 2006). However, in cases where urban colonizers do not have naturally high frequency songs, there is evidence of minimum frequency shifts in response to noisy urban areas in order to avoid masking (Bermúdez-Cuamatzin, Ríos-Chelén, Gil, & Garcia, 2011a; Halfwerk & Slabbekoorn, 2009; Hu & Cardoso, 2010). Thus, passerines in urban habitats may be able to change or adjust acoustic features of song in response to anthropogenic noise as a means to avoid the negative effects of masking (Kirsten M. Parris & Schneider, 2009; Potvin & Parris, 2012). While many studies have investigated the role of frequency shifts in bird song to avoid low frequency masking, fewer studies have addressed the mechanisms songbirds use to accomplish frequency shifts. In this study, I investigate a potential mechanism to explain the observation of frequency shifted songs in noise.

There are three primary mechanisms by which songbirds can accomplish a shift in frequency to avoid being masked in noise. First, one possible mechanism to explain frequency shifts in urban songbirds is that natural selection favors individuals with songs that have higher

minimum frequencies (Hu & Cardoso, 2010; Mikula et al., 2021; Potvin et al., 2011). As an area becomes more urbanized and is impacted by low frequency urban noise, males with a higher minimum frequency songs would be favored because they would be better able to defend territories and attract mates (Perillo et al., 2017). Hence, minimum frequency of song will increase over time resulting in higher minimum frequencies of song in populations of songbirds that occupy noisy, urban areas compared to populations in quieter rural areas.

A second possibility to explain the occurrence of frequency shifted songs in noisy urban areas is through cultural selection. Many songbirds learn songs from other adults as juveniles, during an early sensitive phase for song learning. Juveniles could have biases for learning songs with higher frequencies because higher frequencies would be easier to hear in noisy environments (Moseley et al., 2018; Nordby, Campbell, & Beecher, 1999). Thus, if juveniles are more likely to learn songs with a higher minimum frequency in a loud noisy urban habitat, then over time the population as a whole will have a repertoire of songs with higher minimum frequencies.

Finally, a third possibility is that songbirds use vocal plasticity to alter song frequency as an immediate response to varying levels of noise (Hu & Cardoso, 2010; Leonardo & Konishi, 1999; Kirsten M. Parris & McCarthy, 2013). Male black-capped chickadees (*Poecile atricapillus*) have been shown to use higher peak frequency songs in areas with higher ambient noise (Proppe et al., 2012). Black-capped chickadees commonly use frequency shifting during singing bouts as a natural feature of their singing behavior (Horn et al., 1992; Lazerte, Slabbekoorn, & Otter, 2016). A recent study showed that when male black-capped chickadees were exposed to masking noise, they exhibited immediate vocal plasticity by shifting the frequency in their songs to avoid overlapping with the masking noise (Goodwin & Podos, 2013).

However, it is unclear if songbirds that do not exhibit such frequency shifting as a part of normal song production, are capable of immediate frequency shifts in response to noise.

Frequency shifted songs are observed in many urban populations of species whose songs become crystallized, and in which immediate frequency shifting is not a natural part of singing behavior. Many passerines have crystallized songs, meaning they learn their repertoire of songs as juveniles and do not add any new songs as they age. Though crystallized songs do have variants within the repertoire, where part of the song might be different, but it is still recognizable as the same song type. Songs in species with crystallized song are unlikely to be able to drastically alter acoustic features of the song such as increasing the minimum frequency of notes within the song. However, songbirds with crystallized repertoire of songs may be able to increase the minimum frequency of their song by changing to a different song type with a higher frequency or singing a variant of the same song type with a higher frequency. In those species, it is unknown whether they are capable of immediate frequency shifts or if the observed frequency shifts between urban populations and rural populations are the result of natural or cultural selection over time. Also, while many studies have indicated that songbirds use vocal plasticity by increasing the minimum frequency of their song in the presence of anthropogenic noise (Bermúdez-Cuamatzin, Ríos-Chelén, Gil, & Garcia, 2011b; Gross, Pasinelli, & Kunc, 2010; Montague et al., 2013; Slabbekoorn & den Boer-Visser, 2006; Verzijden, Ripmeester, Ohms, Snelderwaard, & Slabbekoorn, 2010a), alternative strategies may also be effective (Gentry et al., 2017). Of course, these three mechanisms are not mutually exclusive, but could be working in tandem to allow for efficient acoustic communication in some songbird species.

In this study, I will examine the experimental effects of noise on frequency characteristics of song in song sparrows, a species that uses a repertoire of crystallized songs in which frequency

shifting is not a normal part of singing behavior. These songs are learned as juveniles and crystalized before the first breeding season (Akçay & Beecher, 2020; Nordby, Campbell, & Beecher, 2002). Wood and Yezerinac (2006) found that increased noise was correlated with higher minimum frequency of songs, and with songs having more energy in higher frequencies than lower frequencies. However, it remains unknown whether higher frequency songs observed in noisy areas in this species are the result of immediate shifts in frequency, switches to different song types with higher minimum frequencies, or long-term adjustments via natural/cultural selection resulting in frequency shifted songs in males in the population as a whole over time. Song sparrows are an excellent species with which to address the potential mechanisms for explaining songs with increased frequencies in response to anthropogenic noise as a result of immediate vocal plasticity or long-term adjustments of the frequency. Song sparrows are successful colonizers of urban habitats (Foltz et al., 2015; Unfried, Hauser, & Marzluff, 2013; Whittaker & Marzluff, 2012) and have been observed to use higher minimum frequency songs in noisy urban areas when compared song sparrows living in quieter rural areas (Wood & Yezerinac, 2006). When considering vocal plasticity as a potential mechanism for shifts in song frequency, it is important to look at the possibility that song sparrows could be switching the song type in the presence of noise as an alternate means to avoid masking. Therefore, if song sparrows are able to exhibit vocal plasticity, they may do this either by responding to noise and immediately changing the frequency of a current song type, or by transitioning to a new song type that has a higher minimum frequency. In this study, I used experimental playback of noise to determine whether song sparrows can shift the frequency of crystalized song and/or use song type switches (with songs having higher minimum frequencies) to avoid masking. The results of this study will provide insight into potential mechanisms for understanding how urban colonizing

songbirds can change their songs to accommodate urban noise. If song sparrows are capable of immediate vocal plasticity in response to noise, I should find that males can shift the minimum frequency of their current song to be higher during playback of masking noise. If song sparrows use the strategy of switching to another song type, I should find that males switch to a different song type with higher minimum frequency in response to noise playback. In either case, there should be an immediate change in singing behavior suggesting that the male song sparrow has recognized the masking interference of its song and made an adaptive choice to alter its current song to evade masking and to increase audibility of its song. If, however, I find that there is no change in singing behavior during playback of noise, either in shifts of the frequency of a current song, or in a switch to a song type that has a higher minimum frequency, then changes in urban song over time would be more consistent with natural or cultural selection as mechanisms influencing the minimum frequency of songs sung by urban colonizers.

## METHODS

Song sparrows are a common passerine found in a variety of habitats across the United States including urbanized areas. Male song sparrows can be observed singing in March/April and will continue to sing throughout the spring and into late summer, often through July (C. E. Hill, Campbell, Nordby, Burt, & Beecher, 1999). During the breeding season, males sing to maintain territory boundaries and to attract females (Tompa, 1962; Wingfield & Soma, 2002). Thus, during the breeding season it is important for male song sparrows to avoid song masking that may interfere with reproduction. Males have song repertoires of 6-13 song types with a mean of 9 songs that they use interchangeably (Akçay & Beecher, 2020; Searcy, Sewall, Soha, Nowicki, & Peters, 2014; Wood & Yezerinac, 2006). Large repertoire sizes gives males a sexual advantage (Reid et al., 2004; Searcy, 1984) and may also be advantageous for avoiding masking from urbanized ambient noise. Male song sparrows sing with eventual variety, which means that they usually cycle through the song types in their repertoire during song bouts by singing the same song repeatedly before switching to a new song type. (Searcy & Marler, 1981); however, if they are able to use vocal plasticity through song type change, they may change song types more quickly.

### **Study Area:**

Initially, I identified male song sparrow territories across Western Carolina University (WCU) campus in North Carolina ([35.309960, -83.182605](#)). WCU presents an excellent testing site for song sparrows, who have become acclimated to people and common anthropogenic noise sources. Song sparrows in this population are residential and males often stay on their territory year-round (Evans, Boudreau, & Hyman, 2010). Once territories are established, song sparrow males usually do not leave or change territory location (Hughes & Hyman, 2011). Male song

sparrows actively defend their territories that have defined boundaries and do not often overlap with other male territories, especially during the breeding season (Tompa, 1962; Wingfield & Soma, 2002). Defined territories will allow me to test the same males on different days with a high confidence that it is the same male each time on the territory (Hughes & Hyman, 2011), thus minimizing the need for color banding. However, some of the song sparrows in this population are color banded as part of on-going research of this population, allowing me to confirm that territory tenure is long term in this population. Experiments were conducted between May-July of 2022 to coincide with the song sparrow breeding season. During the breeding season, male song sparrows are the most territorial and the perception and discrimination of song is the most important. Experiments were conducted between 0600-1100 since the morning is when song sparrows are most active.

### **Playback Experiment:**

Two treatments were created for this experiment using masking and non-masking noise (Fig.1). Each noise playback had a total duration of 3 minutes, with a 30 second fade-in and 30 second fade-out (Fig.1). Broadband white noise was generated using Audacity 3.2.5 and bandpass filtered using Raven Pro 1.6. The non-masking noise was created using a low frequency limit of 707Hz and an upper frequency limit at 1414Hz creating a one octave band of noise centered at 1kHz (Fig.1 and 2). The masking treatment was created using a low frequency limit of 2121 Hz and an upper frequency limit at 4242 Hz, creating a one octave band of noise centered at 3kHz (Fig.1 and 2). These limits were chosen based on the published critical thresholds for song sparrows (Dooling, 1992). That is, for both noise treatments the noise bands were at frequencies and bandwidths that account for the optimal hearing sensitivity of song



sparrows (Langemann, Klump, & Dooling, 1995; Okanoya & Dooling, 1987). In other words, the non-masking treatment should generate noise that does not mask song sparrow song but is perceived as equally loud to song sparrows as the masking treatment (which masks low frequency components of song sparrow song). Thus, each treatment should be perceived as similar amplitude to song sparrows, but have different masking properties (Langemann et al., 1995; Okanoya & Dooling, 1987).

At least a day before each trial, I scouted out male territories, located favorable perching sites of each male, and marked those sites with flagging tape. I took an ambient noise reading using a Bafx Products BAFX3608 integrating sound level meter (ISLM) set to fast, A-weighted, and using the peak noise to measure the usual environmental noise level at each territory to be used in later analyses. Ambient noise readings were taken a minimum of two times, either during scouting or before each trial. Scouting was often done around noon, to maximize time in the morning for trials since song sparrows are most active in the early mornings. The following day, I would return to the male's territory and begin the trial. I placed a single OontZ Angle 3 ULTRA Bluetooth speaker under the male song sparrows likely perching sites marked with the flagging tape identified from my earlier scouting. The speaker was approximately 2-3 meters below the pre-selected perching site of the male and using the ISLM, I measured the approximate frequency in decibels (dB) of the selected treatment to verify and create a 1m diameter "within range" parameter of the perching site. This allowed me to ensure that within this range, the amplitude of the noise would be approximately 72-80 dB SPL for each experimental treatment.

I conducted playbacks of noise with focal males such that each male was tested with one or the other of the treatments on different days, with an average of 1.32 days between the two trials for 46 sample males. On the day of the first experiment, I randomized the order of

treatment by flipping a coin to control for any bias in order (masking or non-masking). I used non-local song sparrow song playback (from recordings of males located greater than 600 miles from WCU) from Cornell's Merlin app to evoke the male song sparrow to come to his perching site and sing. I recorded trials using a Marantz PMD 661 recorder with a Sennheiser ME66 shotgun microphone at 24-bit, 44.1 kHz sampling rate and stored as .WAV files. Each trial was separated into three sections: before, during and after noise playback, with each of these sections lasting several minutes depending on specific circumstances. During trials, I was located approximately 10 meters away from the perching site and recorded the male's initial territorial song with no outside influence (hereafter known as the *before* songs). After sufficient *before* songs were collected, I started the white noise treatment at a volume that had previously been measured to ensure a level of approximately 75 dB SPL at the location of the focal male. I controlled perch height by adjusting volume to an amplitude of the treatment noise at approximately 75 dB SPL at the pre-determined perch height and only used songs sung within 1 meter from the perch site. I continued to record the male's song during the noise treatments (Hereafter known as *during* songs). Once the playback had ended, I continued recording the song sparrow for approximately 2-6 minutes until sufficient songs were collected (hereafter known as *after* songs). If during the trial the song sparrow stopped singing or flew away, I used playback from Merlin on my phone through the same Bluetooth speaker to stimulate the test subject to return to the designated perching site and sing again. The treatment noise continued playing even when the song sparrow flew out of range and returned to the designated perching site. Songs sung outside the 1-meter range of the perching site were deemed out of range and not used for analysis since the amplitude of the white noise would be lower farther away from the speaker. I completed masking and non-masking trials on 46 male song sparrows.

### **Sound Analysis:**

I used the sound analysis software Raven Pro 1.6 to measure acoustic features of song in response to masking and non-masking noise. I examined songs recorded from each trial and selected songs for analysis that were the highest quality (with minimal overlapping noise), equal representation of song types if they occurred, and songs that were “within range” during noise playback. When possible, 10 songs were selected for each period of the trial (*before*, *during*, and *after*) such that the maximum number of songs analyzed for each trial was 30 songs. For each song, I measured minimum frequency, maximum frequency, frequency bandwidth, and song duration. Songs were recorded at 24-bit, 44.1 kHzs sampling rate. I generated waveforms and spectrograms in Raven 1.6 using a Hanning window at 512 samples, 3 dB Filter Bandwidth was set to 124 Hz. All acoustic measurements used for analysis were based an overall mean of 26.97 songs per male and a mean of 8.99 from each section of the treatment: *before*, *during* and *after*. I used power spectra to determine max and min frequency at -36 dB from peak amplitude as this served as the best compromise between maximizing variation and avoiding the noise floor in song sparrow songs. However, the noise treatments and naturally occurring noise would often be above the -36 dB threshold at low frequency. As a consequence, I used spectrograms to assist the measurement of low frequency for the masking *during* songs if the lowest note was unclear. I used only songs that were of high recording quality which allowed for visualizing all frequency components of songs (Wood & Yezerinac, 2006). I investigated if there was a correlation between naturally occurring ambient noise and minimum frequency of songs for males in my population using the ISLM reading at each territory. I compared ambient noise measurements obtained from each territory with mean measurements of minimum frequency from songs recorded during the *before* portion of trials.

### **Behavioral Analysis:**

Males may respond differently to the noise treatment. For example, males may retreat more often in response to masking noise than non-masking noise. Therefore, I analyzed male behavior in response to noise by determining if they retreated or stayed. Further, males may alter singing behavior differently in response to noise. For example, they could continue singing the same song type, switch song types, or stop singing at different rates in response to noise treatment. Therefore, I analyzed each male reaction to treatments and how they sang at the beginning of each analyzed song in the *during* section. In particular, I examined if males were more likely to leave in response to noise and if they were more likely to switch song types or variants in response to noise. I categorized the response of male song sparrows as: immediately flew away, continued singing same song type, or immediately changed song type. These observations were made according to how the male reacted as soon as the noise started, during the fade in (i.e., within 30 seconds of the start of the *during* section of each trial). I also collected data from spectrograms to determine whether there was any change in song type or variants of song type (i.e., dropping the lower notes or trills from songs). Males can respond to noise by adjusting acoustic features of the same song type to either raise minimum frequency or to shift the overall peak frequency of the song into a higher frequency range during a singing bout to avoid masking, or switch to another song type having acoustic characteristics better suited to avoid masking. Specifically, I observed when each song sparrow changed song type between the different treatment types and when this change occurred in proportion to the treatment reaching full volume. Further, males can change location during the noise playback. I observed males to either remain at the same perching site as before the noise started or within 1 meter of the original perching site (within range) or males moved greater than 1 meter from original perching

site (out of range). The location observations were also categorized into different groups: change occurred out of range before playback reached full volume, change occurred during fade-in, immediately changed at full volume while in range, or stayed in range and eventually changed song types. Song type variations were not considered in this categorization, only complete song type changes.

### **Statistical Analysis:**

For the statistical analysis of acoustic features of song, I used RStudio 2023.03.0 “Cherry Blossom” released for Windows to use a within-individual repeated measures ANOVA to analyze acoustic features and compare the differences within individuals’ responses to the different treatment types (Fox & Weisberg, 2019). I compare each variable together in a pairwise table and made a Tukey-Kramer *a posteriori* comparison of the location in the trial (*before/during/after*) and the treatment type (masking/non-masking) of each acoustic feature to access any significant p-values between sections of each treatment type (Tables 1-4) (Lenth, Singmann, Love, Buerkner, & Herve, 2019). I created box-and-whisker plot graphs for each of the variables to show the comparative differences between the masking and non-masking treatment effects on each of the acoustic variables (Wickham, 2016). I created a scatterplot graph of each individual males change in minimum frequency throughout the trial for both masking and non-masking treatments (Wickham 2016). For the ambient noise comparison, I used a linear regression to analyze the effect of ambient noise on the minimum frequencies of all the *before* songs to assess any significant effects environmental noise may have on the song sparrow’s acoustic features (R Core Team, 2021). The graph was created using the ggplots package (Wickham, 2016). For the behavioral reactions to noise playback, I used a cross tabulation to identify any significant effects in the reaction of each song sparrow and determine when song type switches occurred for each male within each treatment type (Table 5 and 6) (R Core Team

2021). I used cross tabulation to compare how males accomplished a minimum frequency change between their last *before* song and the first *after* in both treatments, which again gave me chi-square values for comparison (Table 7) (R Core Team, 2021). To assess whether immediate changes in the minimum frequency occurred between the last *before* song and the first *during* song in males, I separated males into two groups; males that switched song types and males that continued to sing the same song type. I used a paired t-test to ask whether males from each group differed in their response by comparing minimum frequency of the last song *before* and the first *during* song both treatments (R Core Team, 2021).

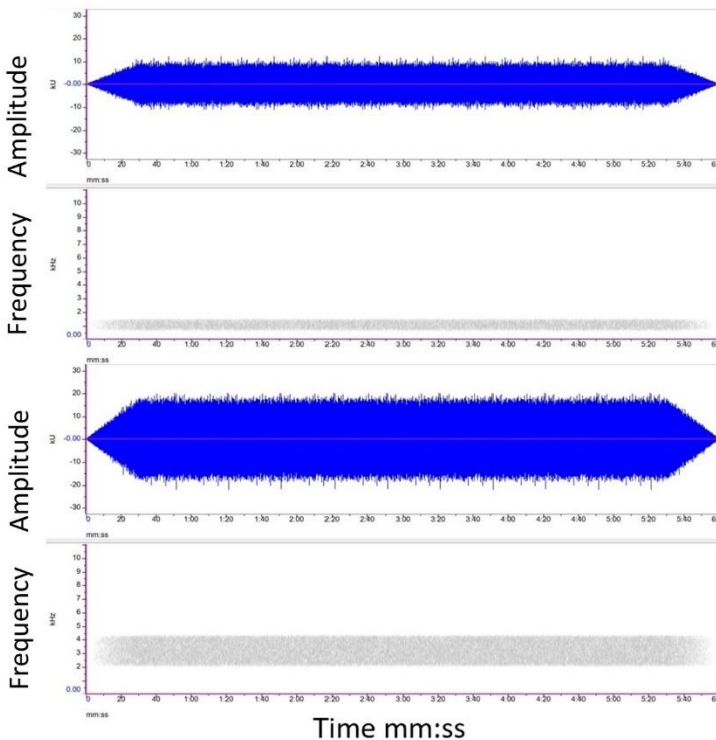


Figure 1. Waveform and sonograms of playback stimuli. The top set is the non-masking noise playback (0.5-1.5kHz). The bottom set is the masking noise playback (2-4.5kHz).

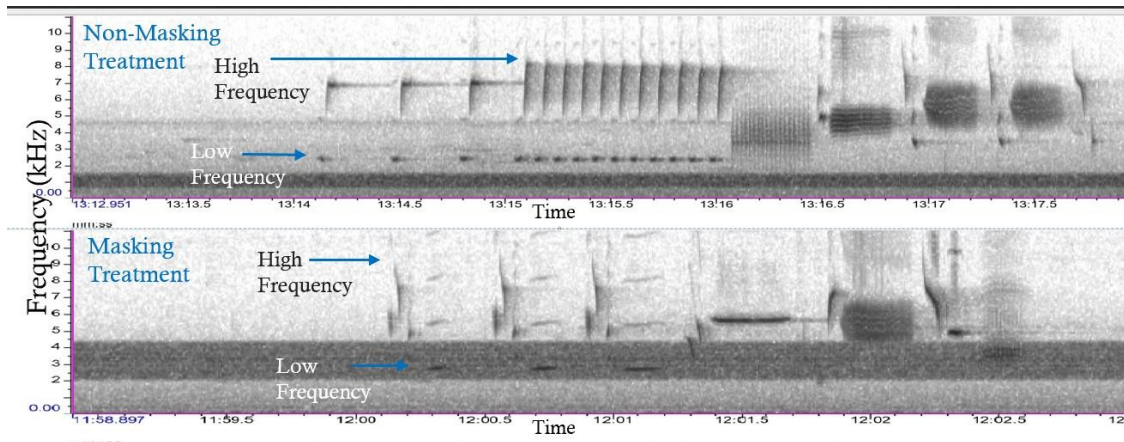


Figure 2. Sonograms of playback stimuli with song sparrow song superimposed to illustrate how song will be non-masked in the 0.5-1.5kHz treatment relative to the masking 2-4.5kHz treatment.

## RESULTS

I completed trials for 46 song sparrow males. I analyzed  $26.98 \pm 3.76$  songs per male for a total of 2,487 songs analyzed.

### Minimum frequency:

I found masking noise treatment had a significant effect on the minimum frequency of songs.

There was a significant increase in the minimum frequency of the male songs during the masking treatment seen in the comparison of masking *before* and masking *during* ( $P = 0.0003$ ) and the masking *during* and masking *after* ( $P = 0.004$ ; Table 1, Fig 3a). There was also a significant increase in the minimum frequency of songs used *during* the masking treatment when compared to the song used *during* the non-masking treatment (Table 1). There was a slight increase in the minimum frequencies of songs during the non-masking treatment, though it was not significant ( $P = 0.14$ ; Table 1, Fig. 3a). Most, but not all males exhibited an increase in minimum frequency of song during the masking treatment (Fig. 3b).

Contrast	Difference	SE	df	t	P value
Masking Before - Non-Masking Before	87.22	55.6	225	1.57	0.6202
Masking Before - Masking During	-240.59	55.6	225	-4.33	0.0003
Masking Before - Masking After	-36.57	55.6	225	-0.66	0.9863
Non-Masking Before - Non-Masking During	-137.47	55.6	225	-2.47	0.1369
Non-Masking Before - Non-Masking After	-100.69	55.6	225	-1.81	0.4610
Masking During - Non-Masking During	190.34	55.6	225	3.42	0.0095
Masking During - Masking After	204.02	55.6	225	3.67	0.0041
Non-Masking During - Non-Masking After	36.78	55.6	225	0.66	0.9859
Masking After - Non-Masking After	23.10	55.6	225	0.42	0.9984

Table 1: Summary of Tukey-Kramer *a posteriori* comparison of the time and treatments of the low frequencies computed against each other. Significant values are highlighted.



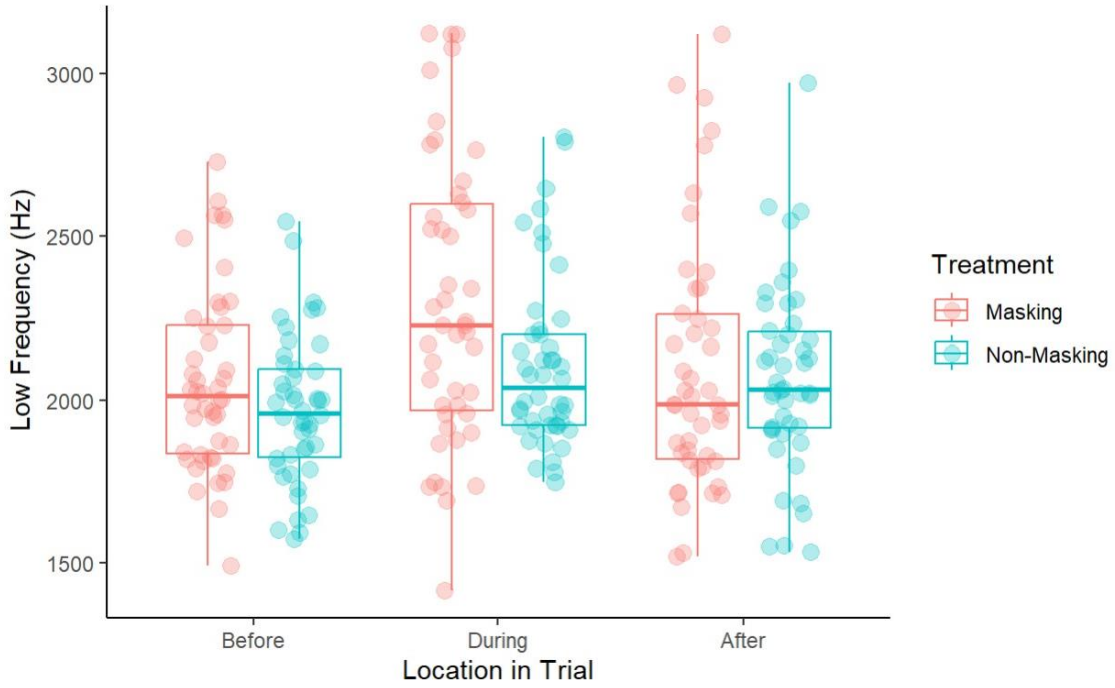


Figure 3a: A box-and-whisker plot indicating the median and the quartiles of the change in average low frequency of male song sparrows' song from one section of the trial to another for both Masking and Non-masking Treatment.

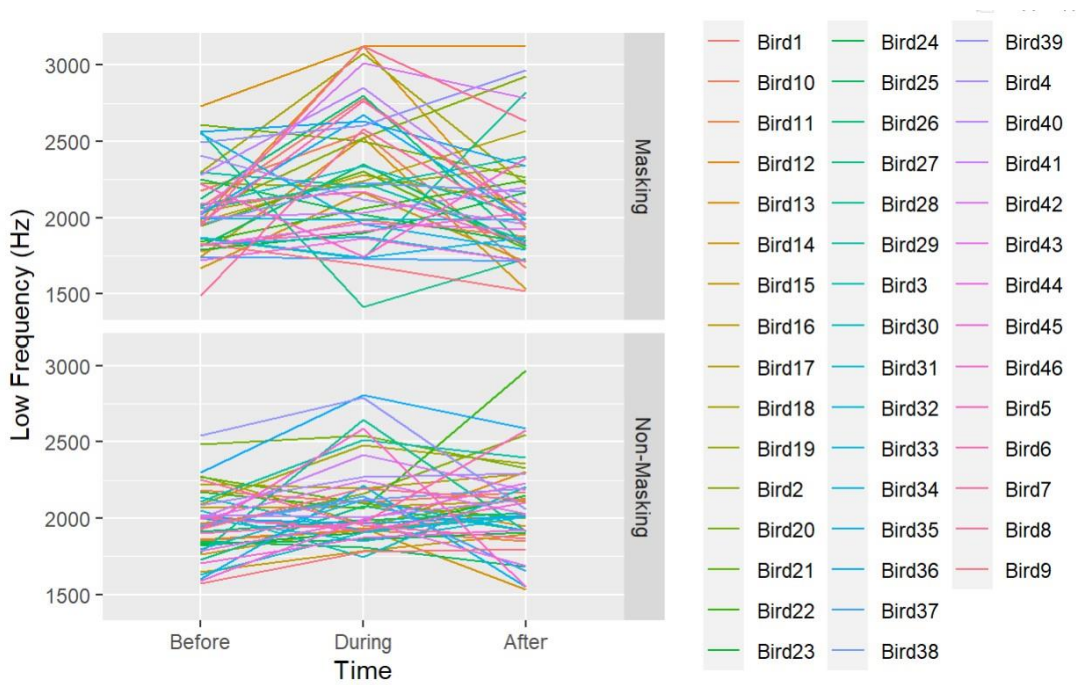


Figure 3b. Individual male song sparrows' change in the average low frequency of their songs across the different sections of the trial for both Masking and Non-Masking Treatments.

### Maximum Frequency:

There were no significant changes in the maximum frequency produced during either of the treatments; all P-values were greater than 0.05 (Table 2, Fig. 4).

Contrast	Difference	SE	df	t	P value
Masking Before - Non-Masking Before	2.63	60.9	225	0.04	1.0000
Masking Before - Masking During	26.32	60.9	225	0.43	0.9981
Masking Before - Masking After	-40.15	60.9	225	-0.66	0.9860
Non-Masking Before - Non-Masking During	13.48	60.9	225	0.22	0.9999
Non-Masking Before - Non-Masking After	-136.85	60.9	225	-2.25	0.2200
Masking During - Non-Masking During	-10.20	60.9	225	-0.17	1.0000
Masking During - Masking After	-66.47	60.9	225	-1.09	0.8841
Non-Masking During - Non-Masking After	-150.33	60.9	225	-2.47	0.1375
Masking After - Non-Masking After	-94.07	60.9	225	-1.55	0.6351

Table 2: Summary of Tukey-Kramer *a posteriori* comparison of the time and treatments of the high frequencies computed against each other. Significant values are highlighted.

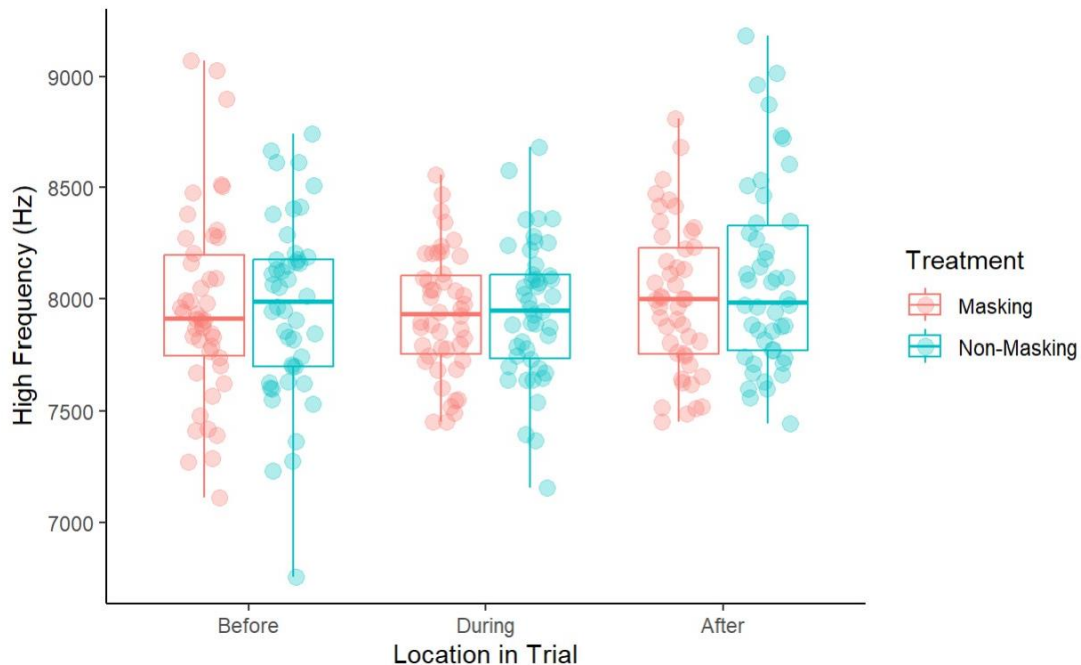


Figure 4: A box-and-whisker plot indicating the median and the quartiles of the change in average high frequency of the male song sparrows' songs from one section of the trial to another for both Masking and Non-masking Treatment.

**Frequency bandwidth:**

There was a significant narrowing in frequency bandwidth during the masking treatment that was not seen during the non-masking treatment ( $P = 0.0062$ ; Table 3; Fig. 5). A statistically significant narrowing of the bandwidth aligns with the minimum and maximum frequency data, indicating that the increase in minimum frequency is significant enough to change the bandwidth. The narrowing of the bandwidth was statistically significant, evident in the significant P-values observed in the *before/during* comparison and the *during/after* comparison in the masking treatment. Though, there was no a significant difference in the *during* songs of the masking and non-masking treatment comparisons (Table 3).

Contrast	Difference	SE	df	t	P value
Masking Before - Non-Masking Before	-84.59	75.2	225	-1.13	0.8705
Masking Before - Masking During	266.90	75.2	225	3.55	0.0062
Masking Before - Masking After	-3.58	75.2	225	-0.05	1.0000
Non-Masking Before - Non-Masking During	150.95	75.2	225	2.01	0.3411
Non-Masking Before - Non-Masking After	-36.16	75.2	225	-0.48	0.9968
Masking During - Non-Masking During	-200.54	75.2	225	-2.67	0.0859
Masking During - Masking After	-270.49	75.2	225	-3.60	0.0052
Non-Masking During - Non-Masking After	-187.11	75.2	225	-2.49	0.1317
Masking After - Non-Masking After	-117.17	75.2	225	-1.56	0.6267

Table 3: Summary of Tukey-Kramer *a posteriori* comparison of the time and treatments of the bandwidth computed against each other. Significant values are highlighted.

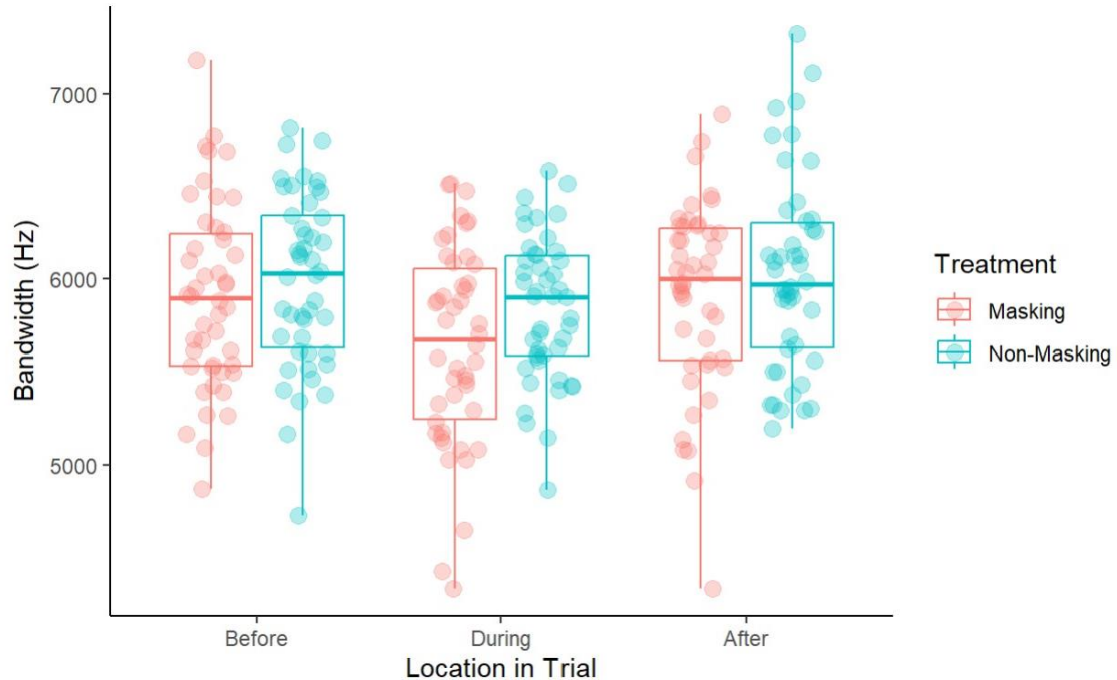


Figure 5: A box-and-whisker plot indicating the median and the quartiles of the frequency bandwidth (difference between max and min frequency) across trials and treatments.

#### **Song duration:**

The only significant change in song length was identified when comparing *during* the masking treatment and *during* the non-masking treatment ( $P = 0.0356$ ) in which the masking songs were shorter compared with the non-masking *during* songs (Table 4). However, none of the *before* or *after* comparisons within treatments were significant, though there was a noticeable downward trend during the masking treatment (Fig. 6).

Contrast	Difference	SE	df	t	P value
Masking Before - Non-Masking Before	0.00	0	225	-0.08	1.0000
Masking Before - Masking During	0.13	0	225	2.69	0.0819
Masking Before - Masking After	0.03	0	225	0.62	0.9894
Non-Masking Before - Non-Masking During	-0.01	0	225	-0.23	0.9999
Non-Masking Before - Non-Masking After	-0.02	0	225	-0.37	0.9991
Masking During - Non-Masking During	-0.15	0	225	-3.00	0.0356
Masking During - Masking After	-0.10	0	225	-2.07	0.3094
Non-Masking During - Non-Masking After	-0.01	0	225	-0.13	1.0000
Masking After - Non-Masking After	-0.05	0	225	-1.06	0.8951

Table 4: Summary of Tukey-Kramer *a posteriori* comparison of the time and treatments of the song length computed against each other. Significant values are highlighted.

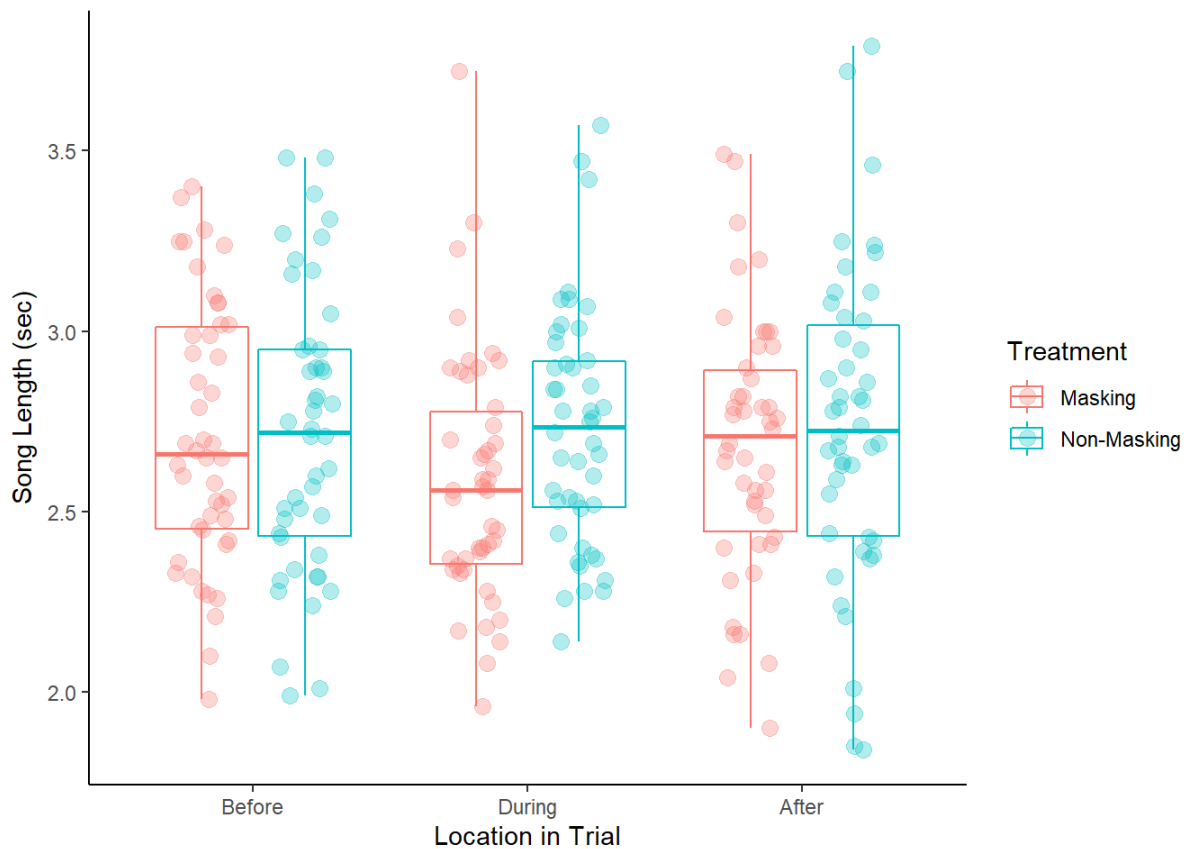


Figure 6: A box-and-whisker plot indicating the median and the quartiles of the change in song length of male song sparrows' song from one section of the trial to another for both Masking and Non-masking Treatment.

### Ambient Noise:

I compared the minimum frequency of all the *before* songs of the overall population of male song sparrows that were sampled against the average ambient noise that occurs in their particular territory during the time of my data collection. A linear regression model revealed a significant positive correlation between the increase in ambient noise of the territory and increase of the minimum frequency of male song sparrow songs ( $P = 0.027$ ; Fig. 7).

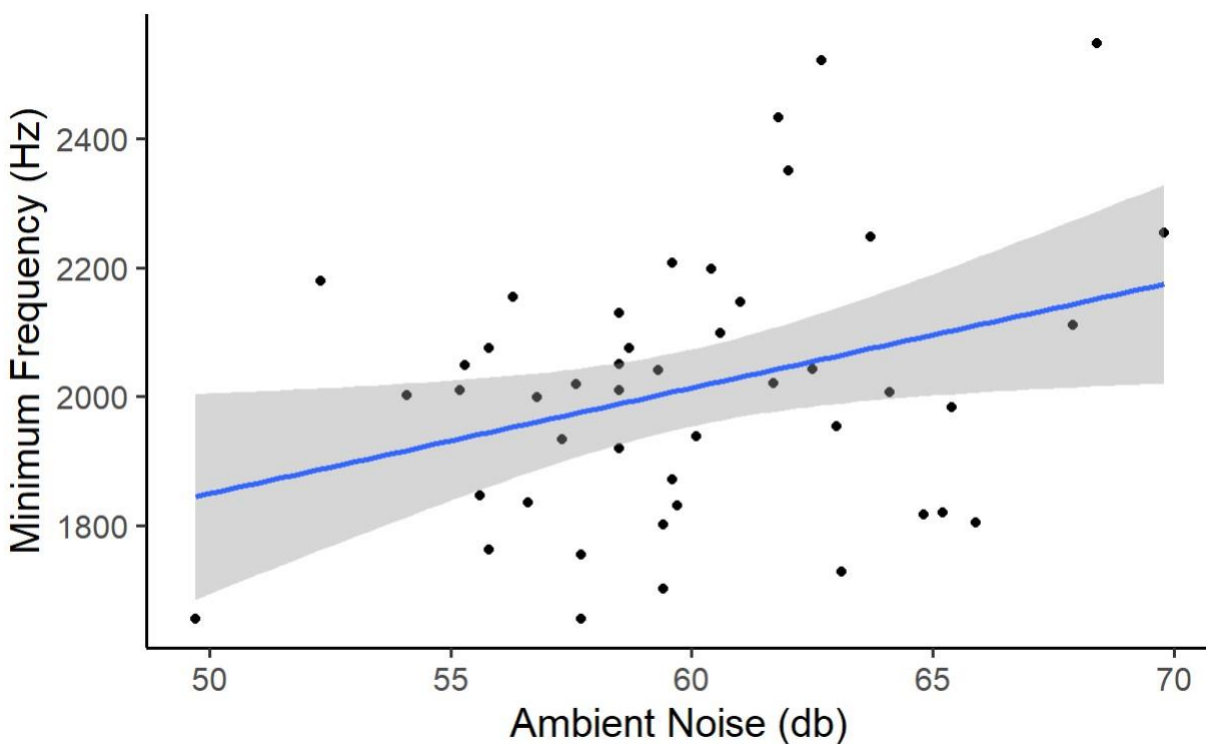


Figure 7: The average minimum low frequency of male song sparrows' songs increased as the mean ambient noise increased. The P-value is 0.027 with 44 degrees of freedom and a standard error of 0.00.

### Behavioral Response to Treatment:

There was no evidence that males behaved differently in response to masking and non-masking noise. Males were no more likely to fly away or switch song types in response to masking versus non-masking noise ( $P = 0.78$ ; Table 5).

	Immediately Flew Out of Range	Continued Singing Same Song Type	Immediately Changed Song Type
Masking	24	14	6
Non-Masking	26	11	5

Table 5: Observed immediate reaction of individual male song sparrows in response to both treatment types during the experiment. There was not a significant relationship between any of the observations despite the treatment type; The ratio of reaction was similar between the two treatments; Chi-Square = 0.48 and P- value = 0.78

### Song Type Change:

All males eventually changed song types throughout trials. However, in response to noise treatments, there was no difference when males changed song types ( $P = 0.13$ ; Table 6).

	Change Occurred Out of Range	Changed During Fade-in	Immediately Changed While In Range	Stayed In Range and Eventually Change
Masking	18	7	8	9
Non-Masking	11	3	14	13

Table 6: The observed occurrence of the first song type change in individual male song sparrows' response to either treatment. There was not a significant relationship between any of the observations; Chi-Square = 5.64 and P-value = 0.13

### Immediate Minimum Frequency Change Between *Before* and *During* Songs:

To examine the increase in the minimum frequency during masking noise, I compared the minimum frequency of the last song *before* the treatment to the first song *during* the noise treatment once it had reached full volume. I found a statistically significant difference between treatments for the increase in the first song *during* noise playback for masking (Paired  $t = 4.48$ ,  $P = 0.000013$ ,  $df = 182$ ; Table 7).

Masking	Non-Masking	Difference	t	df	p-value
2341.33	2011.24	330.1	4.48	182	0.000013

Table 7: A paired t-test of the differences in the lower frequency for the last song *before* the treatment and the first song *during* the treatment for both the Masking and Non-Masking treatments, this does not take into account any song type change.

To assess how the increase in the minimum frequency is accomplished, I compared the last *before* song to the first *during* song I used for analysis and took note of the differences between the two songs. I categorized the observation as either: ‘changed song type’, ‘variant type switch’, ‘frequency shift’, or ‘deletion’. The ‘changed song type’ means that the male started singing a completely different song type between the last *before* song and the first *during* song which would have been once the treatment reached full volume and he was within range of the speaker. A ‘variant type switch’ was a *during* song that was recognizable as the same song type as the *before* song, but with a small difference often seen at the end of the song. A ‘frequency shift’ was recorded if both the *before* and *during* song were the same song type. Often the minimum frequency of these song types was slightly changed in the lower notes. There was no instance of the entire song shifting dramatically, it was a very small shift in minimum frequency. A ‘deletion’ was recorded when the song type did not change but there was an obvious note/s dropped from the song, such as the lowest note/s of the song or if the trill was dropped. I ran a cross tabulation to assess if there were any significant patterns in the way males began to sing during either treatment.



	Song Type Change	Variant Change	Frequency Change	Deletion
Masking	27	3	8	8
Non-Masking	29	4	9	4

Table 8: The observed change between the last ‘before’ song and the first ‘during’ song of male song sparrows in response to the treatment types during the trial. There was not a significant relationship between any of the observations; Chi-Square = 1.61 and P-value = 0.66

There was not a significant pattern in the decision or way the male sang between the last *before* song and the first *during* song between the two treatments (Chi-Square = 1.61; P-value = 0.66). Approximately 60% of the males were observed to change the song type in response to either treatment. To establish if there was a difference in these strategies, I separated out the males that completely changed song types at the start of the treatment and the males that kept the same song type but modified their songs in some way. Again, I compared the actual frequency change in minimum frequency of the last *before* song and the first *during* song in both treatment types for all the males in both groups by using a pair t-test. For the males that changed song types, the minimum frequency of the new song type in the *during* song of the masking treatment increased significantly (P-value of 0.043) and a mean increase from the *before* minimum frequency to the *during* minimum frequency of 370 Hz (Fig. 8). For the non-masking treatment, the minimum frequency of the new *during* song type also increased significantly (P-value of 0.005), but the mean increase between the *before* minimum frequency to the *during* minimum frequency was only 260 Hz (Fig. 8). So, while there was a significant increase in the minimum frequency in both treatments, the masking treatment showed a higher increase compared to the non-masking treatment.

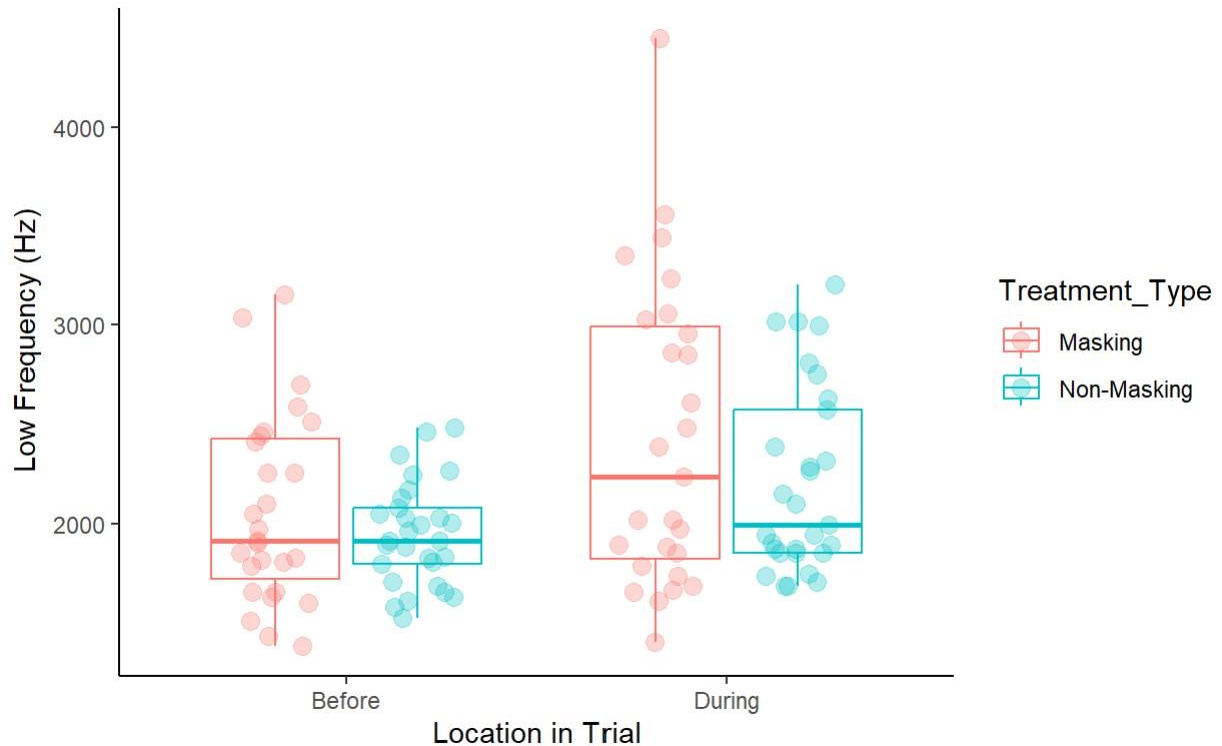


Figure 8: A box and whisker plot indicating the median and the quartiles of the change in low frequency between the last 'before' song and the first 'after' song of male song sparrows' song who changed their song types at the start of the Masking and Non-masking Treatment.

The other three categories (variant change, frequency change, and deletion) were combined since each male sang the same song type in the *before* and *during* sections with some modification to the song. For the masking treatment, the minimum frequency of the *during* song increased significantly compared to the last *before* song (P-value of 0.0015) with an increase in minimum frequency of 532 Hz (Fig. 9). For the non-masking treatment, the minimum frequency of the *during* song did not increase significantly compared to the last *before* song (P-value of 0.073), and the minimum frequency only increased by 130 Hz (Fig. 9). When singing the same song type in *before* and *during* sections of the treatment, the male modified his song in response to the masking treatment significantly by dropping notes or trills.

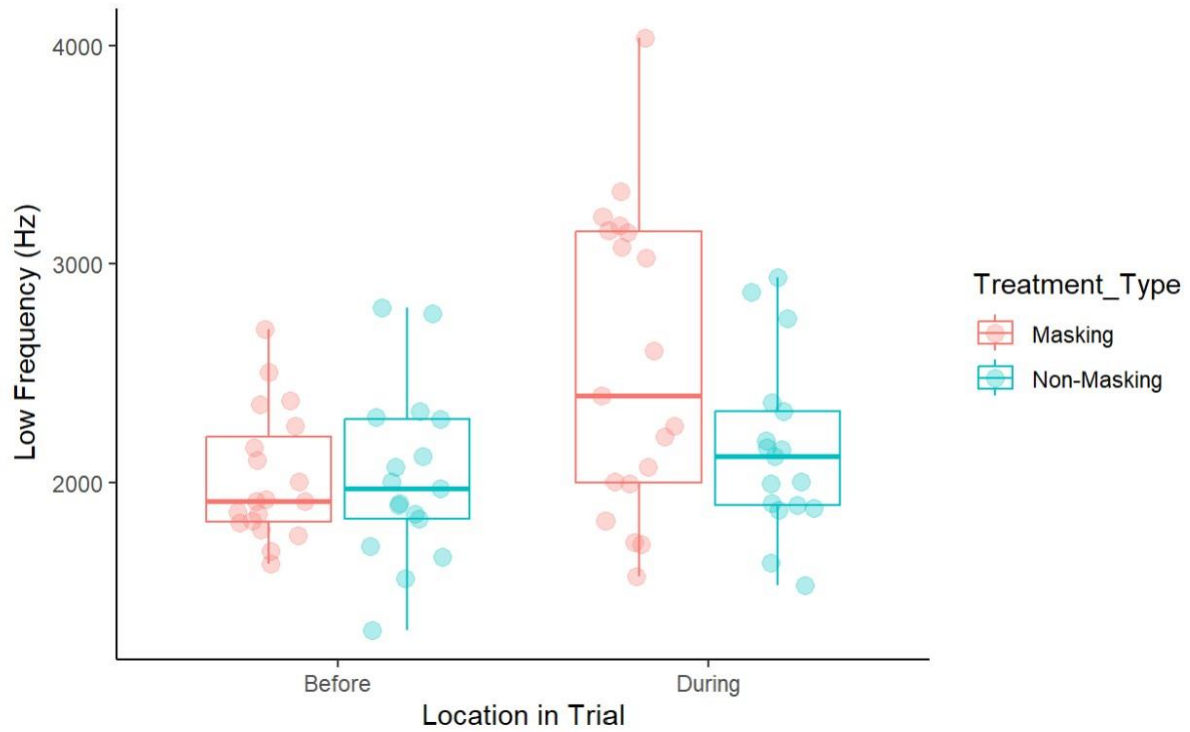


Figure 9: A box and whisker plot indicating the median and the quartiles of the change in low frequency between the last 'before' song and the first 'after' song of male song sparrows' song who kept the same song types at the start of both the Masking and Non-masking Treatment.

## DISSCUSSION

While song sparrows in louder urban habitats have been observed to have a higher minimum frequency within their natural song when compared to those in quieter rural areas (Wood & Yezerinac, 2006), the mechanisms for how this change in frequencies are accomplished have not been fully established. These changes could be the result of song alteration across the generations, either through natural selection or cultural selection, as the song sparrow's habitat becomes more urbanized and thus noisier. Or it could be the result of vocal plasticity in a noisy environment. In this experiment I found male song sparrows were able to accomplish immediate frequency shifts through vocal plasticity in the presence of masking noise. Male song sparrows were able to increase the minimum frequency of their song in response to masking noise (Fig.3a; Table 1). The song sparrows did not change the maximum frequency of their song during either the masking treatment or the non-masking treatment (Fig.4; Table 2). Since the minimum frequency increased and the maximum frequency did not change, the bandwidth became narrower in response to the masking noise and not the non-masking noise (Fig. 5; Table 3). Song duration during the masking treatment was shorter than song duration during the non-masking treatment (Fig. 6; Table 4). This result could be a consequence of dropped notes or trills (alterations to the song), which could act as a means to increase the frequency of the song during masking noise. The results of this experiment align with evidence seen in other songbird studies in which many species increase the minimum frequency of their song as a strategy to avoid the negative effects of low frequency anthropogenic noise (Halfwerk & Slabbekoorn, 2009; Hanna, Blouin-Demers, Wilson, & Mennill, 2011; D. A. Luther & Derryberry, 2012; Proppe et al., 2012; Verzijden, Ripmeester, Ohms, Snelderwaard, & Slabbekoorn, 2010b; Winandy et al., 2021; Wood & Yezerinac, 2006). This is the first study on song sparrows to demonstrate that the males

were able to respond to noise in their environment, specifically noise within the same frequency bandwidth of their song, by exhibiting vocal plasticity and raising the minimum frequency of their song in immediate response. In the non-masking treatment, there was also a trend for males to increase the minimum frequency of their song, but this result was not statistically significant. (Figure 3; Table 1). These results suggest that males were capable of exhibiting vocal plasticity in the presence of masking noise as a strategy to avoid masking, resulting in maximizing transmission and increasing clarity of their song in a noisy environment (LaZerte et al., 2017).

### **Effects of Ambient Noise**

The song sparrows in this study population also showed a positive correlation between an increase in ambient noise within their territory and a higher minimum frequency of their natural song. I.e., in a parallel observational study, males whose territories had louder environmental noise naturally, sang at a higher minimum frequency when compared with those in territories having lower levels of ambient noise (Figure 7). These findings contribute to a growing number of studies on song sparrows and other oscine passerines that have found higher overall minimum frequencies of song in areas where ambient noise has increased as a result of urbanization (Hu & Cardoso, 2010; Potvin et al., 2011; Proppe et al., 2012; Verzijden et al., 2010b; Winandy et al., 2021; Wood & Yezerinac, 2006). Males in urban areas may be pre-adapted to show vocal plasticity compared with males of the same species in rural habitats. Such studies show some variation in mechanisms of frequency adjustments in song. A study on Nuttall's white-crowned sparrows (*Zonotrichia leucophrys nuttalli*), for example, found that the males in rural areas were unable to immediately adjust their signal in response to experimental masking noise, but males in urban areas showed immediate vocal plasticity by shifting the frequency of their songs (Gentry et al., 2017). Similarly, male urban black-capped chickadees increased the minimum frequency of their song in response to masking noise, while males in the

rural populations decreased the minimum frequency of their song (Lazerte et al., 2016). Black-capped chickadees may be especially plastic in adjusting song frequency, as other previous studies have shown that males will shift the frequency of their song in an immediate way, exhibiting vocal plasticity during normal singing, and to song match with rival males (Goodwin & Podos, 2013; B. Hill & Lein, 1987; Horn et al., 1992; Ratcliffe & Weisman, 1985). However, black-capped chickadees have a single-song repertoire with a relatively simple song usually consisting of two notes (Horn et al., 1992). On the other hand, song sparrows have a large repertoire of 6-13 songs that are more complex (Akçay & Beecher, 2020; Searcy et al., 2014). Many passerines, like song sparrows, learn their repertoire of songs as juveniles which become crystallized within their first year (Nordby et al., 2002). They do not add new songs to their repertoire later, but they do regularly make adjustments while singing, such as changing the trills within the song, or dropping notes (Podos, Peters, Rudnický, Marler, & Nowicki, 1992). My results indicate that vocal plasticity is achieved within the crystallized songs of this species during noise exposure via this plasticity in the song structure, since the overall song type a male song sparrow was singing did not change, only specific elements within the song type the male was already singing.

While my findings are consistent with the ability of male song sparrows to exhibit vocal plasticity in the presence of masking noise, they do not discount natural or cultural selection as an additional mechanism to accomplish frequency shifts observed in urban habitats. On the contrary, all three strategies could be working concurrently to maximize song clarity in anthropogenic noise. In white-crowned sparrows, cultural selection appears to be a mechanism for increased minimum frequency in urban environments (Moseley et al., 2018). Indeed, natural selection on acoustic signals results in songs that have better transmission in environments that

include natural sources of noise (Wiley & Richards 1982, Klump 1996). Yet, the ability to use vocal plasticity in noise could give male song sparrows an additional advantage in urban environments, with more immediate flexibility, to enhance the effects of natural and cultural selection (Francis et al., 2011) . Together the results of studies on mechanisms for the observed increases in minimum frequency in songs of urban songbirds suggest that vocal plasticity is one of multiple avenues in songbird adaptation to urban landscapes (Bermúdez-Cuamatzin et al., 2011b; Gentry et al., 2017; Goodwin & Podos, 2013), but one that may give specific males an advantage when competing to be heard above the background noise.

### **Song Duration**

Another strategy identified by some studies as a way to maximize transmission of songs in anthropogenic noise is by increasing the duration of those songs, making them potentially more detectable over time, particularly when noise is more periodic and less continuous (S. D. Hill, Aryal, Pawley, & Weihong, 2018). However, I found that in the presence of masking noise, song sparrows actually sang shorter songs in comparison to songs sung in the non-masking treatment (Table 4). I saw a noticeable shorting of song duration when comparing the *before/ during* songs in the masking treatment (Fig. 6), though it was not statistically significant. The songs increased in duration when comparing the *during/after* songs of the masking treatment (Fig. 6), suggesting the masking treatment was affecting song length even if it was not statistically significant (Table 4). A possible explanation for these counter-intuitive results comes from the mechanism by which male song sparrows accomplished an increase in minimum frequency. If males are dropping the lower notes or some trills in the song, this change could result in temporarily shortening their song in the presence of masking noise. Similar results were seen in the chiffchaff (*Phylloscopus collybita*), a bird that also increased minimum frequency with decreases in duration of their song resulting from dropped notes in their song (Verzijden et

al., 2010b). In some species, such as chiffchaffs and song sparrows, song duration might not be as important as song clarity for increased song transmission.

### **Behavioral Response**

I was able to assess how shifts in minimum frequency during masking was accomplished by observing the behavioral patterns of the males in both treatments. There was no statistically significant pattern to how the males reacted initially to the treatment (Table 5). Over 50% of the song sparrows flew away initially at the start of either treatment, which indicates that masking noise did not frighten the males off their territory at a higher rate compared to non-masking noise. Thus, it was not masking noise specifically that may have startled males away from the speaker, but rather an instinctual response to move away from any noise whether masking or non-masking (Liu, Slabbekoorn, & Riebel, 2020; Rosa & Koper, 2018; Slabbekoorn & Ripmeester, 2008). It is likely, at least for some males, that when confronted with either noise treatment, often the initial reaction of the male is to escape the noise and return after the noise has ended. After using male playback in tandem with the noise treatment, males returned to their original perches and often changed their song, depending on the treatment during the trial.

Since song sparrows have a large repertoire of songs, a change in song type is one way in which individuals could change the minimum frequency during the masking treatment. Song type changes have been observed in great tits (*Parus major*), who change to a higher frequency song type when the ambient noise is prominent at low frequencies (Halfwerk & Slabbekoorn, 2009). I assessed if males in each trial changed their song type in response to either treatment. However, there was no significant difference in terms of song type changes when comparing masking versus non-masking noise. For both trials, many of the males changed their song type while out of range (Table 6), and treatment type did not influence when the males changed song type as a direct response to masking frequencies over non-masking frequencies. I did use non-



local playback to provoke the male back into range to collect ‘in range’ data, the use of other male song may have influenced a song type switch from the focal male; however, regardless of the playback used, the males did still consistently increase the minimum frequency of their song in the masking treatment and not in the non-masking treatment. Since louder anthropogenic noise is often temporary (Shannon et al., 2016b), any initial move away from the noise may eventually be followed by moving back closer to the initial perching site, especially if provoked by a rival male or playback. There were slightly more males who continued singing the same song type in the masking treatment than in the non-masking treatment, but it was not statistically significant (Table 6). For the song type analysis, I did not consider any changes within the same song types, as these were assessed in a subsequent analysis (below). These results would indicate that male song sparrows do not rely on song type switched in response to anthropogenic noise but may achieve increases in song detectability in other ways when it comes to vocal plasticity.

### **Immediate Vocal Response**

When considering vocal plasticity during masking noise, the response may be immediate or to take some time for the male to assess the acoustic properties of the noise and then adjust his singing accordingly. As there was a significant increase of the minimum frequency in the male’s song during the masking treatment and not in the non-masking treatment, I compared the last *before* and the first *during* song in both treatments to gauge if there was an immediate increase in minimum frequency in response to the masking treatment. Though there was an increase in minimum frequency in both treatments, there was a statistically significant increase in the minimum frequency during the masking treatment (Table 7). These results would support the conclusion that vocal plasticity in male song sparrows is an immediate response to masking urban noise.

I categorized observed changes between the last *before* and the first *during* song to identify patterns that could explain how the song sparrows of this population were utilizing different strategies to increase minimum frequency. I observed four strategies used in response to either treatment: song type change, variant change, frequency change, and deletion (Table 8). I combined the males who used variant change, frequency change, and deletion since all these strategies involved altering the current song type. I took all the males in this study and divided them into 2 groups based on the main strategies used: males who changed song types and males continued singing the same song type. While almost 50% of the males changed their song type between the last *before* song and the first *during* song, others sang the same song type but modified the song structure in a way that increased the minimum frequency (Table 8). When comparing the change in minimum frequency of those males who changed song types as a response to either treatment, there was only a slightly greater change in the masking treatment compared with the non-masking treatment (Fig. 8). Males shifted minimum frequency up by 370 Hz during the masking treatment and increased minimum frequency by 260 Hz in the non-masking treatment. Both increases in minimum frequency were statistically significant, though there was a greater increase in the masking treatment compared to the non-masking treatment. Though song sparrows have a moderately-sized repertoire of songs, the repertoire is still finite, and the songs in their repertoire may vary only slightly in minimum frequency (Podos et al., 1992).

Alternatively, males may choose to modify their current song type in the presence of noise by dropping the lowest notes in song, dropping trills, or otherwise singing a variant of the song type with slightly different elements, raising the minimum frequency of their song as a consequence. Those males that did not change the song type between the last *before* song and

first *during* song, modified their song in the presence of noise before eventually changing song type. In these males, there was a significant difference between the frequency change for the masking treatment compared with the non-masking treatment (Fig. 9). For the masking treatment, the males increased their minimum frequency by approximately 532 Hz which was statistically significant and in the non-masking treatment the minimum frequency increased by only 130 Hz which was not statistically significant. The strategy of changing song variants or dropping notes, while more effective in raising the minimum frequency during masking noise, may negatively impact the perception of their song by other songbirds. The tradeoff between modifying the same song type and greatly increasing frequency against switching song types and only slightly increasing the frequency may influence the males' response to low frequency anthropogenic noise.

#### **Trade-Offs: Detectability**

The song sparrows in this study were able to temporarily increase the minimum frequency of their song either through changing song types or changing song variants by modifying some part of their original song type (through dropping the trill or the lower notes in the middle/end of their song). One advantage for males who significantly increase the minimum frequency of a their song may be that a higher minimum frequency also increases the chances of signal detection in low frequency anthropogenic noise (Pohl et al., 2012; Winandy et al., 2021). By increasing the minimum frequency of their song, either through dropped notes or by changing song types, allows for all or at least most of the song to be heard above masking noise, thus making the song clearer for the receiver (Pohl et al., 2012). Also, by increasing the minimum frequency and narrowing the bandwidth, the male potentially increases the active space of his song in noise (Lohr et al., 2003). Active space is the distance around the singer in which the song can be perceived by the receiver (Brenowitz, 1982; Lohr et al., 2003; Marten & Marler, 1977).

Often, birds' songs with more tonal or narrower bandwidth are more easily detected by other birds in a noisy environments (Hanna et al., 2011; Lohr et al., 2003; D. Luther & Magnotti, 2014; Pohl, Slabbekoorn, Klump, & Langemann, 2009). By dropping low frequency elements of their songs and thereby increasing minimum frequency, birds may redistribute energy to best maximize perception and increase active space. Detectability of song, especially for males is important for mating and defending their territory from other males (Halfwerk et al., 2011; Kleist, Guralnick, Cruz, & Francis, 2016). Thus, to avoid masking, an increased frequency would allow the male to be heard above the noise via increased detectability, allowing the male to be heard at greater distances by potential rivals. However, there is more than one approach to accomplish an increase in detectability. For instance, in a study on white-crown sparrows, the minimum frequency of the song did not change, but rather the maximum frequency decreased in the presence of noise (Gentry et al., 2017). Though, the males still reduced the bandwidth of their song, thus potentially increasing the detectability of their song (Gentry et al., 2017). Another challenge facing songbirds in anthropogenic noise is the ability to not only detect a signal, but to be able to discriminate different calls and songs from both conspecific and heterospecific. Males may be increasing minimum frequency in a way that not only improves detectability but also improves discrimination. For example, males need to be identifiable as an individual so if parts of songs are so degraded by noise, they may no longer be recognizable which could bring increased attention from neighbors. The 'dear enemy effect' describes the relationship in which neighboring males often act less aggressive towards a male with adjacent territories (Fisher, 1954). Especially during breeding season when males are defending not only territory, but also parentage of the female's offspring, they are more likely to escalate their aggression towards a stranger than towards their neighbor (Briefer, Rybak, & Aubin, 2008). However, in song

sparrows specifically, males may view neighbors as more of a threat when the female is at peak fertility during the mating season (Moser-Purdy, MacDougall-Shackleton, & Mennill, 2017). The ability to not only detect a neighbor crossing over into a territory, but also discriminate the individual and level of threat they present, particularly during mating season could be crucial to male territorial defense and aggression. By increasing minimum frequency in low frequency anthropogenic noise, males maybe increasing their detectability, but discrimination of their song may decrease from nearby conspecifics. It is unclear if conspecifics can identify their neighbor with more accuracy from complete songs that are degraded by masking noise or from familiar songs with altered song elements that have an increased minimum frequency in noise.

#### **Trade-off: Female Perception**

While it may initially be advantageous of males to increase the minimum frequency of their song to be heard over low frequency anthropogenic noise, there are trade-offs when it comes to changing the frequency of their song, such as being perceived as lower quality by females and other rival males (Ballentine, Hyman, & Nowicki, 2004; Grabarczyk & Gill, 2019; D. A. Luther, Phillips, & Derryberry, 2016). Females often use song as an honest signal of male quality. In certain songbirds, like song sparrows, higher quality males will provide better genes for the offspring and may also provide more parental care (Linhart, Slabbekoorn, & Fuchs, 2012; D. A. Luther et al., 2016). Though song sparrows are social monogamous, both the male and female have been observed to have extra-pair offspring (C. E. Hill, Akçay, Campbell, & Beecher, 2011; Sardell, Arcese, Keller, & Reid, 2011). Thus, it is still very important for a male song sparrow to impress and keep his mate, but also potentially find extra-pair females to increase the number of his offspring. Especially during breeding season, female perception of quality is very important. Low frequencies in songs have been shown to be correlated with the body size and age of the male (Gil & Gahr, 2002; Hu & Cardoso, 2010; Ryan & Brenowitz,

1985). Female swamp sparrows (*Melospiza georgiana*) judge the quality of the male based on their song performance and displayed more for males with higher quality songs, such as songs which had either a strong trill or wide bandwidth (Ballentine et al., 2004). If females are using males song as an honest signal for fitness and body quality, then the presence of anthropogenic noise is skewing perception of males (Cardoso, 2012; Gil & Gahr, 2002; Huet des Aunay et al., 2014; Linhart et al., 2012). Some of the song sparrows in this study immediately dropped the trill as a means to increase the minimum frequency of their song, this subsequently lowers the quality of their song in both loss of trill and narrowing of the bandwidth. The altered song leads to an inaccurate assessment of the male's quality and singing ability since the increase in minimum frequency is only temporary as an attempt to be heard above the noise. The complexity of a male's song is another feature females and rival males will use as an honest signal to judge the signaler's quality (Ballentine, 2009). Even songbirds like song sparrows, who have crystalized repertoire of songs, the complexity of the song often increases with maturity (Kochvar, Peters, Zippel, & Nowicki, 2022). Older males are often of higher quality since it shows they are able to survive longer, tend to have better territories, and generally give more parental care (Yasukawa, McClure, Boley, & Zanolco, 1990). The loss of song complexity and narrower bandwidth even temporarily could negative effect conspecific judgment and cause the male to exert more energy in the presence of noise.

Similarly, while male great tits also sang their lowest frequencies during female peak fertility, when tested against masking backgrounds noise, males with increased minimum frequencies had a stronger response from the females then the males with a lower frequency songs (Halfwerk et al., 2011). This would suggest that thought lower frequencies may be a preferred trait in some species of songbird, that if a female cannot perceive the low frequency,

then higher minimum frequencies may be a more favorable song element. If the female cannot detect the song, then it may affect her mate choice to a song that can be heard above the noise (Halfwerk et al., 2011). There does not appear to be ideal strategy in terms of this trade-off: if high detectability over perceived as low quality is better for a male or if it is better to have a high-quality song that does not reach as far and cannot be heard over anthropogenic noise. It seems to depend highly upon the environment at the time. A study on ovenbirds (*Seiurus aurocapilla*), suggest that females would choose a lower quality male in quieter territory than a bigger male in a noisier territory because of the negative affects the environmental noise has on song detectability and overall reproductive success (Habib, Bayne, & Boutin, 2007a). The study also inferred that lower quality males may simply get stuck with lower quality territories (Habib, Bayne, & Boutin, 2007b). The trade-off between being detectable or being perceived as better quality may change female choice in an urban environment and may lead to a change in female preference if she is unable to gain adequate information on the male from his song (Huet des Aunay et al., 2014). Urbanization is not only changing the way males sing in noise, but overtime could be influencing the traits females perceive as good qualities in a mate.

### **Trade-off: Male Perception**

Increased minimum frequency in the presence of noise may not only skew the females' perception of the males, but also may negatively affect male-male competition. From a male song, rivals are able to size up their opponent and assess the potential levels of threat (Patricelli & Blickley, 2006). As song sparrows raise the frequency of their song to be heard above the noise, then the bandwidth and increased lower frequencies they project will not be an accurate representation of their fitness and body size, which could misrepresent the vocalist and negatively affect conspecific competition (Gil & Gahr, 2002; Ryan & Brenowitz, 1985). Males have been shown to be less responsive to songs with a narrower bandwidth, suggesting that these

songs are less potent in comparison to songs with wider bandwidths (Phillips & Derryberry, 2017). In a study on male white-crown sparrows, songs with higher minimum frequencies and consequently narrower bandwidth received less of a response from other males (D. A. Luther et al., 2016). This suggests that males perceived the higher minimum frequency songs as an indication of a lower quality opponent (D. A. Luther et al., 2016). Similar results were found with song complexity and trill rate in song sparrows, males had a much stronger response to songs with a trill than songs without a trill (Duke, 2017). Song features such as bandwidth and song complexity are likely indicators of a male's quality and therefore used by other males to assess the level of threat they pose to their territory and female mate. Again, increasing frequency as a means to be heard above the noise also skews other males' perception of the singer. Even a temporary increase in frequency could cause conspecifics to view a male as less of a threat, thereby forcing the territorial male to escalate their aggression and incite more conflict instead of scaring other males off their territory with their initial song (Phillips & Derryberry, 2017). This would exert more energy and time than could be used for foraging. By increasing the minimum frequency, males are making their songs more detectable, but less recognizable by neighbors and other conspecifics.

Similarly, if males cannot gauge an intruder's size and quality in anthropogenic noise, he may not respond adequately to the threat which may lead to a loss of resources and paternity. A study on chipping sparrows (*Spizella passerine*) and spotted towhees (*Pipilo maculatus*) demonstrated with increased background noise, males were less likely to detect rivals songs and may inhibit signal discrimination (Kleist et al., 2016). If males are unable to detect or discriminate signals correctly, then they cannot accurately defend their territory and may take unnecessary risk. When mountain chickadees (*Poecile gambeli*) were presented with urban song



stimuli and rural song stimuli, mountain chickadees living in a noisy urban habitat showed a higher level of aggression towards all stimuli whereas the chickadees living in a quieter rural habitat were able to differentiate between the two different stimuli and show less aggression to the rural song stimuli; suggesting there was a lower discrimination threshold for the urban chickadees than the rural chickadees (LaZerte, Slabbekoorn, & Otter, 2019). Urban males may then be exerting all their strength to defend their territory against all intruders, instead of discriminate potential neighbors or other males that may be of lower quality and therefore, less of a threat.

### **Conclusion**

This trade-off between increased detectability but lower discrimination from conspecifics, may be reduced through the use of vocal plasticity in song sparrows during masking noise and allow males to maximize transmission of their song in noise, while retaining their lower frequencies in the absence of noise. Though during the noise, the increase in minimum frequency songs may increase detectability but still be difficult to perceive the quality of the male; however, most anthropogenic noise is temporary. So vocal plasticity may be one of the best ways to maximize transmission in temporary masking anthropogenic noise. When analyzing the last *before* song and the first *during* song, just over half the males changed to a new song type that usually had a higher minimum frequency, this allowed for the more or all of the new song type to be heard above the noise. However, a greater increase in minimum frequency was accomplished by dropping notes and trills of the current song type. The males would have to be vigilant and hyper aware of the songs they were singing and the current ambient noise on the territory for this to be an efficient strategy. The change may also not be immediate but may happen over the course of a few minutes. When comparing the mean minimum frequency in the masking treatment compared to the mean of the minimum frequency

in the non-masking treatment, the masking treatment had a much more significant increase (Fig. 3a.). This would suggest that there was not only an immediate change in minimum frequency once the noise started, but a continuation of higher minimum frequency songs used throughout the entirety of the masking treatment. The higher minimum frequencies then decreased and returned to approximately the same frequency as the *before* songs. For some males, it may have taken more time to adjust their song frequency, but considering the mean of all the songs in the *during* section had a higher minimum frequency, then the change did occur and continued until the masking noise stopped. While a complete understanding of how changes in minimum frequency come about, this study does provide some of the first evidence that song sparrows do exhibit vocal plasticity in the presence of masking noise. Males are able to recognize masking noise in the lower frequencies that cover part of their song and increase the minimum frequency either through changing song types or dropping lower notes. They do not increase the maximum frequencies of their song. Which consequentially narrows the bandwidth of their song, again, only seen during the masking treatment. Slight increases were observed in the non-masking treatment, but it was not as great or as statically significant as observed in the masking treatment. Song duration also shortened during the masking treatment, likely as a result of dropped notes as an attempt to increase minimum frequency. The behavioral pattern remained the same despite the treatment used at the time. The only difference the masking and the non-masking treatment elicited was in the acoustic features of the males' song and not in the reactions they had to the treatment noise.

One consideration for this study is that I did not measure any potential amplitude change in the acoustic characteristic of either treatment. It was outside the scope of this study to analyze fluctuations in amplitude; however, in certain species it has been suggested that an increase in

amplitude is one strategy to overcome negative masking effects of anthropogenic noise (Brumm & Todt, 2002; Lohr et al., 2003; Nemeth & Brumm, 2010). Another suggestion is when songbirds increase the frequency of their song, it naturally leads to an increase in amplitude to enhance detection above noise (Nemeth et al., 2013). Though it has also been suggested increasing amplitude is very costly for songbirds (Brumm, 2004). A future study should consider comparing changes in amplitude alongside increases in minimum frequency in song sparrows' song during low frequency masking noise. Since there are multiple strategies to overcome the negative effects of low frequency masking noise, song sparrows may be utilizing more than one. It would be interesting to compare song sparrows who drop notes in their song against the males who switch song types, to identify any predilection of either strategy towards increasing amplitude.

Another aspect future studies should focus on is the response of both males and females to frequency shifted songs in the presence of masking and non-masking noise. For song sparrows, it may be advantageous to increasing minimum frequencies in noise, if it makes the signal more detectable and thus illicit a greater response from females. Studying female response to songs with increased minimum frequency in anthropogenic noise could help our understanding of how noise is affecting sexual selection and the efficiency of vocal plasticity in males. Likewise, a noisy environment may be changing both male and female song sparrows' perceptions of higher minimum frequency songs and narrower bandwidth. A future study should focus on a males' response and level of aggression in masking and non-masking noise. And study could also focus on males' levels of aggression towards songs degraded by masking noise against males' songs with elements altered to be heard above the noise by increasing the minimum frequency to identify which strategy is more effective in increasing detectability in

noise while retaining discrimination from neighboring conspecifics. Since there have been other studies on passerines and the different receivers' response during low frequency anthropogenic noise (Halfwerk et al., 2011; D. A. Luther et al., 2016), a future study should focus on behavior in both male and female song sparrows and the use of vocal plasticity in masking noise.

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