

**THE FUNCTION OF SONG OVERLAPPING IN
HERMIT THRUSH (*CATHARUS GUTTATUS*)**

by

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B.Sc. (Honours) Biology-Psychology, (University of New Brunswick, 2020)

A Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree of

Master of Arts

in the Graduate Academic Unit of Psychology

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This thesis is accepted by the
Dean of Graduate Studies

THE UNIVERSITY OF NEW BRUNSWICK

July 2022

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Abstract

Male songbirds may mediate aggressive competition by singing concurrently with their rival, termed song overlapping. Support and criticism for overlapping functioning as an aggressive signal exist; many species adjust their singing to avoid sound interference, including during male competition. In this study, natural rates of overlapping were measured using past recordings of hermit thrush. Playback studies were used to examine overlapping in a male-male aggressive context versus in response to different bird species' songs. No association was found between overlapping and physical aggression. The conspecific playback and counter-singing groups showed similar degrees of overlapping avoidance, with birds that were exposed to the heterospecific playbacks showing the least amount. These results suggest that overlapping is not an aggressive signal in this species and may occur for other reasons, such as avoiding acoustic interference. This study expands on the understanding of how aggressive signaling and acoustic interference affect patterns of birdsong.

Keywords: hermit thrush, acoustic interference avoidance, song overlapping, playback, aggression

Acknowledgements

I would like to thank my thesis supervisor Dr. Sean Roach of the department of Psychology at the University of New Brunswick for his invaluable advice and mentorship throughout the two years of writing my thesis. I am extremely grateful for the chance to work with him for the duration of this project.

I would also like to thank my committee members, Dr. David Speed, Dr. Drew Rendall, and Dr. Jeff Houlahan for their insight and guidance on this dissertation. In addition, I would like to thank Adrienne Thornton, Jillian Jessulat, and my parents for their valuable assistance with the large amount of field work that made this study possible.

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The Function of Song Overlapping in Hermit Thrush (*Catharus guttatus*)

Birdsong has captivated and been the inspiration for countless artists and writers for centuries. Scientists have equally been enthralled by these songs. Research has shown that there are two primary functions of birdsong: mate selection and attraction and as a signal of aggression (Searcy et al., 2006). When males of a species sing, females can listen and gather information from their songs that is important to help determine which male they will select to mate with (Nowicki & Searcy, 2005). In comparison, aggressive signals occur between two male conspecifics when one tries to invade the other's established territory. The ability for song to function as an aggressive signal is important as it helps the male protect and maintain their territory where he can attract a female and be the only individual with access to the territory's resources (Nowicki et al., 1998; Nowicki & Searcy, 2005).

Song, which is important to a bird's ability to survive in its environment, only achieves its intended goal if it reaches the listener. When a bird sings, it is important to recognize that this specimen is not the only source of noise in the environment. There could be noise from other species, abiotic noise from natural sources such as a brook or a river, as well as abiotic noise from anthropogenic sources. These types of noise, especially songs of other birds, can mask the bird's signals, thus impacting their ability to adequately pass on information. The masking of signals can impact both mate attraction and the ability to signal aggression. This can have negative consequences such as a decreased ability to attract a mate; the females may not be able to judge the quality of a male or may not be able to hear a male when he sings his location, as the signal was not being transmitted successfully (Nowicki & Searcy, 2005). Signal masking can also

impact a male's ability to protect their territory. When masked, signals that convey information, such as a male's level of aggression and fighting ability, may not reach the intended rival, and thus limit a male's ability to maintain their territory, which may further impact their ability to attract a mate (Nowicki et al., 1998).

In response to noise in their environment, birds may alter their vocal behaviour to help relieve the negative effects of the different noise sources on their signals, as explained by the acoustic interference hypothesis (Brumm, 2006; Wilson et al., 2016). One proposed method of avoidance occurs when a bird changes its song timing to prevent song overlapping. Song overlapping occurs when two individuals sing simultaneously and can result in the masking of signals (Brumm, 2006; Wilson et al., 2016). However, other researchers have suggested that birds may alter the timing of their songs to intentionally overlap the songs of a rival male conspecific to convey their level of aggression (Baker et al., 2012; Dabelsteen et al., 1997). For songbirds to adequately communicate in their environment, they need to be able find a balance between these competing pressures of avoiding acoustic interference and still being able to have competitive relationships with other conspecific males in relation to mate attraction and aggressive interactions (Brumm, 2006).

Song overlapping has been proposed to be related to and interconnected with aggression and acoustic interference avoidance. The objective of the current project was to untangle this relationship to better understand the function of song overlapping in hermit thrush (*Catharus guttatus*). This thesis will first discuss one of the main functions of bird song by focusing on song as an aggressive signal. This will be followed by an overview of the acoustic interference hypothesis and the methods used by animals to avoid different types of noise interference.

Aggression

One of the major functions of birdsong is to act as a signal to send information such as the bird's level of aggression and fighting ability to a rival conspecific bird that has invaded the bird's territory (Bischoff et al., 2009; Searcy et al., 2006). Many different signals of aggression have been proposed by researchers, such as song-type switching, song-type matching, song rate, soft songs, novel and abridged songs, and song overlapping. However, many of these signals are controversial as they show inter- and intraspecific variation in how they are used. To be classified as an aggressive signal, Searcy and Beecher (2009) suggest that a signal must meet three different criteria: context criterion, response criterion, and predictive criterion. The context criterion refers to whether the vocal signal is more common during an aggressive context (Searcy & Beecher, 2009). The response criterion is satisfied if the signal elicits a response from the target bird (Searcy & Beecher, 2009). The predictive criterion involves whether or not the signal is predictive of further aggression and an escalation in aggression in individuals (Searcy & Beecher, 2009).

Proposed Signals of aggression

Song-Type Switching. One proposed signal of aggression is song-type switching, which occurs when a bird switches between the different song-types in their repertoire. By switching between song-types, a bird is able to show the size of their song repertoire, with larger repertoires being associated with a healthier and stronger bird, and thus a better fighting ability. As well, the larger repertoire acts as a signal to females of the quality of a male, as larger repertoires have been shown to be more attractive to females, such as seen in western meadowlarks (*Sturnella neglecta*; Horn & Falls, 1991;

Logue & Forstmeier, 2008). There are some interspecific differences in how song-type switching is related to aggression. For example, when looking at banded wrens (*Thryophilus pleurostictus*), Molles (2006) found that low levels of song type switching, termed repetitive singing, was associated with higher levels of aggression. Chaffinches have also been shown to show more aggressive behaviour, such as flying toward a speaker during a simulated territorial intrusion, when faced with a rival with a low degree of song-type switching (Deoniziak & Osiejuk, 2020).

Song Rate. Another vocal behaviour shown to be associated with aggression is song rate. Song rate involves the number of songs a bird sings during a specific time period. Increases in song rate have been shown in multiple studies to be an aggressive signal. They have also been shown to be a good predictor of attack by a bird, such as seen in black-capped chickadees (*Poecile atricapillus*). Chickadees that increased the rate of their songs were more likely to attack a taxidermic mount than those that did not change their song rate (Baker et al., 2012). Similar results were seen in a study done by Szymkowiak and Kuczynski (2017) using wood warblers (*Phylloscopus sibilatrix*) where higher song rates were more likely lead to an escalation in aggression.

Song-Type Matching. Song-type matching has also been proposed to be a common signal of aggression. Song-type matching occurs when a bird attempts to match their song-type to those being sung by a rival in an aggressive context. Song-type matching can be considered a directed signal of aggression, as it involves matching the song with a specific individual (King & McGregor, 2016). This signal can be used to illustrate the concept of a signaling hierarchy for aggression, as proposed by Searcy et al. (2013). Signals that appear lower on this hierarchy are considered signals of lower levels of aggression (Searcy et al., 2013). Lower-level signals are predictive of the next

signal on the hierarchy at above chance levels, but cannot directly predict that a bird will attack a rival, as a bird may de-escalate the situation (Searcy et al., 2013). As a bird uses signals higher on the hierarchy, the signals become more predictive of a final attack. This has been shown in song sparrows, who song-type matched when aggressive; however, it was considered to be a signal of low or intermediate aggression and not predictive of a final attack by a bird, as a bird could de-escalate the situation by not matching song-types with the rival (Searcy et al., 2013; Vehrencamp, 2001).

Soft Song. One of the most strongly supported signal of aggression is soft song. Soft songs are low-amplitude vocalizations that can come from a bird's normal repertoire (or novel vocalizations) and are sung at a lower-than-normal amplitude (Ballentine et al., 2008; Anderson et al., 2008). Studies have pointed out that when examining soft song, it is important to note novel vocalizations that do not fall within a bird's repertoire (Reichard & Welkin, 2015). It is suggested that these special song types have a distinct function as an aggressive signal and may convey different information in comparison to soft songs that fall within a bird's repertoire (Reichard & Welkin, 2015). A possible explanation for the common use of soft song when aggressive is its potentially lower metabolic expenditure, they may let the bird reserve its energy in case of a physical interaction with the rival (Zollinger et al., 2011).

The use of soft song can be seen in studies using song sparrows, where soft song was the vocal behaviour with the highest utility to predict an attack and was therefore considered a signal of high levels of aggression in this species (Akçay et al., 2011; Anderson et al., 2007; Ballentine et al., 2008; Templeton et al., 2012). Another example of soft song's association with aggression is seen in Savannah sparrows (*Passerculus sandwichensis*), which also used this signal when aggressive. Moreover, during a

playback experiment soft song was the vocal behaviour most predictive of an attack on a taxidermic mount (Moran et al., 2018). Soft song was also shown to be predictive of attacks in black-throated blue warblers, Bachman's sparrows, and brownish-flanked bush warblers (*Horornis fortipes*; Ali & Anderson, 2018; Hof & Hazlett, 2010; Xia et al., 2013). According to Hof and Hazlett (2010), the signal of soft song is the only signal that has the ability to adequately predict an aggressive attack by a bird.

Novel and Abridged Vocalizations. Other less studied signals of aggression include novel and abridged vocalizations. Novel vocalizations are songs that do not fall within a bird's normal repertoire. Abridged songs appear when a bird does not sing a section of a specific song type, such as the introductory note. This has been primarily illustrated in the veery (*Catharus fuscescens*), as they were shown to drop the introductory note of their songs when aggressive. Individuals producing higher levels of these abridged song types exhibited more swoops at a taxidermic mount than those that produced lower levels of these vocalizations, which is considered an aggressive behaviour (Belinsky et al., 2015). The use of abridged songs as an aggressive signal has been used in hermit thrush, where abridged song only appeared in an aggressive context. Novel songs have been suggested to be a possible aggressive signal in hermit thrush, as they produced unique song types in an aggressive context (Roach, 2016).

Song Overlapping as an Aggressive Signal

Describing song overlapping as an aggressive signal is controversial. Some researchers argue that a bird changing the timing of their songs to exhibit song overlapping could be considered aggressive, while others argue that this signal does not meet the criteria of an aggressive signal suggested by Searcy and Beecher (2009). Other

researchers propose that if song overlapping is shown to increase in an aggressive context it may be a consequence of changes in song rates when aggressive, (Baker et al., 2012; Benedict et al., 2012; Wilson et al., 2016; Vehrencamp et al., 2007; Naguib & Mennill, 2010).

Some researchers have argued that the signal of song overlapping, where individuals may change the timing of their songs and sing simultaneously, can be considered an aggressive signal. A study done by Naguib et al. (1999) shows that presence of song overlapping may be a highly aggressive signal in nightingales (*Luscinia megarhynchos*) and occurred most often during a simulated aggressive context (Todt & Naguib, 2000). Naguib and Kipper (2005) further suggest that as nightingales increase their levels of song overlapping, their aggression also increases. This signal was also shown to be a high-level threat in the corn bunting (*Emberiza calandra*), as shown by Osiejuk et al. (2006). In their study, corn buntings were exposed to an overlapping and non-overlapping treatment. In the overlap treatment, the birds spent less time close to the speaker and it took longer for a bird to approach it, with the researchers suggesting that the slower approach occurred due to overlapping may be a highly threatening signal and it may elicit a more cautious response from the subject, in comparison to alternating singing which showed the birds quickly approaching the speaker and spending more time around it (Osiejuk et al., 2006). Sprau et al. (2010) also showed that song overlapping is an aggressive signal in nightingales, and it may be considered a directed threat signal, as a bird is changing their song timing and singing behaviour to overlap and mask the song of a specific rival.

Baker et al. (2012) found song overlapping may be associated with aggression in black-capped chickadees; however, it was shown to be less predictive of an attack in

comparison to signals such as song frequency matching and increase in song rate. American robins (*Turdus migratorius*) have also been shown to use overlapping as a signal of high levels of aggression and may lead to an escalation in aggression, as those who showed high levels of overlapping in response to a simulated territorial intrusion by a conspecific individual were most likely to approach the speaker (Dabelsteen et al., 1997). A study done by Maynard et al. (2012) showed that long-tailed manakins (*Chiroxiphia linearis*) naturally avoided overlapping the songs of other known conspecifics when trying to attract a mate; however, during a simulated territorial intrusion, they increased their level of overlapping in this aggressive context. Mennill and Ratcliffe (2004) showed that song overlapping by a conspecific elicits higher levels of arousal in an aggressive context. Different results were seen in banded wrens, where increased levels of overlapping were predictive of a retreat of an individual during territorial intrusion (Vehrencamp et al., 2007). Hall et al. (2006) also suggested that in banded wrens overlapping could be an aggressive signal. The observed changes to song timing to avoid overlapping and show lower than chance levels of overlapping could be seen as a way to de-escalate an aggressive situation.

While some studies show that song overlapping could be an aggressive signal, others, such as a study done by Fitzsimmons et al. (2008) showed that higher levels of overlapping were not associated with higher levels of aggression and did not lead to an escalation of aggression in black-capped chickadees. Similar results were seen in the great tit, as when exposed to an overlapping and an alternating treatment there was no difference in response, and when being overlapped the birds did not show the higher level of aggression suggested to be linked to song overlapping (Dabelsteen et al., 1996). Similar behaviour was seen in Eurasian wrens (*Troglodytes troglodytes*) where in

response to a simulated conspecific intrusion they exhibited lower than chance levels of overlapping (Yang et al., 2014). As Yang et al. (2014) increased the song rate of their stimulus, the Eurasian wrens continued to change their song timings and avoid overlapping, and in all treatments with varying song rates the rate of overlapping was at below chance levels.

Another study done by Akçay et al. (2019) also showed that song overlapping was not a signal of aggression in the great tit (*Parus major*), where there was a negative correlation between aggression and overlapping. Akçay et al. (2019) showed that birds with the highest levels of aggression were those that did not vocalize during the playback experiment, in comparison to those that overlapped the rival's songs, and suggested that the birds may be changing the timing of their singing to avoid song overlapping and avoid acoustic interference. Brindley (1991) has also proposed that while overlapping may not be an aggressive signal, it may be a strategy to mask the vocalizations of a rival as to prevent females from hearing a stranger's song. Wilson et al. (2016) also showed that black-capped chickadees avoid overlapping the songs of other conspecifics, as well as abiotic noise. Recent studies have shown more evidence supporting the idea that the changes to song timing that cause song overlapping may be associated with other aspects of vocal behaviours, such as acoustic interreference avoidance, where birds may change their song timing to avoid song overlapping and thus acoustic interference from other conspecifics in their environment as this noise would have a negative impact on their ability to communicate their aggressive intent (Searcy & Beecher, 2011; Wilson et al., 2016).

Acoustic Interference Avoidance

For vocalizations to meet their intended goal of communicating information they need to be received or heard by the intended individual. The acoustic interference hypothesis suggests that animals will attempt to avoid having their vocalizations masked by noise in their environment. Specifically, in regard to songbirds, this hypothesis offers an alternative explanation for song overlapping, suggesting that birds alter the timing of their songs to prevent being overlapped by the songs of conspecifics, other species (heterospecifics), and other noises in their environment to facilitate communication. In line with this hypothesis, a bird not changing the timing of their song to avoid overlapping the songs of a rival could be seen as counterproductive for communicating information in an aggressive context, as it would mask the information travelling from an individual to their rival (Helfer & Osiejuk, 2015).

When signalling in their environment, there are multiple noise sources an animal needs to take into considerations. Noise can be classified as biotic (i.e., the noise from other animals in the environment) or abiotic (e.g., running water, waves, wind) noise which includes those from anthropogenic sources (e.g., planes, cars, boats; Baumann-Pickering, 2015; Farina, 2014; Naguib, 2013). High levels of these different kinds of noises in an animal's environment cause a low signal-to-noise ratio, meaning the high noise levels can mask the signals, which has a negative impact on the animal's ability to communicate as the intended receiver may not be able to hear the signal (Naguib, 2013). It has been shown in many studies that animals have the ability to alter their signalling behaviour to be heard better over the noise in their environment.

Interference Avoidance in Non-avian animals

Marine Mammals. The avoidance of acoustic interference of both biotic and abiotic noise and its importance for aiding in effective communication can be seen in many diverse species. One way that animals avoid this interference is through the Lombard effect, where the animal may increase the amplitude (i.e., volume), of their song to effectively communicate over the noise. The Lombard effect has been shown as a method to avoid interference in multiple marine mammals such as right whales (*Eubalaena glacialis*), belugas (*Delphinapterus leucas*), and killer whales (*Orcinus orca*; Baumann-Pickering, 2015; Parks et al., 2010).

Frog Species. Different frog species also have methods for avoiding acoustic interference. For example, gray treefrogs (*Hyla versicolor*) have been shown to alter their song timing in response to being in both small and large groups where levels of call overlapping were increased. Particularly in small groups, changes in call timing in grey treefrogs were shown to be effective to avoid overlapping conspecific neighbours; however, the effectiveness of this strategy decreased as the group size increased (Schwartz et al., 2002).

In response to noise from heterospecific frogs, Wong et al. (2009) showed that male strawberry poison-dart frogs (*Oophaga pumilio*) will lower their signal rate when faced with high levels of interference. This study also showed that these frogs responded selectively to what noise sources they would modify their signalling behaviour to avoid, as the frogs would avoid overlapping calls with cicadas and tree crickets, but not with ground crickets (*Acanthoplus discoidalis*).

Frogs also alter their calling behaviour in response to abiotic, specifically anthropogenic, noise such as seen in a study done by Vargas-Salinas et al. (2014)

looking at the signal modification of anurans in response to highway noise. Green frogs (*Rana clamitans*) and American bullfrogs (*Lithobates catesbeianus*) were shown to have very low levels of signalling during times of high traffic and noise, as their low frequency songs are easily masked by the similarly low frequency noise, while this behaviour was not seen in other frogs with high frequency calls (Vargas-Salinas, 2014).

Insect Species. Insects, such as crickets, have also been shown to avoid acoustic interference by changing their song rate. When faced with either a heterospecific or a conspecific that may sing with the same frequency; however, this avoidance is not seen with those exhibiting different call frequencies (Latimer & Broughton, 1984). Similar results were shown in multiple species of katydids occurring in a single habitat, where all their signal had similar spectral properties such as frequency and amplitude and could easily mask one another if they occurred simultaneously; however, the katydids were shown to change the temporal patterns of their signals to avoid overlapping and interference from the other species (Tiwari & Diwakar, 2018).

Acoustic Interference Avoidance in Birds

Multiple studies have shown that birds, like many other groups of animals, avoid acoustic interference from noise in their environment; however, not all birds respond the same way and show multiple different strategies to avoid interference and masking. Strategies of avoiding or decreasing interference used by songbirds are similar to those used by other animals such as the Lombard effect of singing with a higher amplitude, as well as changing the timing and frequency of their song to prevent song overlapping and masking which would have a negative impact on the birds' ability to adequately send signals (Dominoni et al., 2016). These different modifications of vocal behaviour have

been exhibited when exposed to abiotic noise and biotic noise from both birds of the same species and those of different species (Dominoni et al., 2016).

Abiotic and Anthropogenic Noise. In response to high levels of abiotic noise, some bird species may increase the amplitude of their songs as described by the Lombard effect. Birds may also increase the frequency of their songs in conjunction with an increase in amplitude, with studies suggesting that the increased amplitude for the Lombard effect may be associated with changes in song frequency, such as seen in the elegant crested tinamous (*Eudromia elegans*) as they sang at a higher frequency and amplitude when noise levels were high; however, this coupling of frequency and amplitude is not commonly seen in songbirds (Dorado-Correa et al., 2017; Nemeth et al., 2013; Schuster et al., 2012;). This difference in songbirds has been suggested to be due to physiological consequences of the vocal structures of these birds, such as the syrinx, which may be more refined in songbirds allowing for the uncoupling of the two different song properties (Dorado-Correa et al., 2017; Elemans et al., 2008). The Lombard Effect was also shown by Brumm (2004) in nightingales, where nightingales living in urbanized areas and experience a higher level of noise in their environment sang (at a higher amplitude) than their rural counterparts.

Multiple studies show the effect of increasing anthropogenic noise on bird vocalizations over the past 50 years. Recently, a study was done by Derryberry et al. (2020) that investigated the effect of abnormally low levels of human noise due to the COVID-19 lockdowns in California on white-crowned sparrow (*Zonotrichia leucophrys*) vocalizations. Derryberry et al. (2020) show that birds took advantage of this reversal in noise levels by producing songs with lower amplitude than those that appeared pre-lockdown, as they did not need expend extra energy to produce loud songs

to be heard over high noise levels. Birds also sang more high-performance songs, with a suggested explanation being that due to the low noise levels there is a decrease in masking of signals, meaning more females are able to hear the songs and rivals can more easily hear songs which impacts competition in male-male aggressive interactions.

Derryberry et al. (2020) further inferred that young birds learning during lockdown had a higher exposure to these high-performance songs, which may further impact how these birds sing post-lockdown when noise levels return to normal.

When in these noisy environments, birds can make other modification to their songs to be better heard by the receiver of their messages, for example, the great tit was shown to sing at higher frequencies to help prevent being masked by the common low-frequency noises in cities (Slabbekoorn & den Boer-Visser, 2006). In response to low frequency, anthropogenic noise song sparrows have been shown to change aspects of their songs (Wood & Yezerinac, 2006). Song sparrows living in noisy environments sang at higher frequencies than those living in quieter areas, as songs of low frequency would be masked by the noise. When singing songs of lower frequency, song sparrows also sang at a lower amplitude; therefore, not expending energy on signal that would not be easily heard by another conspecific (Wood & Yezerinac, 2006). Similar to the song sparrow, in response to noise, Black-capped chickadees were also shown to switch to a different frequency song to prevent being masked (Goodwin & Podos, 2013). Blackbirds (*Turdus merula*) were also shown to sing songs of higher frequency and amplitude when in the city to avoid noise interference in comparison to birds living in a forest, which also illustrated the connection of frequency and amplitude suggested by the Lombard effect (Nemeth et al., 2013).

Fuller and colleagues (2007) showed that European robins (*Erithacus rubecula*) modify their normal singing behaviour in response to anthropogenic noise by only singing at times where the interference from the noise is minimal, such as during the night. Another study done by Dominoni et al. (2016) showed similar results, where bird species living close to airports in Germany, where there are high noise levels, differed in the onset of their dawn chorus by starting 5-10 minutes earlier to have a longer period of dawn singing with low interference and would stop singing during the takeoff of planes to avoid the masking of their songs. In response to white noise, black-capped chickadees changed their vocal behaviour to avoid overlapping the stimulus and showed below chance levels of overlapping, which suggests that these birds may avoid abiotic noise in their environment that could interfere with the transmission of their songs (Wilson et al., 2016). The great tit also modified their signing behaviour in response to abiotic noise, as they sang at a higher song rate in comparison to birds living in rural areas, which was suggested to be a strategy to increase the likelihood of their songs being heard in a noisy environment (Slabbekoorn & den Boer-Visser, 2006).

While many species have been shown to use avoid being masked by abiotic and anthropogenic noise, there have been some contrary results surrounding avoidance of abiotic noise. This is seen in Bermúdez-Cuamatzin and colleagues (2018) on acoustic interference in Mexican bird species. It was shown that none of the species in the study actively avoided being masked by anthropogenic noise; however, all species studied avoided song overlapping from other conspecifics.

In summary, birds have multiple strategies to help them cope with acoustic interference. First, birds can increase the amplitude or loudness of their songs to help them be more likely to be heard over the noise in their environment. Second, birds can

change the frequency of their songs to avoid being masked by noise of the same frequency. Third, they can avoid overlapping their songs with the noise, to prevent the masking of their songs, as well as primarily singing during silent periods and avoid singing when noise levels are high. These strategies are used in response to both abiotic and biotic noise.

Biotic Noise from Heterospecific Songbirds. One strategy used by songbirds in relation to biotic noise of heterospecifics is the aforementioned avoidance of song overlapping. Planqué and Slabbekoorn (2008) investigated 20 different tropical bird species in Peru and demonstrated that all species avoided overlapping other species who sang at the similar frequencies and therefore had a high potential to mask their songs. Only 0.7% of the recordings used in the experiment showed overlapping and simultaneous singing by three or more species.

Similar results were seen in a study using 19 species in a northern forest in Wisconsin. Like the tropical birds, these birds changed their song timing to avoid overlapping each other's songs and would sing immediately after a particular heterospecific sang; for example, ovenbirds (*Seiurus aurocapilla*) would always sing directly after chestnut-sided warblers (*Setophaga pensylvanica*) had finished singing (Ficken & Popp, 1985). However, the wood thrush (*Hylocichla mustelina*) did not show similar vocal behaviour and did not avoid overlapping as often as other species, and Popp et al. (1985) showed that the other birds changed their song timing to actively avoid overlapping with this species or that the wood thrush may be more concerned with other conspecifics than members of other species. Also, in response to heterospecific songs, nightingales also alter the timing of their songs to fit in the silent intervals between other birds' songs, thus preventing song overlapping (Brumm, 2006).

Another concept related to acoustic interference is the birds' placement in the environment and the division of the acoustic environment to best avoid interference from other birds in the same environment. Luther (2009) performed a study looking at an acoustic environment with 82 different rainforest birds to investigate the species' methods of avoiding acoustic interference. This study showed that the species positioned themselves around the environment, as to avoid neighbours that may have similar songs that would mask theirs. Birds on the outer edges of the environment were shown to be more spread out, and therefore face less interference and masking than birds positioned closer to the centre of the environment as there was less space between neighbours and more opportunity for interference. To compensate for this and help ensure their song is being heard by other conspecifics, the birds near the centre would sing more than those living near the edges (Luther, 2009).

While birds can face much interference and noise from other bird species in their environment, they also face potential interference from non-avian species. For example, cicadas have been shown to sing at medium and high frequencies that could mask a birds' songs, causing the birds to sing at lower frequencies (Planqué & Slabberkoorn, 2008). In addition, frogs can also impact signaling efficacy (Planqué & Slabberkoorn, 2008).

Biotic Noise of Conspecifics. In relation to avoiding songs of other conspecifics, the main method to avoid masking and interference is to alter song timing to avoid overlapping songs with another individual, as discussed when looking at the connections between song overlapping and aggression where avoiding overlapping is important to adequately convey information. For example, Nielsen and Vehrencamp (1995) show that avoidance of song overlapping is seen in song sparrows. In their study, song sparrows

were shown to avoid song overlapping while counter-singing to avoid being masked by the other birds' song, particularly in an aggressive context (Nielsen & Vehrencamp, 1995). In a study done by Wilson and colleagues (2016), black-capped chickadees were exposed to a stimulus of conspecific songs to investigate song overlapping and its relation to interference avoidance. In response to the conspecifics, 96% of subjects were shown to overlap the stimulus at below chance levels, possibly suggesting that the birds changed their song timing to avoid overlapping another bird's songs, and therefore avoided acoustic interference (Wilson et al., 2016).

Still more studies have investigated the avoidance of song-overlapping in a non-aggressive context. Ovenbirds have also been shown to avoid overlapping their songs with those of other conspecifics (Ficken et al., 1985). The white-throated sparrow (*Zonotrichia albicollis*) showed similar behaviour, where in response to other conspecifics they avoided overlapping their songs. This avoidance was shown to be highest in neighbouring conspecifics due to their spatial location and therefore increased possible acoustic interference with one another (Wasserman, 1977). This avoidance of overlapping neighbouring conspecifics was also seen in European robins, in comparison to stranger songs the birds showed higher avoidance of overlapping for neighbour songs and the highest avoidance of those neighbours closest to them due to the higher level of interference that may cause (Brindley, 1991).

In summary, the active avoidance of acoustic interference can be seen throughout the animal kingdom. In songbirds in particular, the research shows that they actively and selectively avoid noise that would mask their signals and impair their communication abilities, while not responding to those noises that do not inhibit the recognition of their signals by conspecifics, such as those at a different frequency level to their own songs.

Changes to song timing to avoid overlapping has been shown to be a primary method to avoid interference from other birds, and not just in aggressive contexts. Some researchers have suggested, since it is used as a way to avoid songs of both conspecifics and heterospecific, as well as have an important function in helping to attract a mate as females are better able to hear their songs.

In relation to abiotic noise, birds commonly show other behaviour such as changes in song frequency, song rate, and song amplitude. Some species also attempt to minimise the interference by avoiding the noise altogether by singing during quiet periods, or predictable periods of lower noise levels. There are also implications of noise and noise avoidance on mate attraction and selection, since when a bird sings to attract a mate and their signals are masked the female loses the ability to assess the male's quality as a mate. This means they are not able to adequately assess the repertoire size or the song rate of the male, which lowers the male's fitness as they may have difficulty attracting a mate. Also, the female may not be able to detect the male's *sexy syllables*, which are song portions that are highly complex and energetically expensive to produce and are especially attractive to females (Vallet et al., 1998). The relationship between high noise levels and the ability to attract a mate can be seen in a study done by Luther et al. (2015), where birds facing high levels of anthropogenic noise were suggested to have a decreased signaling performance and a decreased ability to attract a mate. Avoidance of overlapping abiotic noise is not seen as commonly in the literature as abiotic noise shows more variation and less predictability in duration and its acoustic properties, especially with anthropogenic noise. Meaning, depending on the abiotic noise stimulus presented to the birds, the appropriate method to remove the interference may change, which suggests avoidance of the specific noise may not be the most beneficial

option. It is possible that birds may treat conspecific songs as they treat any other noise that may interfere with communications and try to avoid being masked by their noise; however, this remains to be seen.

Current Study

Background on Hermit Thrush

The current study investigated the function of song overlapping specifically in hermit thrush. The hermit thrush is a species of territorial songbird that is native to North America. They spend their breeding season during the spring and summer in the Northern United States and Canada and migrate to the southern United States and areas surrounding the Gulf of Mexico for the winter (Dellinger et al., 2012). Based on variations in song characteristics, such as frequency and length of songs, some researchers suggest that there are multiple subspecies of hermit thrush, with suggested numbers of subspecies being as high as 12; however, the divisions and the exact number is debated (Rivers & Kroodsma, 2000; Roach & Phillmore, 2017). One of the most commonly seen divisions of this species is into Western and Eastern populations, and the birds are classified based on where they spend the breeding season and show some variation in their songs (Dellinger et al., 2012; Roach & Phillmore, 2017). Some researchers have gone as far as to suggest that birds in these two different groups could be considered separate species due to significant genetic differences (Alvarado et al., 2014). The population of this study will be individuals of an eastern population.

The repertoire of these birds ranges from 6-12 distinct song types, with the number varying depending on where a bird lives (Rivers & Kroodsma, 2000; Roach et al., 2012). An example of an individual's repertoire can be seen in Figure 1. Specific

song-types are unique to an individual bird, creating unique repertoires that have been shown to be helpful in discerning specific individuals (Rivers & Kroodsma, 2000; Roach et al., 2012). While each bird has their own set of song types, all song types are composed of two sections: a single introductory note, followed by a complex post-introductory section containing a flurry of notes (Dellinger et al., 2012; Rivers & Kroodsma, 2000). The introductory note of these songs usually falls above 4000 hz or below 3000 hz, leaving a frequency gap which allows for the division of their song types into high or low songs, with high songs falling above 4000 hz and low songs falling below 3000 hz (Roach et al., 2012).

Hermit thrush have been shown to follow some syntactical rules while they sing. They have been shown to produce bouts of low songs that are interrupted with a high song, and the same song types are not used in consecutive sequence (McLean & Roach, 2020; Rivers & Kroodsma, 2000; Roach et al., 2012). Rivers and Kroodsma (2000) also show that hermit thrush may sing with a moderate level of predictability, where some song types are more like to follow a specific type than another in the bird's repertoire, which has been supported by other studies (Roach et al., 2012)

In regard to song overlapping in eastern populations of hermit thrush, preliminary data collected from using a simulated territorial intrusion showed that hermit thrush would overlap their rival at below chance levels, suggesting that they were avoiding the possible interference of their signals by their rival; however, the association between song overlapping and level of physical aggression could not be investigated due to lack of precision in measuring physical behaviour (DeMerchant & Roach, 2021).

Current Study

In this study, song overlapping was further investigated in both aggressive and non-aggressive contexts. Song overlapping in an aggressive context was explored using playback experiments to simulate a territorial intrusion by another hermit thrush. Aggression was also measured for each bird to further investigate the link between the amount of physical aggression shown by a bird and levels of song overlapping. In addition to this, playback experiments were also performed using a stimulus of songs from a congener species, the white-throated sparrow, to investigate overlapping in connection with heterospecific songbirds in the environment. This method of using playbacks to study song overlapping has been seen in studies that include Wilson et al. (2016), where overlapping of conspecifics and abiotic noise was explored in black-capped chickadees. To look at avoidance of overlapping during counter-singing interactions between conspecifics, recordings of counter-singing between hermit thrush from past field seasons were analyzed.

The objective of this study was to further our understanding of the function of song overlapping in songbirds, specifically the hermit thrush, and how this species balances the pressures of aggressive behaviour and acoustic interference avoidance. The primary objective of this study was to investigate song overlapping in response to an aggressive conspecific. The secondary objective is to investigate song overlapping during counter-singing with a neighbouring conspecific and in response to a heterospecific songbird in their environment. Based on the interconnectedness of aggressive signalling and acoustic interference, with the concepts not being mutually exclusive, and the current lack of understanding on how this species uses song overlapping in different behavioural contexts, no specific hypotheses were made.

Method

There were two components to this study: playback experiments and recordings of counter-singing interactions between hermit thrush. The playback experiments were used to investigate song overlapping in response to songs of a rival conspecific and songs of a heterospecific songbird. Natural counter-singing was assessed using past recordings from the 2018 and 2019 field seasons.

Recording Sites and Subjects

The playback data was collected in Saint John, New Brunswick and surrounding areas between May and July 2021. Subjects were selected when encountering individuals exhibiting spontaneous singing, with locations chosen based on previous knowledge of hermit thrush territories in Kingston, Hampton, Kennebecasis Valley, and Saint John. Playback experiments were performed around dawn (5:00am-10:00am), as this is the time when male hermit thrush have the highest levels of spontaneous singing.

Part I: Conspecific and Heterospecific Playback

To assess how overlapping relates to aggression in conspecific playback, and how these levels of song overlapping when aggressive compare to those seen in response to heterospecific playback, this study had a between-subjects design. Between-subjects designs are commonly used when investigating song overlapping, especially when there is relatively large sample size, such as seen in studies done by Wilson et al. (2016) and Naguib and Kipper (2005). In regard to hermit thrush in New Brunswick, it is possible that they have larger territories in comparison to other populations such as those in Nova Scotia, and in response to a conspecific stimulus they will move to other parts of their larger territories. This has caused issues when using within-subject playback

experiments in the past as it becomes difficult to relocate and identify individuals for future treatments. This makes the between-subjects design the more feasible option when multiple treatments are being used. Each bird was presented with either a stimulus of conspecific songs or a stimulus of heterospecific songs.

Playback Stimuli

The conspecific stimulus used for the aggressive treatment were composed of previously recorded hermit thrush songs from 2018-2019 (see Figure 2A). The selected recordings were from birds that were thought to be unfamiliar to the those used in the study. Using unfamiliar birds is important as it has been shown that birds react differently to the songs of a neighbour bird, which they recognize, and those of a stranger (Skierczynski et al., 2007). The birds used for the playback stimuli were divided into three categories based on where they were recorded in Saint John: East, West, and Central. Birds were always presented with a stimulus that were not recorded in their area, meaning a bird in West Saint John was never presented with a stimulus created from a bird in the same area. This means, the target bird and stimulus bird were recorded approximately 17 km apart. It has been shown that using neighbouring birds for a stimulus can alter the response of the target bird, and by using birds unfamiliar to the subject the confounding effects of familiarity can be avoided (Temeles, 1994). Other criteria for selecting recordings included having high quality and clear vocalizations, and low background noise levels in the recordings as to not impact the clarity of the songs. The created stimuli were manipulated to have relatively the same song rate of 13 songs per minute, which was similar to the average natural song rate of the hermit thrush (Roach et al., 2012). This song rate was determined by averaging the song rate from recordings of hermit thrush collected in 2020. The use of a rate similar to the natural

song rate is commonly used when investigating song overlapping, such as seen with Wilson et al. (2016). All manipulations were done by using Audacity, an audio editing software. A high pass filter (1500hz) was also applied to the selected song sequences to remove background noise to ensure stimuli of high clarity.

For the playbacks investigating song overlapping in relation to heterospecific song, stimuli were composed of songs from white-throated sparrows (see Figure 2B). This species was selected as they are commonly seen in the same environment as hermit thrush and could have the potential to mask the songs of the hermit thrush as they sing at a similar frequency range. Like the hermit thrush stimuli, the song rate will be similar to the species' normal song rate and will be made from recordings with low levels of noise and high clarity of vocalizations. Both types of stimuli were three minutes long, as this has been shown to be an adequate duration to elicit a response by a bird, but not cause a lasting disruption to its behaviour (Nesbitt, 2020; Roach, 2016). The recordings were selected from Macauley Library and Xeno Canto, which are databases of songbird recordings. The stimuli recordings originated from Maine, New Hampshire, Quebec, and Prince Edward Island. The ID numbers of the recordings used for the stimuli were XC296910, XC424319, XC626756, XC600773, XC294259, XC139053, and XC13627. The quality of recordings was controlled for to ensure that different levels of background noise were not impacting a bird's responses to the introduced stimulus.

Playback Equipment and Procedure

In regard to playback experiments, both treatments followed the same procedure. Once a hermit thrush is located, a Sony SRS-XB12 wireless speaker was set up on the bird's territory and markers indicating distances of 4m and 8m from the speaker were placed to create an arena with an 8m radius. The bird was recorded for approximately

five minutes as a pre-playback session to understand different aspect of the bird's vocal behaviour, such as their song rate and timing, which could then be used to see how the bird may change its vocal behaviour response to the presented stimulus. All vocalizations were recorded using a Zoom H6 recorder held by the experimenter. After the pre-playback session, a stimulus selected by the researcher on an iPhone was played from the speaker at a sound level of 80 dB from one metre.

The experimenter narrated the target bird's physical behaviour and movements throughout the playback session to understand the response the stimulus elicited from the bird. Measures of behaviours included the average distance a bird approached the speaker, the distance of the closest approach to the speaker, the length of time a bird spent within 5 m of the speaker, the number of times the target bird swoops within 5 m of the speaker, the length of time it takes for a bird to approach to within 5 m of the speaker, and the latency of the first swoop within 5 m of the speaker. These six variables have been shown to adequately describe the physical response of a bird to a playback stimulus (Nesbitt, 2020; Nielsen & Vehrencamp, 1995; Roach, 2016). The bird was recorded for another five minutes after the stimulus ended as a post-playback session to see how the bird's singing might have changed as a result of the stimulus. Each individual was exposed to only one of the two treatments, with a total of 31 birds receiving the conspecific stimulus and 32 birds being exposed to the heterospecific stimulus.

Analysis of Vocalizations

Both sections of this experiment had similar methods of analysis. Recordings were analyzed by viewing spectrograms of the recordings on Raven Pro 1.5. The window size of each recording was set to 1000, while other settings such as brightness

and contrast were adjusted for each individual recording to maximize the clarity of the bird's vocalizations. In Raven, selection boxes were drawn around each of the subjects' vocalizations, as well as the vocalizations of the playback stimulus. The Raven measurements "Begin Time" and "End Time" indicated the start and end of each vocalization. These values were used in the analysis of overlapping, as described below.

Song Overlapping. Song overlapping of playback songs by the subjects were analyzed using the package Song Overlapping Null Model Generator (SONG; Masco et al., 2016) in R (R Core Team, 2020). SONG, which compares the amount of observed overlapping behaviour to that expected by chance, has been used in recent studies of song overlapping behaviour in birds (Hart et al., 2021; Hutfluss et al., 2021) and other animals (Allen-Ankins & Schwarzkopf, 2021). SONG analyzes overlapping behaviour via two methods. In one, the observed number of subject songs that overlap playback songs is compared to the expected number of subjects songs that do so. In the other, the amount of time the subject spends overlapping subject songs is compared to that expected by chance. Thus, in each case, the value representing observed overlapping behaviour is calculated by SONG based on the data related to song timing generated by Raven and imported into R. Assessment of overlapping in terms of number of subject songs that overlap playback aligns most closely with how signal overlapping has been analyzed in the past (Ficken, 1974). Assessment in terms of amount of time subject spend overlapping playback has also been used and provides a non-binary approach. Thus, both methods were included here.

In both cases, expected overlapping was calculated based on the amount of overlapping within randomized interactions constructed by SONG. To do so, SONG generated 1000 randomized interaction between subjects and playback, which

represented a null distribution representing expected overlapping behaviour for comparison to observed overlapping. Among the null models available, the SampleGaps method, which maintains information about song duration and randomizes the gaps between signals, was used. According to Masco et al. (2016), this model is suited to highly variable timing, as seen in hermit thrush males during playback sessions. The observed amount of overlapping was then statistically compared to the expected amount of overlapping according to the null distribution, thus testing the null hypothesis that the subject overlapped playback songs at expected, or chance, levels. Using an alpha level of 0.05, significant deviation from chance levels of overlapping were represented by p -values less than 0.025 (interpreted as overlapping more than would be expected by chance based on the null distribution) and p -values greater than 0.975 (interpreted as overlapping less than expected by chance).

In order to better compare the amount of overlapping seen in each behavioural context and to assess the relationship between overlapping and physical responses to playback, normalized rates of overlapping were calculated. This was done by dividing the observed overlapping by the expected overlapping value that were provided by SONG. Thus, a normalized overlapping rate of 1.0 represented chance overlapping, while values above and below 1.0 represented overlapping that occurred at greater than and less than chance levels, respectively.

Song Rate. Song rate was calculated for the pre-playback section of the conspecific treatments to determine the baseline song rate of the bird. Depending on the quality of the recording, a range of three-to-five minutes of the pre-playback session were analyzed to determine song rate. The song rate was also calculated during each playback session to see how it may have changed as a result of the stimulus. This aspect

of vocal behaviour is important to consider as there may be changes to the base song rate in response to a stimulus to avoid song overlapping, especially when aggressive, as suggested by Yang et al. (2014). Song rate was defined as the number of songs a bird sings per minute and was calculated by dividing the total number of songs a bird produces by the total length of the recording.

Measurements of Physical Response. During the playback recordings, the experimenter narrated the physical behaviour of the target bird, as mentioned above. The amount of overlapping was compared to the measurements of physical response to determine if there is a connection between aggression and song overlapping, as suggested by some researchers.

Statistical Analysis

Statistical analyses for this study were performed using SPSS and R statistical software. As described above, observed overlapping was statistically compared to that which would be expected by chance using the R package SONG. In that case, $p \geq 0.975$ was interpreted as representing overlapping below chance levels and $p \leq 0.025$ was interpreted as representing overlapping at above chance levels.

To investigate the relationship between rates of overlapping and measurements of physical response, a principal component analysis (PCA) was run using SPSS to determine how many variables would be taken into consideration to determine the relationship. Once this was done, bivariate correlations were run to investigate the relationship between the variables of aggression and the normalized rates of overlapping for the conspecific treatment.

To compare the amount of overlapping seen in both the conspecific and heterospecific playback groups, a t -test was run. To determine if there were differences

in the proportions of overlapping on non-overlapping birds seen in the two groups, a binary logistic regression was run.

To further investigate the relationship between aggression and song overlapping, bivariate correlations were run between the song rate and changes in song rate and each of the two measures of overlapping. A change in song rate was considered to be the absolute difference between the base song rate which was determined during the pre-playback section of the recording and the song rate determined from the playback section of the recording. A *t*-test was also run to determine if the change to song rate as a result of the stimulus was significant. For the conspecific playback group, a total of 29 birds were included in the analysis, with two birds being removed due to the lack of clarity in the recordings and the presence of a second bird. For the heterospecific playback group, two subjects were removed due to lack of vocal response in one and lack of clarity in another, for a total of 31 individuals included in the analysis.

Part II: Recordings of Counter-singing

In the second part of the experiment, song overlapping was assessed among males engaged in natural vocal interactions. As only a few usable recordings containing counter-singing were collected during the 2021 field season, this group of recordings was supplemented recordings from previous years that contained bouts of counter-singing. The criteria for selecting a recording were high quality with low levels of background noise and three-to-five minutes of consistent counter-singing behaviour. In total, 21 pairs were included in the analysis for this group, for a total of 42 birds. To make comparisons among groups, a random sample of 21 birds (one from each pair) were selected to meet the fundamental assumption of independence of observations.

Analysis of Vocalizations

In relation to the recordings of spontaneous singing, these recordings were also analysed using Raven for song overlapping, as done with the playback recordings in Part I.

Song Overlapping. For overlapping with recordings of spontaneous singing, observed proportions of overlapping were calculated in the same way as done with the playback studies, using Masco et al.'s (2016) method. In these recordings, there were vocalizations from two different birds and overlapping was assessed from the perspective of each individual, meaning each bird was given observed and expected measures of overlapping, with each bird acting as a stimulus for the other.

Statistical Analysis

Each bird's singing will be used to determine the expected value for the other bird. To make comparisons across the three groups (aggressive conspecific, heterospecific songs, and counter-singing) the normalized rates of overlapping were first calculated. As mentioned above, only 21 randomly selected birds using an online random number generator (numbergenerator.org), with one bird from each pair being included in this part of the analysis to maintain independence of observations. As the counter-singing group was non-parametric, a Mann-Whitney U test was used to compare counter-singing to both playback groups in relation to both measures of overlapping. A binary logistic regression was also run, with the outcome variables being whether the bird overlapped the stimulus at below chance levels, to determine if the proportion of individuals that avoided song overlapping varied between the three groups.

Results

SONG Analysis

The R package, SONG, was used to assess rates of overlapping relative to chance in the three groups (i.e., conspecific playback, heterospecific playback, and counter-singing); the raw data relating to all subjects in each behavioural context can be found in appendices A-C and the results of the SONG model are summarized in Table 1.

Examples of song overlapping in the cases of conspecific and heterospecific playback can be seen in Figure 3. In the conspecific playback group, a total of 29 birds were included. Of these 29 individuals, 15 exhibited below chance levels of song overlapping (i.e., avoided song overlapping; $p > 0.975$) based on time spent overlapping. Based on the second measure, the number of times the bird overlapped the stimulus, 12 of the 29 birds had below chance levels of overlapping. No birds were shown to have above chance levels of overlapping (i.e., actively overlapping the stimulus).

For the heterospecific treatment group, a total of 31 individuals were included in the analysis. Of these 31 birds, only three individuals avoided overlapping the stimulus when looking at each measure of overlapping. One bird overlapped the stimulus more than expected by chance and the other 27 birds showed chance levels of overlapping.

For the counter-singing group, 21 pairs of birds were included in this part of the analysis for a total of 42 individuals. In total, 31 birds avoided overlapping while counter-singing, based on time spent overlapping, with the rest showing chance levels of overlapping. Based on the time spent overlapping, 12 pairs showed avoidance of overlapping by both birds involved. In six of the pairs, it was shown that one individual was avoiding overlapping. In the other three pairs both birds showed chance levels of overlapping. Based on the number of times overlapping occurred, 26 birds avoided

overlapping and all other birds showed chance levels. For this measure of song overlapping, overlapping avoidance exhibited by both birds occurred in nine pairs. For seven pairs, overlapping avoidance was shown by one bird in a pair while the other showed chance levels of overlapping. In the five other pairs, neither bird avoided overlapping the other and showed chance levels of overlapping. In summary, in roughly half of the counter-singing bouts included in the study, both participants timed their songs to avoid overlapping each other. In other cases, this was exhibited by only one – or occasionally neither – participant.

Once the SONG model was run, the normalized rates of overlapping were determined for all individuals for each of the two measures of overlapping. A comparison of the normalized rates of overlapping for each group can be seen in Figure 4.

Differences in Overlapping Between the Conspecific and Heterospecific Playback Groups

To determine if there was a difference in the mean rate of overlapping between the heterospecific and conspecific playback groups a *t*-test was used. It was shown there was a significant difference between these groups for both the amount of time spent overlapping, $t(58) = 8.865, p < .001$, and the number of times overlapping occurred, $t(58) = 12.064, p < .001$. Based on the means of these groups, the heterospecific groups showed higher levels of overlapping for both measures.

To determine if the proportion of individuals that avoided overlapping varied between the heterospecific and conspecific playback groups a binary logistic regression was run on each of the two measures of song overlapping. The predictor variable used

was social context (conspecific and heterospecific). This variable was found contribute to the overall model, in regard to both time spent overlapping, $\chi^2(1) = 13.42, p < .001$, and the number of times overlapping occurred, $\chi^2(1) = 6.412, p = .011$. Relative to the heterospecific group, the conspecific group showed significantly higher proportions of overlapping avoidance for both time spent overlapping ($p = .001$) and the number of times overlapping occurred ($p = .017$). The results of these two tests suggest that the conspecific group is showing more overlapping avoidance than the heterospecific group.

Differences in Overlapping among the Three Groups

The normalized rates were compared between the counter-singing group and conspecific playback group, and the counter-singing group and heterospecific playback group on both measures of overlapping. This was done using a Mann-Whitney U test, as the normalized rates of overlapping for the counter-singing group were not normally distributed.

When comparing the conspecific playback and counter-singing groups both the number of times the birds overlapped, $U = 272, p = .523$, and time spent overlapping, $U = 301, p = .945$, showed no difference between the two groups.

When comparing the heterospecific playback and counter-singing groups both the number of times the birds overlapped, $U = 181, p = .007$, and the time spent overlapping, $U = 130, p < .001$, showed there was a statistically significant difference between the two groups. Based on the mean, the normalized rates of overlapping are higher for the heterospecific playback group than the counter-singing group.

To determine if the proportion of individuals that avoided overlapping varied among the three groups a binary logistic regression was used for each measure of song

overlapping. The predictor variable, social context (conspecific playback group, heterospecific playback group, counter-singing group), was found to contribute to the overall model in regard to time spent overlapping, $\chi^2(1) = 22.08, p < .001$, and the number of times overlapping occurred, $\chi^2(1) = 12.59, p = .002$. For time spent overlapping, it was shown that relative to the conspecific group, counter-singing showed a similar proportion of overlapping avoidance ($p = .293$). In addition to this, it was shown that relative to the heterospecific playback group, the proportion of birds that avoided overlapping was significantly higher in the counter-singing group ($p = .001$) and the conspecific group ($p < .001$). For the number of times overlapping occurred, it was shown that relative to the conspecific playback group, the counter-singing groups did not show a significant difference in the number of birds that avoided overlapping ($p = .273$), Relative to the heterospecific playback group the counter-singing group ($p = .002$) and the conspecific group ($p = .017$), showed a significantly higher number of individuals that avoided overlapping.

Association Between Aggression and Song Overlapping

In response to the conspecific playback, 27 of the 29 birds showed a physical response associated with aggression. The criterion for a physical response was the entrance into the arena by the individual. None of the birds in the heterospecific playback group entered the area, meaning they exhibited not physical response. Because only the conspecific group showed aggressive responses to playback, aggression and overlapping were compared only in the conspecific playback group. Response variables were not measured for the counter-singing recordings selected from the database and counter-singing was considered a non-aggressive conspecific interaction.

A PCA was run to group related variables together and reduce dimensionality of data. The analysis included the six variables of aggression that were measured during the conspecific playbacks. The PCA resulted in two principal components extracted that had eigenvalues greater than one, together explaining 89.729% of variance in the six measured variables, as shown in Table 2. Based on the factor loadings in Table 2, principal component one (PC1) represented a bird's location and approach towards the speaker. Principal component 2 (PC2) represented flight and swooping behaviours exhibited by a bird.

In terms of times spent overlapping, normalized rates of overlapping were associated with neither PC1 ($r = .075$, $p = .816$; see Figure 5A) or PC2 ($r = .045$, $p = .654$; see Figure 5B). Similar results were detected between the normalized number of times a bird overlapped the stimulus and PC1 ($r = .087$, $p = .654$) and between this measure and PC2 ($r = -.252$, $p = .187$). In addition to this, there were no significant correlations between either measure of song overlapping and the six individual measures of physical aggression, as shown in Table 3. In summary, there was no association between the aggressiveness of the birds' physical responses to conspecific playback and the degree to which they overlapped the playback songs.

Association Between Song rate and Song overlapping

The baseline song rate was determined from the pre-playback section ($M = 12.01$ songs/minute, $SD = 2.29$) of the conspecific playback, along with the during-playback song rate ($M = 9.95$ songs/minute, $SD = 5.09$), and it was shown that there was shown to be a statistical decline in song as a result of the stimulus, $t(28) = 10.529$, $p < .001$. To see if there was an association between song rate and song overlapping, bivariate

correlations were run between the song rates exhibited by subjects during the conspecific playbacks and both measures of normalized song overlapping. No significant correlations were seen between song rate and number of times overlapped ($r = .088, p = .649$) or between song rate and time spent overlapping ($r = .146, p = .451$).

The relationship between changes in song rate and overlapping was also assessed for the conspecific treatment. There was no significant relationship between changes in song rate and either number of times a bird overlapped the stimulus ($r = -.082, p = .672$; see Figure 6) or the amount of time spent overlapping ($r = -.274, p = .150$). In addition to this, changes in song rate were shown to not be associated with either PC1 ($r = -.156, p = .418$) or PC2 ($r = -.079, p = .683$). In summary, there was no association seen between song rate and degree of physical aggression, or between song overlapping and song rate. This suggests that changes in song rate are not responsible for the appearance of overlapping behaviour.

Discussion

The purpose of this study was to explore the extent and function of song overlapping in hermit thrush, and how this species balances the pressures of aggression and acoustic interference avoidance. This was investigated by looking at song overlapping in response to conspecific and heterospecific playback, as well as during natural counter-singing interactions between neighbouring males. Overlapping was compared across the three groups and the link between song overlapping and aggression was explored. When comparing the levels of overlapping for each group, the counter-singing and conspecific playback groups showed similar levels of overlapping avoidance. The majority of the birds in the heterospecific playback group did not avoid

overlapping and showed chance levels. Based on proportions of birds avoiding overlapping, the counter-singing group and conspecific group had the most birds avoid song overlapping, and the heterospecific group had the fewest amount of birds avoid overlapping. Overall, there was shown to be no association between aggression and song overlapping. Some findings were in line with past research on other species, such as the lack of relationship between aggression and song overlapping; however, other findings were not. For example, in this study the birds did not avoid the acoustic interference from another songbird species in their environment which is shown in many other types of songbirds. The results from each of the three groups will be discussed in turn.

Vocal Behaviour and Aggression

One of the primary goals of this study was to investigate the proposed link between song overlapping and aggression and its use as an aggressive signal. Many past studies have shown results that both support and refute this relationship, where some species showed above chance levels of song overlapping while others showed at chance or below chance levels when aggressive. In this study, the relationship between song overlapping and aggression was investigated by looking at the physical and vocal response of the conspecific playback group. The vocal behaviours that occurred during simulated territorial intrusions, including song overlapping, were examined in a previous study on hermit thrush. In the study done by DeMerchant and Roach (2021), song overlapping avoidance was shown in just over 50% of individuals in the sample, with the rest showing chance levels of overlapping and no birds overlapping the stimulus at above chance levels. Similarly, in the current study, above chance levels of song overlapping were not present in the aggressive context. In addition to this, just over half

of the birds in the study ($n = 15$, 52%) avoided overlapping the playback stimulus, while the remaining birds in the study ($n = 14$, 48%) showed chance levels of overlapping. Although the hermit thrush showed chance and below chance levels of song overlapping in both studies, according to Naguib and Mennill (2010) this does not discount song overlapping as a potential adaptive behaviour or discount it as a behaviour and the context of its use needs to be considered.

Unlike in the study done by DeMerchant and Roach (2021), the current study directly examined the relationship between song overlapping and aggression using six different physical response variables to reliably determine the aggressiveness of a bird. In this study, 27 of the 29 birds included in the analysis exhibited a physical response to the stimulus, as indicated by entry into the arena.

There was no association between aggression, as represented by the two principal components, and the amount of song overlapping. The relationship between song overlapping and aggression is highly debated, with some studies showing support for the relationship. This was seen in a study done by Naguib and Kipper (2005) who investigated song overlapping in nightingales, which showed that birds who had the highest degree of overlapped songs were the most aggressive, and that as overlapping increased so did aggression. In a study using corn buntings, Osiejuk et al. (2006) suggested that overlapping may be a high-level threat, based on the reluctance of birds to approach the speaker. In their study, Maynard et al. (2012) looked at overlapping in long-tailed manakins using recordings of natural interactions and playback studies. Birds showed above chance levels of overlapping in response to the simulated rival during the playback and it may be an important signal to convey aggressive intent (Maynard et al., 2012).

In contrast, many studies including most recent ones, have found no association between aggression and song overlapping. Playback studies like the current study have found that overlapping is either unassociated with aggression (Dabelsteen et al., 1997; Hutfluss et al., 2021; Yang et al., 2014) or negatively associated with aggression (Ackay et al., 2019; Wilson et al., 2016). Interactive playback studies have shown similar results, for example Dabelsteen et al. (1996) explored whether song overlapping was an aggressive signal in the great tit. There was no difference in the response of a bird when it had its songs alternated compared to when it had its songs overlapped (Dabelsteen et al., 1996). In another study by Dabelsteen et al. (1997) that looked at song overlapping in robins, there was no change in aggressiveness in response to having their songs overlapped at the varying amounts of the three conditions. Similar results were also seen when looking a natural conspecific interaction, such as seen Fitzsimmons et al. (2008) which showed no relationship between song overlapping and aggression in black-capped chickadees. Another study showed that there is no association between song overlapping and aggression in Eurasian wrens (Yang et al., 2014). Wilson et al. (2016) also showed below chance levels of overlapping in black-capped chickadees in response to a simulated territorial intrusion.

To further investigate the link between song overlapping and physical aggression, one can refer to the criteria of aggression suggested by Searcy and Beecher (2009) that need to be met for a signal to be aggressive. The current study was able to establish that two of the three criteria were not met. First, the context criterion was not met in this study because the rates of overlapping were not significantly different between the aggressive playback group and the non-aggressive counter-singing group. Second, the predictive criterion not met, as increased aggression and the measures of

aggression themselves were not associated with the levels of overlapping seen in the birds, and song overlapping was independent of aggression. The results seen in the study agree with those seen in some studies, but it is in contradiction to what is seen in others.

One explanation for the avoidance of song overlapping in this group is acoustic interference avoidance. According to this explanation, the birds are not avoiding overlapping because they are aggressive, but they are instead potentially avoiding overlapping because it is more conducive to their ability to communicate with their rival by allowing their rival to hear their signals. Acoustic interference avoidance can be seen in a variety of different taxa, including mammals, amphibians, and insects. Animals have been shown to avoid interference from a variety of different sources, such as biotic noise from the same and other species in their environment, abiotic noise such as from wind and running water, as well as anthropogenic noise. This explanation for avoiding song-overlapping in songbirds was explored by Brindley (1991), where it was proposed that instead of song overlapping and avoidance of overlapping associated with, specifically the avoidance of song overlapping could instead be a way to avoid acoustic interference and aid in adequate conveyance of signals between individuals. This is especially relevant when interacting with neighbouring birds within a close range. Similarly, in the study done by Wilson et al. (2016), black-capped chickadees exhibited below chance levels of song overlapping, with the lowest levels of overlapping being seen in those individuals who had the closest approach to the sound source during the playback experiments. This means the highest levels of avoidance are seen when a bird is in a position where the potential for interference from the stimulus is highest. In addition to this, when the amplitude or loudness of the stimulus was manipulated, the birds increased their levels of avoidance as the amplitude increased. Wilson et al. (2016)

suggests that a primary function of song overlapping when interacting with conspecifics is not aggression, but instead a mechanism used to avoid acoustic interference.

While many birds did avoid song overlapping when aggressive, there were many that showed chance levels of overlapping. Based on acoustic interference avoidance a possible explanation for this is looking at how far a bird was away from the speaker. For example, if a bird was far away from the speaker projecting the stimulus, it may perceive less of a need to avoid overlapping the stimulus songs as they may not be perceived to be causing acoustic interference (Naguib & Mennill, 2010). The different use of song overlapping by these birds illustrated the idea proposed by Logue (2021), which suggests the importance of context when investigating this signal.

Recent reviews of research done on song overlapping behaviour show that most species exhibit below chance levels of overlapping, especially when interacting with other conspecifics in their environment, lending support to the idea that song overlapping is primarily a method of avoiding acoustic interference (Masco et al., 2015; Searcy & Beecher, 2009). In summary, the hermit thrush is potentially not avoiding song overlapping to illustrate aggressive intent or use it as an aggressive signal; they are instead attempting to avoid overlapping the songs of another conspecific that could potentially mask their songs, which in this context would impede their ability to convey aggressive intent to a rival.

Another possible explanation for the results seen in the current study is suggested by Hutfluss et al. (2021), where there was no association between aggression and song overlapping in great tits. Like with the hermit thrush, this species showed both overlapping avoidance and chance levels of overlapping. Hutfluss and colleagues (2021) further suggested that while song overlapping is not aggressive, it may still be used in

aggressive context as a method to indicate ‘non-engagement’ by an individual. In this study, by using playback studies, just over 20% of birds avoided overlapping when aggressive, and almost 77% of birds showed chance levels of overlapping. To explain this, they proposed the idea of nonengagement, which is connected to a bird’s motivation and willingness to engage in an aggressive interaction.

Another possible explanation for the results of the current study is that song overlapping, and the avoidance of overlapping may be a by-product of changes in a bird’s song rate when they are aggressive (Baker et al., 2012). In the current study, while song rate did not predict aggression, hermit thrush decreased their song rate in response to the conspecific stimulus, which was also seen in previous results (DeMerchant & Roach, 2021). While in the current study song rate decreased significantly during the aggressive conspecific playback, song rate during the playback and the change in song rate from the pre-playback to playback sessions were not significantly related to the amount of song overlapping exhibited by the birds. In addition to this, song rate and changes in song rate were not associated with the measures of aggression, meaning song rate and changes to song rate do not predict aggression in this species.

In regard to the relationship between song overlapping and song rate, the results of this are contrary to what is seen in other species such as wood warblers (Vehrencamp et al., 2007). In the study done by Vehrencamp et al. (2007) higher song rates were associated with higher levels of song overlapping. In addition to this Yang et al. (2014) suggested that variations in song overlapping avoidance in Eurasian wrens can be explained by changes in song rate. The findings of the current study do not support the idea that levels of song overlapping would be dependent on changes to song rate when a bird is aggressive. Species may change their song rate when aggressive, as the hermit

thrush did in the current study, but that does not mean that they also avoid overlapping or show above chance levels of overlapping a stimulus. This can be seen in a study done by Baker et al. (2012), where birds changed their song rates in response to rival but did not use song overlapping as an aggressive signal. While they may change their song rate, it does not mean it has to be connected to song overlapping, as all correlations with song overlapping and song rate were statistically non-significant.

Based on the large variability in results of overlapping studies, it is possible that song overlapping is a species-specific signal of aggression, unlike signals such as soft songs. Soft songs are typically considered a universal aggressive signal among songbirds. Some species use song overlapping to show aggression and others showing overlapping avoidance to aid in communication, and others still potentially use it as a signal of non-engagement. This is seen with other potential signals of aggression such as changes in song rate, which occurs when a bird changes their song rate, more specifically when they increase their song rate. In some species, such as Claudia's leaf warblers (*Phylloscopus claudiae*) and the wood warbler, this is shown to be an aggressive signal with the higher song rates being associated with higher levels of aggression (Opaev et al., 2018; Szymkowiak & Kuczyński, 2016). In contrast, other birds, such as the hermit thrush may decrease their song rate when aggressive and song sparrows show no change (DeMerchant & Roach, 2021; Peters et al., 1980). As with song rate, song overlapping may also show interspecies variation. This would suggest that while some birds can use song overlapping or the avoidance of it to convey their aggressiveness to a rival, other species may use it for other reasons that are independent of aggression, as was the case with the hermit thrush in this study.

In summary, conspecific playback group showed that hermit thrush avoid song overlapping when aggressive and song overlapping is not associated with aggression in hermit thrush and therefore is not an aggressive signal in this species. The main explanation for this, which is supported by many studies, is that song overlapping avoidance results from other reasons, primarily being used as a method to avoid acoustic interference that could impede their ability to adequately communicate with other conspecifics in their environment. The current study aligns with numerous ones that argue against song overlapping being an aggressive signal.

Song Overlapping During Counter-singing Interactions

One can also further understand the function of song overlapping and song timing by looking at counter-singing interactions and investigating song overlapping in a different, non-aggressive context. The counter-singing group did not show significant difference in the amount of overlapping in comparison to the conspecific playback group. This supports the idea that avoidance of overlapping may simply be a method of avoiding acoustic interference from other conspecifics in the environment, as it appeared in equal amounts in both the aggressive and non-aggressive context.

While comparisons can be made between the conspecific playback and counter-singing groups, these are made difficult by the number of variables that could be controlled for in the conspecific group but were not able to be controlled for the counter-singing group, as well as the difference between the two scenarios. First, the location of the birds causes an issue as in the conspecific playback group the stimulated bird was on the target birds' territory, whereas for the counter-singing pairs the location of the birds relative to one another was not measured, but it was assumed they were on separate

territories. In addition to this, the nature of the interaction is an important factor to consider as the conspecific playback group involves a territorial intrusion; however, for the counter-singing group the birds stay within their own territories. In addition to this, familiarity may be playing a factor. Based on the *dear enemy hypothesis*, birds will respond differently, especially less aggressively, to other birds they are familiar with (Skierczynski et al., 2007; Temeles, 1994). Although this factor was controlled for in the playback studies by using a stimulus with songs from a stranger bird, it was not controlled for in the counter-singing group which could be influencing how the birds are interacting. In future research it would be crucial to collect this information to help further explore the usage of song overlapping, specifically when comparing the counter-singing and conspecific playback groups.

Similar to the results seen in the current study, avoidance of overlapping when counter-singing has been seen in species such as the canyon towhee (Bermúdez-Cuamatzin et al., 2018). In a study done by Ficken et al. (1985), ovenbirds also avoided overlapping the vocalizations of other conspecifics when counter-singing. Other studies done on nightingales also showed avoidance of song overlapping when counter-singing, specifically during nocturnal interactions (Todt & Hultsch, 1999).

The levels of avoidance seen in the counter-singing group in the current study are not always seen in songbird species, with some varying in their extent of song overlapping avoidance. For example, in a study looking at ovenbirds which used playback studies where the songs were broadcast from an area off of the territory of the target bird to emulate counter-singing, the birds only overlapped 10 out of over 250 songs (Ficken et al., 1985). This could suggest other factors are influencing the response of the birds in the current study, such as reliance on other additional strategies to avoid

acoustic interference, familiarity of individuals, and the location of the birds relative to one another, as was the case with white-throated sparrows (Wasserman, 1977).

As with the conspecific playback group, not all birds avoided overlapping, with just less than half showing chance levels of overlapping. In many instances, both birds in a pair showed below chance levels of song overlapping. In a few pairs, only one of the birds avoided overlapping, while the other would show chance levels. Other pairs showed chance levels in both birds. One of the primary explanations for avoidance behaviour in this group is acoustic interference avoidance, with birds avoiding each other's songs to in turn be able to adequately communicate with the other. In addition, the high levels of overlapping avoidance, especially when exhibited by both birds in a pair, could indicate higher familiarity, as has been seen with white-throated sparrows (Wasserman, 1977). The influence of familiarity was explored by Brindley (1991) who suggested birds may overlap with stranger birds more than their known neighbours. This suggests that birds interacting with known neighbours would be those showing below chance levels of overlapping, and birds showing chance levels may be interacting with less familiar birds.

The effects of familiarity were not controlled for in this part of the study. As the recordings were from previous field seasons, the effects of familiarity described by Brindley (1991) could not be assessed or controlled for. Therefore, it was unknown if the birds were a pair of neighbouring birds or if one was a stranger bird without a well-established territory in that area; however, based on location, each pair were likely familiar neighbours. In future research, it would be important to determine the effects of familiarity on counter-singing by comparing the behaviour seen when interacting with a known neighbour to the behaviour when interacting with a stranger bird.

In the counter-singing context, the location of the birds within the acoustic environment could also play a factor in the amount of overlapping seen in these pairs (Logue, 2021). Birds that are far away from each other may perceive less interference from the other, and the sound may not carry far enough to have to avoid overlapping it to prevent it from impeding communication (Wilson et al., 2016). This was illustrated in a study by Wilson et al. (2016) with black capped chickadees, which showed lower levels of overlapping when close to another conspecific. This could suggest that pairs where both individuals avoided overlapping could be closer together than pairs that show chance levels of overlapping. This mean they have the higher potential of interfering with each other's songs and have a higher need to avoid overlapping; however, in the current study, the location of the birds relative to each other is unknown. In future research, the effects of location on song overlapping should be assessed to better understand overlapping behaviour while counter-singing.

As described by Logue (2021) and Naguib (2005), a possible explanation for the three different variations of overlapping seen in the counter-singing pairs may be an interaction of the factors of familiarity and location of the birds relative to one another. According to Naguib (2005), the interplay of these factor creates unique social contexts where specific vocal behaviours may be more beneficial over other types of vocal behaviour. For example, a bird they are singing with could be a neighbour on a territory nearby or one on a territory farther away, or it could be a stranger bird outside a bird's territory, with each context potentially warranting different amounts of song overlapping behaviour (Logue, 2021; Naguib, 2005). In the current study, this would suggest that depending on the interplay of these two factors, avoidance of song overlapping may be

more beneficial and occur more frequently in specific social contexts compared to others.

Another possible explanation for the results seen for the counter-singing group, especially when looking at those pairs where one bird showed overlapping avoidance and the other showed chance levels of avoidance, relates to the dominance status and motivation of each individual in a pair. In studies looking at counter-singing in black-capped chickadees, it was proposed that degrees of overlapping behaviour were directly related to the bird's status or dominance (Fitzsimmons et al. 2008; Foote et al., 2008). For black-capped chickadees, dominance ranking was directly related to the quality of the individual, and in turn could influence vocal behaviour in interactions such as counter-singing. According to Fitzsimmons et al. (2008) birds may want to avoid overlapping other birds with a higher rank of dominance to avoid aggressive contests, but not avoid overlapping those of a lower dominance ranking. Although this hypothesis was refuted in both of these studies and overlapping was independent of dominance ranking, it is still possible it can explain the differences seen in this group of hermit thrush, and warrants future research.

Todt and Naguib (2000) also suggest another explanation for differences of the amount of overlapping seen in the counter-singing group, which is similar to the idea of ranking and dominance. They suggest that overlapping may be related to eavesdropping. During interactions, there can be another individual eavesdropping on the interaction between a pair of birds. This third individual could be a male conspecific assessing dominance of the birds in the interaction, or a female assessing the males in the interaction on their quality as a method of choosing a mate. Todt and Naguib (2000) suggest that overlapping could be seen as a dominant behaviour or show that a bird is of

high quality, and they overlap the other bird to demonstrate their dominance or quality to this other bird eavesdropping on the interaction. For example, in a study done by Naguib and Todt (1997) on nightingales, eavesdroppers showed different responses to individuals based on whether they had their song overlapped in an interaction. The birds responded more intensely when interacting with the overlapping and possibly more dominant bird. In the context of the current study, this would suggest that birds that overlapped the other in the pair, even at chance levels, may be the more dominant of the pair if the other bird in the pair showed below chance levels of overlapping.

In future research, it would be important to explore the different facets that could be influencing the song overlapping behaviour in counter-singing. It would especially be important to take location of the birds into consideration by measuring the distance between the birds in each pair and seeing if there is an association between location and song-overlapping. In addition, familiarity, although more difficult to determine, would be important to assess to see if this factor is influencing the degree of overlapping seen in this social context. In turn, it would be important to also see how these two factors interact to determine overlapping behaviour.

Song Overlapping in Response to Heterospecific Vocalizations

The individuals that were exposed to a stimulus of heterospecific songs showed the lowest levels of song overlapping avoidance. The majority of birds in this group showed chance levels of song overlapping, only three birds showed below chance levels of overlapping, and one showed above chance levels. Though research on this topic is limited, these results contrast with most existing ones. For example, nightingales actively avoided songs of multiple different species and showed more song production

during the period between the heterospecific songs (Brumm, 2006). In a study looking at 20 different Peruvian songbird species, birds avoided overlapping species that sang at similar song frequencies and had high potential for masking their songs (Planqué & Slabbekoorn, 2008). In another study looking at multiple songbird species in a forest environment it was shown that they would order their songs in a way to minimize overlapping each other and in turn prevent acoustic interference from the other species in the environment (Ficken & Popp, 1985; Popp et al., 1985).

In addition to avoiding overlapping the songs of other heterospecifics in their environment, songbirds have also been shown to avoid abiotic noise. Although song overlapping is not the only method of avoiding acoustic interference when faced with high levels of abiotic noise, some birds do use overlapping avoidance as a strategy to mitigate the effect of the noise on their ability to communicate. For example, in a study done by Wilson et al. (2016) black-capped chickadees avoided overlapping a stimulus of white noise.

Although the avoidance of heterospecific songs is often shown in songbirds, it is not always the case. For example, in a study done with flycatchers, which showed high levels of avoidance to overlapping vireo songs; however, like the hermit thrush in the current study, the vireo did not show as much avoidance of overlapping the songs of the flycatcher (Ficken et al., 1974). One proposed reason for this difference seen between species had to do with the propagation of sound. Sound can take time to travel through a given acoustic environment. This suggests that where the speaker for a playback experiment is placed relative to the target bird, could impact the propagation of sound, and potentially impact the degree of overlapping behaviour. According to Ficken et al. (1974), it is possible any degree of song overlapping can be explained by the birds not

hearing the songs of the other species before they start their own songs, thus leading to overlapping. Another explanation has to do with the length and different acoustic aspects of the individual's songs. In the case of these two species, the vireo had longer songs than the flycatcher, meaning even if overlapping occurred some of their song could still be communicated, giving less incentive to avoid overlapping.

For the hermit thrush, length of song may not be the most important driving factor that determines if it will avoid overlapping a heterospecific, it may be other acoustic properties of their song such as frequency. Furthermore, hermit thrush cycle through song types that all have varying frequencies, although other birds in their environment may have a single song type which means they sing at a constant frequency and may be able to avoid interference by singing at a different frequency. The impact of frequency can be seen in a study done by Planqué and Slabbekoorn (2008), where the main determinant of whether a bird overlapped a heterospecific song or not was the frequency of the songs, with the majority of birds in the study avoiding songs with similar frequencies to their own. This would imply that hermit thrush may not have the same pressures to avoid song overlapping to the same extent seen in other songbirds, as they have the ability to avoid acoustic interference from songs with similar frequencies as they cycle through their different song types.

One possible explanation for song overlapping in this context relates to the choice of the heterospecific stimulus. In the current study, the white-throated sparrow songs had a similar frequency to the hermit thrush songs, as the songs of the white-throated sparrow have a frequency range of 1.5-6.6 kHz; in comparison, the hermit thrush song have a frequency range from 1.7-5.0 kHz, yet the hermit thrush did not avoid overlapping the stimulus songs (Dellinger et al., 2020; Falls & Kopachena, 2020).

White-throated sparrows were selected for this study because they have the potential to mask the songs of the hermit thrush, they are a congener species, and they share some degree of similarity with a whistle-like intro note. In the current study, the songs of the white-throated sparrow were much longer than the songs of the hermit thrush. This raises the possibility that it is difficult for the hermit thrush to alter their vocal behaviour to avoid overlapping while still maintaining some degree of normal song timing. However, there could have been other species in the environment that had more similar frequencies and similar song structure which may have a better ability to mask the hermit thrush's song and is prioritized over the songs of the white-throated sparrow.

It is possible other acoustic characteristics of the stimulus songs are influencing the degree of overlapping avoidance exhibited by the hermit thrush. The song of a white-throated sparrow different acoustic properties than the songs of a hermit thrush, with potentially less variation and more simplicity, while hermit thrush have complex songs with an introductory note that can be masked by the songs of the white-throated sparrow, followed by a flurry of notes at varying frequencies less likely to be masked by the other's songs. Like with the vireo in the study done by Ficken et al. (1974), the sparrow's songs may mask some part of the hermit thrush's song, but they can still transmit some of it and may not have that incentive to avoid overlapping. According to Todt and Naguib (2000), the post-introductory section of song is usually the section that contains the most important information that a bird is trying to convey, such as individual quality. In the case of the current study, the white-throated sparrow may be masking the introductory note of the hermit thrush's songs, but they may not see the need to avoid overlapping since the more important post-introductory section may still be able to be conveyed to the intended target. In future research this idea can be explored

by presenting hermit thrush with songs of various types of songbirds, such as ovenbird as they are another species commonly seen in the same environment and have highly different acoustic properties in comparison to the hermit thrush. Other types of thrush, such as the wood thrush, could also be used as they have similar song structure. It would be important to look at species that have similar and increasingly different song structures to their own to see what potential song properties could influence their degree of overlapping.

While many birds avoid overlapping the songs of other species in their environment, this is not always the case, such as seen in thrushes. This is shown in a study done by Popp et al. (1985) that investigated how different species of birds in a northern forest environment ordered their songs to avoid overlapping those of other species. For example, in this study, one species would vocalize and then a second species, and then a third and this ordered singing would prevent the overlapping with other species in the environment; however, one species did not follow this pattern. The wood thrush overlapped other species in their environment and not fall into the pattern of ordered singing seen in the other species. Popp et al. (1985) and Ficken and Popp (1985) explain this behaviour by suggesting that birds like the wood thrush may be prioritizing avoiding songs of the same species over the songs of others. It is possible that the hermit thrush may behave similarly to the wood thrush, a species that did not avoid overlapping the other birds' songs. This could be explained by considering that hermit thrush cycle through song types of varying frequencies which may lead to less masking by other species in their environment and it may be more important to avoid songs of other hermit thrush.

The collective finding of these studies was similar to those seen in a study done by Hodgson et al. (2018), which investigated vocal responses of hermit thrush during the dawn chorus. In this study, birds that sing early in the morning were more likely to have their vocal behaviour influenced by other conspecifics in their environment in comparison to heterospecifics which the birds tended to not attend to. In the current study, playback studies were conducted during the dawn chorus as this is when birds show the highest levels of singing, and like what was shown by Hodgson et al. (2018), the hermit thrush in this study were suggested to attend more to the other conspecifics. This suggests that it is a strategy to avoid overlapping primarily used when avoiding the songs of other conspecifics in their environment.

Song overlapping in response to heterospecific songs in the environment could be explored in future research by doing a similar study to that done Popp et al. (1985), where the natural singing of multiple species is recorded. Using this methodology, it could be determined if hermit thrush avoid overlapping other heterospecific in their environment, instead of just looking at one. To further look at the acoustic interference hypothesis in this species, it would be important to identify what methods they use, or if they even do avoid interference from these noise sources, such as if they use the Lombard effect or show shifts in song frequency like those seen in black-capped chickadees or show changes in the number of vocalizations produced (Goodwin & Podos, 2013; Luther, 2009).

Limitations of the Current Study

One limitation of this study is the use of playback experiments. While many animal communication studies use this method and it is especially prevalent in songbird

research, it has its flaws. One major critique of playback studies, and specifically more traditional designs like those used in the current study, is that it is too artificial. In nature, communication involves two or more individuals interacting with each other; however, with a playback its one individual reacting to a stimulus that does not alter its behaviour in response to their signals (Douglas & Mennill, 2010; King, 2015). In future research, it would be worthwhile to perform interactive playback studies with the birds where each stimulus song is selected by the experimenter in real time to be simulate interactive communication.

Another limitation of this study is the number of differences seen between the three groups, which limits the ability to interpret and make firm conclusions about the differences seen in song overlapping between the three groups. As previously mentioned, differences in the locations of the birds, the differences in social contexts, and the familiarity of individuals are all factors that are all different between the groups and can have impacts on the birds' interactions in each context. It is also important to note that the location for all birds relative to the microphone used to record them was not always known. This could potentially cause a small shift in the timing of the songs, especially for those birds that were father away from the microphone; however, the effects are probably small, if not negligible.

The use of recordings from past field seasons to study counter-singing was also a limitation for this study. This made it so that approximate distance between counter-singing pairs could not be determined, which would have helped to explain why in the counter-singing groups not all birds showed avoidance of overlapping. In this study there are many things that are unknown about the bird that could be influencing their behaviour. For example, age of the birds used in the study. Logue (2021) explains that

age in some species can determine the amount of overlapping exhibited by birds; however, it is difficult to control or to assess in studies. Other unknowns that could be influencing behaviour are familiarity of individuals, breeding status, and motivation.

The one type of stimuli used, specifically in the heterospecific condition offers another limitation. Although most birds did not avoid overlapping the song of another species in their environment, it is important to note that this does not mean the results of non-avoidance are generalizable to all species within that environment that could potentially be interfering with their songs.

The sample size of birds used in the study also presented a limitation by decreasing the power of the study. This was especially true when looking at relationships between song overlapping and aggression, where small effects may not be detected. Although the sample size of the study may be considered small in many disciplines, it had a significantly larger sample size than many birdsong studies.

In addition, for both playback studies, the stimuli were three minutes long. Although this is standard for most playback studies, it may not be long enough in this context to fully understand song overlapping. It is possible that some birds do not have immediate vocal plasticity and it may take them time to get a sense of the vocal behaviour of the other bird and in turn adjust their vocal behaviour to avoid interference.

Conclusion

In conclusion, the current study gave insight into the function of song overlapping and song overlapping avoidance in hermit thrush. It establishes that there is no link between song overlapping and aggression. In addition to this, overlapping avoidance was suggested to be a method to avoid acoustic interference, primarily when

interacting with other conspecifics in their environment, independent of the social context. However, more studies are needed to fully understand the use of song overlapping avoidance. Specifically, it would be important to investigate other factors that could be influencing the degree of overlapping seen in each group, such as the location of the birds relative to one another, the presence of other birds in the environment, and other acoustic factors that could determine whether there is a need to show overlapping avoidance. These future studies will help to give more insight into the use of song overlapping avoidance as a mechanism of acoustic interference avoidance in hermit thrush.

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Table 1

Percentage of individuals in each context that exhibited above chance, at chance, and below chance levels of overlapping based on each of the two measures of song overlapping

Context	Time Spent Overlapping			Number of Times Overlapping occurred		
	Above Chance	At Chance	Below Chance	Above Chance	At Chance	Below Chance
Conspecific Playback	0	48.3	51.7	0	58.6	41.4
Heterospecific Playback	3.2	87.1	9.7	3.2	87.1	9.7
Counter-singing	0	28.6	71.4	0	40.5	59.5

Table 2

Factor loadings of physical aggression variables measured during conspecific playbacks for principal components with eigenvalues greater than 1

Variable	PC1	PC2
Closest Approach	.956	.157
Average Distance	.947	.214
Time in Arena	-.795	-.482
Latency of Entry	.795	.498
Number of Swoops	-.173	-.936
Latency Swoops	.349	.856
Eigenvalue	4.372	1.012
Variance Explained (%)	72.863	16.866

Table 3

Correlations between both measures of song overlapping and the two PCs extracted from the PCA, as well as between the measures of overlapping and each variable of aggression.

Variable	Number of times overlapping occurred		Time Spent overlapping	
	Pearson Correlation	Sig.	Pearson Correlation	Sig.
Closest Approach	.025	.896	-.083	.667
Average Distance	.067	.731	-.069	.724
Time in arena	.066	.733	.008	.968
Latency of Entry	-.071	.714	-.041	.834
Number of Swoops	.221	.230	.008	.967
Latency of Swoops	-.175	.363	.044	.819
PC1	.075	.816	.087	.654
PC2	.045	.654	-.252	.187

Figure 1

A spectrogram of an individual hermit thrush's song repertoire (DeMerchant, 2020)

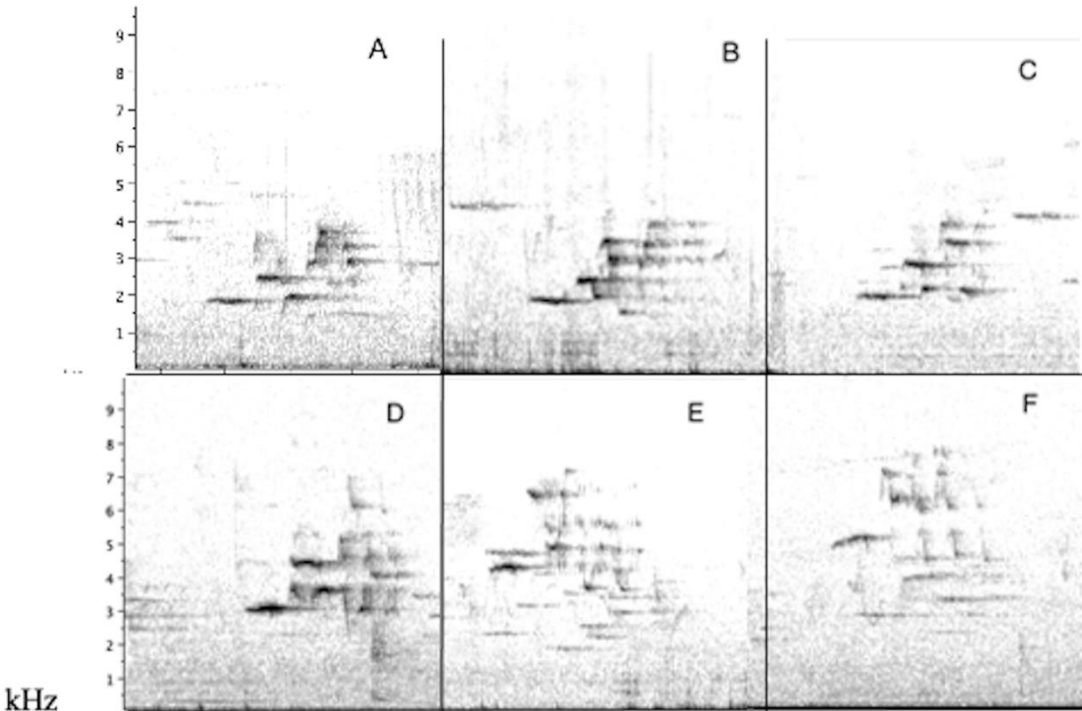
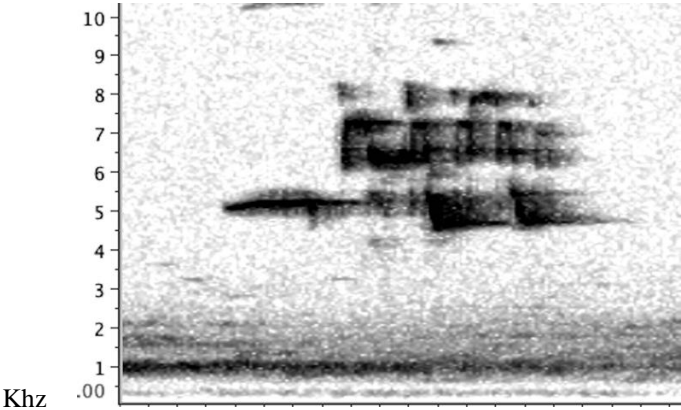


Figure 2

Spectrogram of a hermit thrush vocalization (A) and a white-throated sparrow vocalization (B)

A



B

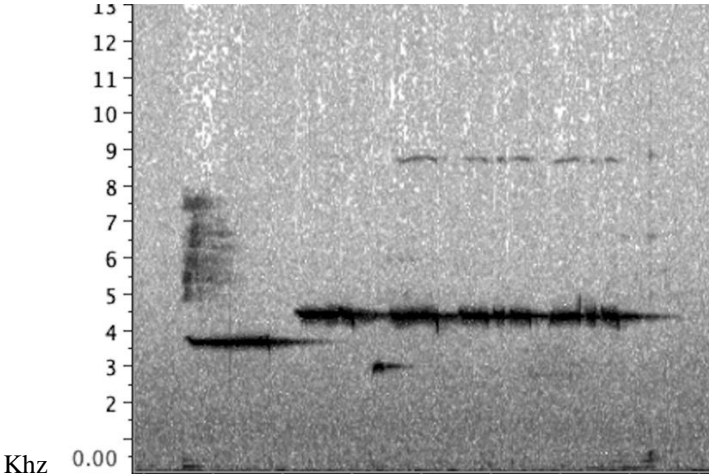
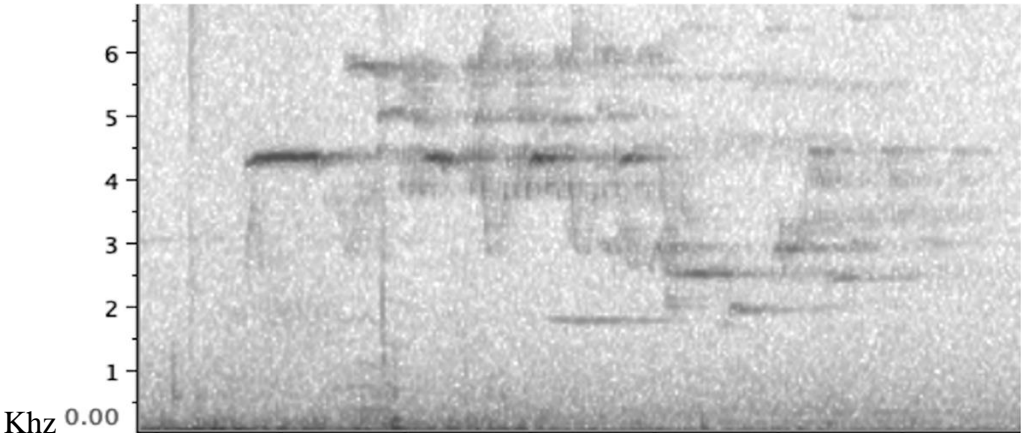


Figure 3

Spectrogram of song overlapping by a hermit thrush with a conspecific stimulus (A) and song overlapping with a heterospecific stimulus (B)

A



B

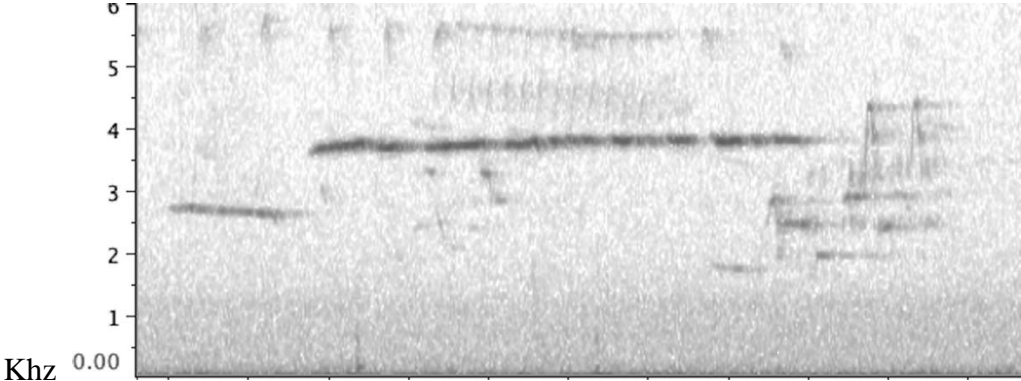
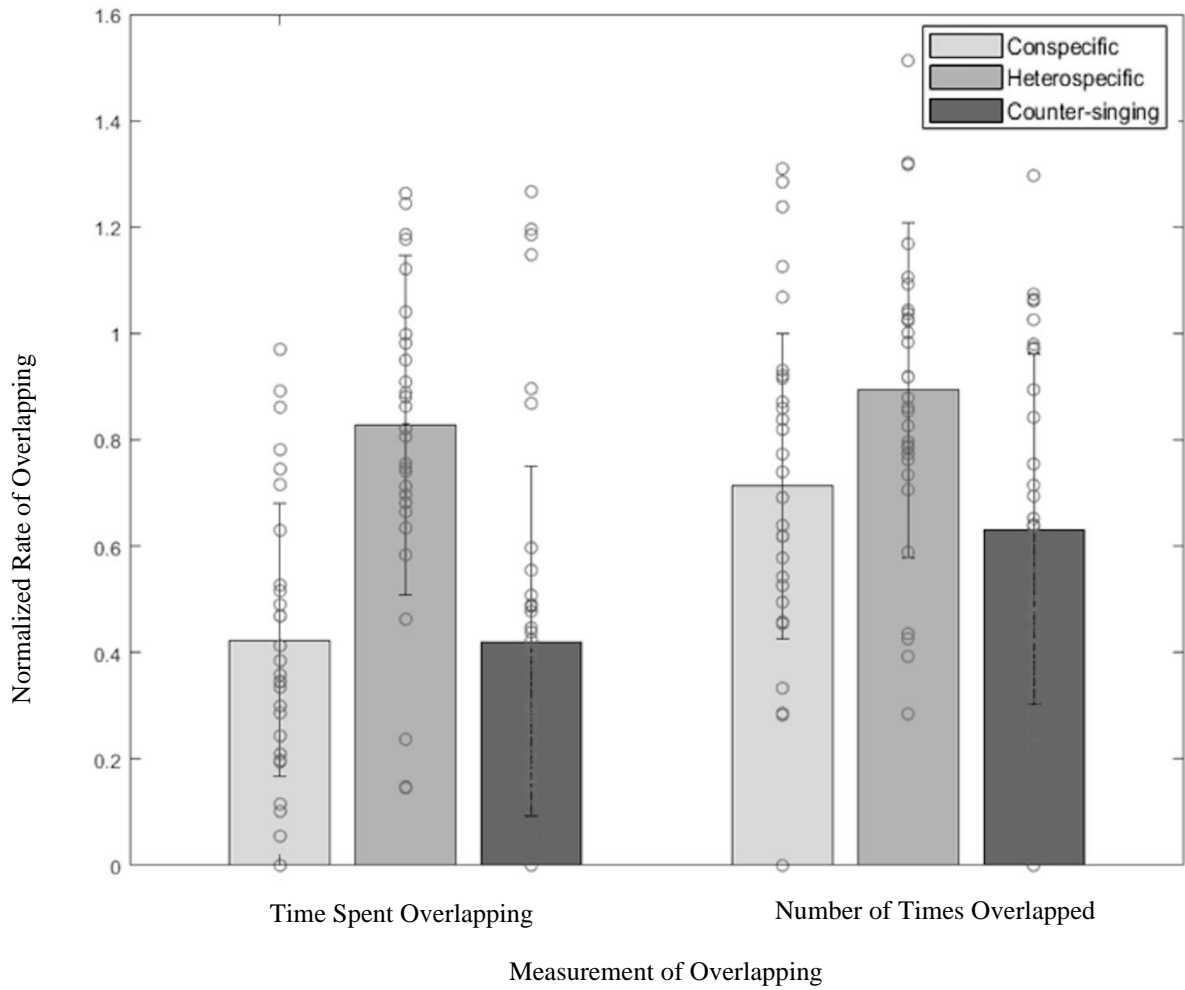


Figure 4

Comparison of the normalized rates of overlapping between the three groups

(conspecific, heterospecific, and countersinging)

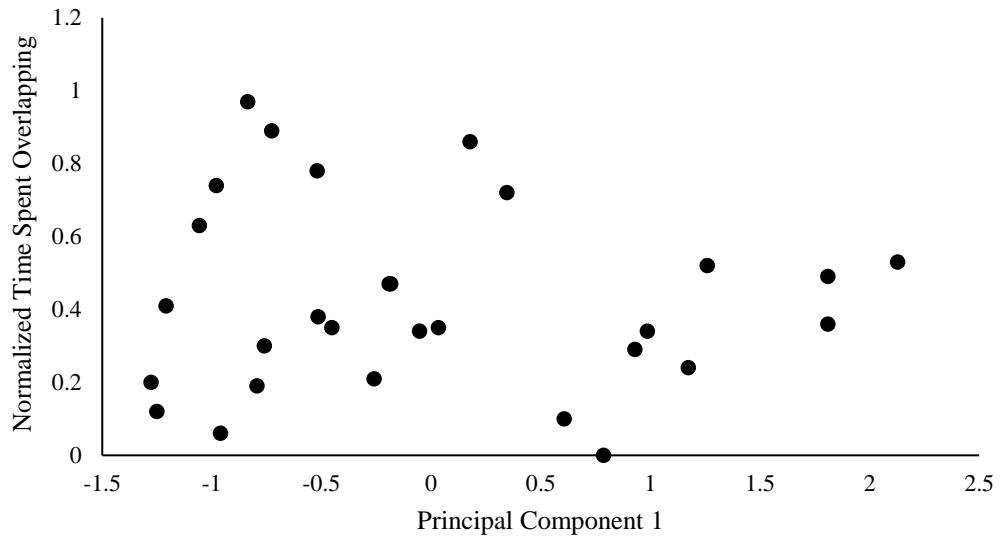


Note: Each circle represents a single individual.

Figure 5

*Correlations between the normalized time the bird spent overlapping the stimulus and
PC1 (A) and PC2 (B)*

A



B

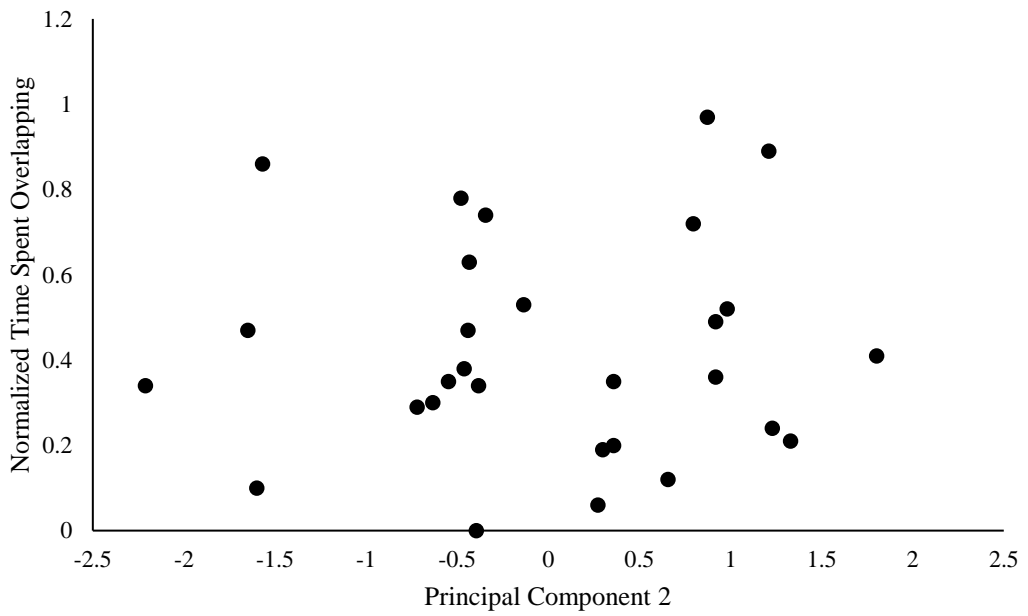
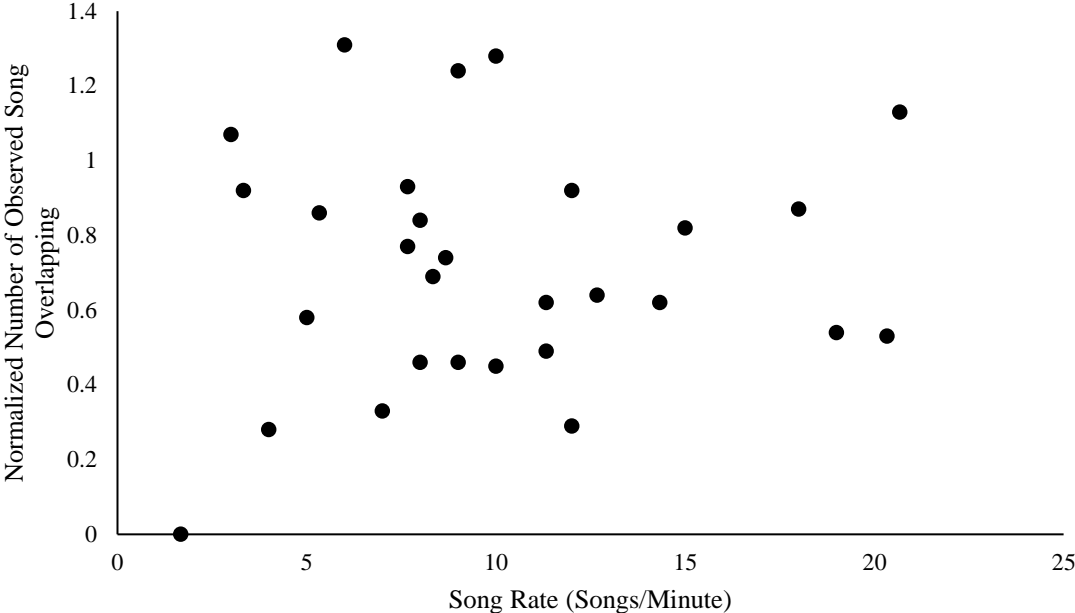


Figure 6

Association between song rate and the normalized number of times the birds overlapped the stimulus



Appendix A

Data Collected from the Conspecific Playback Studies

Subject	Number of overlapping songs				Time spent overlapping (s)			
	Total songs	Observed	Expected	<i>p</i> -value	Total duration	Observed	Expected	<i>p</i> -value
1	57	11	20.29	1.000	74.70	3.11	15.72	1.000
2	10	3	3.26	0.681	14.73	0.74	2.48	0.916
3	34	6	12.12	0.996	47.29	2.27	9.35	1.000
4	15	3	5.19	0.951	17.00	1.54	3.72	0.921
5	45	14	17.08	0.902	49.69	9.60	12.88	0.917
10	27	11	8.89	0.233	30.31	5.26	6.11	0.672
11	23	5	5.37	0.695	26.77	2.98	3.34	0.995
12	24	7	8.35	0.805	28.64	2.18	6.32	0.987
13	27	4	8.74	0.992	40.96	7.06	7.28	0.519
18	30	12	9.34	0.178	34.55	3.11	6.63	0.966
19	21	2	6.00	0.995	18.98	0.48	4.15	0.998
20	62	21	18.65	0.264	80.44	10.11	12.94	0.887
21	36	3	10.49	1.000	44.19	2.66	6.91	0.993
22	26	6	8.11	0.879	35.53	2.85	5.81	0.954
24	12	1	3.54	0.991	15.18	0.14	2.49	0.982
26	38	8	12.52	0.978	59.31	2.08	9.90	1.000
28	38	8	12.94	0.986	51.07	1.94	9.96	1.000
30	23	5	6.47	0.836	35.15	2.52	4.77	0.881
31	16	5	5.82	0.782	21.39	1.47	4.39	0.968
38	34	8	12.91	0.981	48.16	3.76	10.49	0.995

Subject	Number of Overlapping Songs				Time Spent Overlapping (s)			
	Total Songs	Observed	Expected	<i>p</i> -value	Total Duration	Observed	Expected	<i>p</i> -value
46	36	11	12.01	0.711	44.52	4.21	8.96	0.981
47	9	3	2.81	0.583	12.01	0.57	1.99	0.888
50	5	0	1.53	1.000	6.18	0.00	1.12	1.000
54	25	6	8.68	0.933	38.22	3.63	7.02	0.939
57	30	4	8.80	0.993	39.22	2.39	6.92	0.988
61	16	3	5.70	0.971	24.80	0.48	4.77	0.993
63	24	4	8.78	0.992	29.03	2.39	6.91	0.992

Appendix B

Data Collected from the Heterospecific Playback Studies

Subject	Number of overlapping songs				Time spent overlapping (s)			
	Total songs	Observed	Expected	<i>p</i> -value	Total duration	Observed	Expected	<i>p</i> -value
7	41	16	15.63	0.509	64.71	19.24	19.27	0.508
8	26	9	8.14	0.423	42.01	7.84	9.72	0.767
9	36	11	10.54	0.498	53.85	7.50	11.82	0.945
14	27	4	6.79	0.968	44.71	3.61	7.80	0.960
15	36	12	13.66	0.836	56.54	13.01	17.23	0.914
16	31	10	7.59	0.154	48.21	11.81	9.34	0.172
17	21	8	6.06	0.223	28.11	7.29	6.19	0.306
25	22	4	5.45	0.850	28.29	3.70	5.43	0.808
27	31	11	11.99	0.746	48.74	12.77	14.81	0.749
29	34	9	8.99	0.592	45.49	9.42	9.92	0.577
32	26	4	9.18	0.999	37.02	1.47	10.09	1.000
33	36	4	9.39	1.000	52.99	1.47	9.90	1.000
34	33	11	12.78	0.850	47.80	12.27	14.95	0.819
35	33	6	7.87	0.899	49.42	7.11	9.52	0.820
36	17	4	5.10	0.821	24.36	3.16	5.42	0.845
37	31	7	9.04	0.875	53.02	8.17	11.02	0.837
40	11	3	2.75	0.559	17.22	2.47	3.46	0.693
41	30	11	11.19	0.615	49.69	13.29	14.62	0.653
44	21	5	5.44	0.691	34.95	6.58	6.32	0.435
45	30	8	7.79	0.560	50.45	10.96	9.25	0.255
48	30	7	8.87	0.880	52.97	7.92	11.60	0.863

Subject	Number of overlapping songs				Time spent overlapping (s)			
	Total Songs	Observed	Expected	<i>p</i> -value	Total duration	Observed	Expected	<i>p</i> -value
51	33	13	8.60	0.028	50.22	16.66	9.77	0.005
52	28	2	5.09	0.984	43.59	3.01	4.53	0.797
53	42	11	10.61	0.517	63.78	14.30	11.49	0.143
55	17	3	4.25	0.862	24.96	4.43	4.66	0.517
56	41	10	7.57	0.175	61.93	6.62	6.75	0.494
58	35	9	10.54	0.833	51.69	8.72	12.51	0.921
59	25	8	10.05	0.889	38.88	9.72	11.04	0.691
60	36	2	7.02	1.000	60.30	1.57	6.63	0.991
62	40	17	14.55	0.203	59.68	19.23	17.15	0.226

Appendix C

Data Collected from the Counter-singing Interactions.

*Note: The bolded individuals were included in the group used for the comparison between group.

Subject	Number of overlapping songs				Time spent overlapping (s)			
	Total songs	Observed	Expected	p-value	Total duration	Observed	Expected	p-value
1A	30	2	8.97	1.000	36.73	0.74	5.60	1.000
1B	49	3	10.58	0.999	71.94	1.25	7.56	1.000
2A	43	4	10.64	0.999	74.47	1.78	8.54	1.000
2B	36	7	8.31	0.776	48.33	6.42	5.59	0.320
3A	50	4	12.37	1.000	83.47	1.00	9.51	1.000
3B	37	4	9.73	0.997	48.21	1.82	6.41	0.996
4A	56	16	17.89	0.762	81.53	6.45	13.27	0.989
4B	84	10	20.46	1.000	141.40	6.45	16.67	0.998
5A	34	4	8.17	0.995	58.81	3.09	6.93	0.962
5B	25	2	6.73	0.998	37.12	0.77	5.14	0.992
6A	27	1	2.73	0.939	41.99	0.58	1.90	0.877
6B	26	2	2.06	0.621	21.10	0.49	1.22	0.753
7A	20	4	3.77	0.539	21.51	2.48	2.08	0.322
7B	28	5	4.66	0.517	39.41	1.51	3.09	0.875
8A	54	7	12.89	0.990	73.42	1.44	8.54	1.000
8B	42	8	11.52	0.943	51.91	2.14	7.33	0.996
9A	48	9	6.94	0.239	65.91	3.88	4.33	0.582
9B	39	11	6.44	0.036	51.96	5.51	4.65	0.287
10A	55	9	15.81	0.997	88.38	5.28	12.05	0.999

Subject	Number of overlapping songs				Time spent overlapping (s)			
	Total Songs	Observed	Expected	p-value	Total duration	Observed	Expected	p-value
10B	41	6	12.09	0.994	50.99	3.05	7.65	0.988
11A	65	10	15.61	0.990	93.45	3.52	10.88	0.999
11B	38	13	13.27	0.617	46.58	4.65	8.37	0.966
12A	50	10	13.25	0.918	72.36	4.55	9.27	0.980
12B	39	8	12.26	0.962	52.45	2.50	8.42	0.998
13A	33	0	4.93	1.000	51.02	0.00	3.59	1.000
13B	24	3	4.32	0.852	34.10	0.47	3.03	0.976
14A	38	5	8.89	0.981	56.91	3.23	6.37	0.958
14B	29	7	6.83	0.549	34.57	3.57	4.11	0.600
15A	54	8	11.19	0.940	77.01	3.81	7.96	0.976
15B	31	12	11.27	0.451	44.85	10.40	8.21	0.164
16A	52	9	14.12	0.979	79.48	4.36	10.29	0.995
16B	45	4	11.62	1.000	57.32	3.14	7.69	0.992
17A	60	4	16.24	1.000	84.46	0.62	10.97	1.000
17B	52	6	13.95	1.000	63.94	2.25	8.76	0.998
18A	48	5	11.47	0.996	71.37	1.96	8.43	0.999
18B	36	5	10.63	0.992	50.24	1.49	7.41	0.999
19A	53	6	14.64	1.000	74.37	2.72	10.15	1.000
19B	42	6	12.99	0.999	54.27	1.46	8.66	1.000
20A	117	9	18.18	1.000	173.25	4.01	13.45	1.000
20B	43	17	17.52	0.641	61.39	7.72	12.93	0.977
21A	194	18	35.23	1.000	294.58	4.83	24.52	1.000
21B	98	16	25.98	0.997	109.20	5.36	14.97	1.000

CURRICULUM VITAE

Kendra Brooke DeMerchant

Universities attended:

University of New Brunswick – Bachelor of Science – 2016-2020

University of New Brunswick – Master of Arts – 2020-2022

Publications:

DeMerchant, K., Roach, S.P. (2021, December). *Vocal responses of hermit thrush (Catharus guttatus) males to territorial playback of conspecific song*. Paper published in the International Journal of Avian Science.

Conference Presentations:

DeMerchant, K., Yoo, J., & Roach, S.P. (2022, July). *Abridged Song Use During Territorial Defense in Hermit Thrush (Catharus guttatus)*. Virtual poster session at the 2022 Animal Behaviour Society Conference

DeMerchant, K., Jessulat, J. & Roach, S.P. (2021, August). *Characterization of Hermit Thrush (Catharus guttatus) song overlapping during simulated territorial intrusions and natural countersinging*. Virtual poster session at the 2021 American Ornithological Society Annual Conference.

Roach, S. P., DeMerchant, K., & Nesbitt., M. (2019, October). *Division of labor: the communicative functions of hermit thrush (Catharus guttatus) song components*. Poster session at 2019 Wilson Ornithological Society