IS SYNTAX A SIGNAL OF AGGRESSION IN HERMIT THRUSH (*CATHARUS GUTTATUS*) SONG?

by

Morgan Nesbitt

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Supervisor: Sean Roach, PhD, Dept. of Psychology

Examining Board: David Speed, PhD, Dept. of Psychology
Drew Rendall, PhD, Dept. of Biology
Mary Ann Campbell, PhD, Dept. of Psychology

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ABSTRACT

Syntax, which classifies the order song types must follow within a bird's song to convey functional meaning, is thought to play a role in songbird communication. Vocal cues are crucial to male-male interactions and certain species have been shown to alter their songs in response to territorial intruders (Hedley, Denton, & Weiss, 2017). The current study focuses on the use of syntax in aggressive contexts in the hermit thrush, a migratory songbird common to North America. Using playback sessions, this research evaluated the importance of species-typical syntax in conveying aggression in territorial disputes between two males. It was expected that the hermit thrush would react more strongly to songs which contained species-typical syntax than those which did not, however there was no difference in aggressive reactions between the two stimuli. These findings suggest that the hermit thrush may use syntax for other evolutionarily relevant behaviours, such as mate attraction. Vocal responses, including song overlapping and frequency matching, were also assessed and were both found to occur at below chance levels, indicating that birds actively avoided these behaviours during playback. Based on past research, it could be possible that birds are altering their songs to avoid acoustic interference, thus maximizing their signal transmission efficiency.

Keywords: aggression, male-male interactions, hermit thrush, playback

ACKNOWLEDGEMENTS

Table of Contents

List of Tables

List of Figures

Is syntax a signal of aggression in hermit thrush (*Catharus guttatus*) song?

It is hard to deny the beauty of birdsong which has been an inspiration for poets and composers (Messiaen, 2015). However, this form of communication transcends a simple collection of notes. There are several reasons why birdsong is an important subject to study, one of which is the similarities between vocal learning in songbirds and humans (Abe & Watanabe, 2011; Brainard & Doupe, 2013; Yip, 2013). The process of learning songs resembles the acquisition of speech in human infants, including similar stages of sound development, which presents an opportunity to use birdsong in the study of human language and its development (Abe & Watanabe, 2011; Brainard & Doupe, 2013; Yip, 2013). Unlike most other animals, both birds and humans have the capacity for vocal learning through imitation and possess a critical period of language learning which is influenced by social interaction with adults (Doupe & Kuhl, 1999; Phan et al., 2006; Wilbrecht & Nottebohm, 2003).

Similar to speech in human infants, birdsong is learned in stages (Chen et al., 2016; Phan et al., 2006; Wilbrecht & Nottebohm, 2003). Signal production learning in birds includes both a sensory and sensorimotor phase during a sensitive period of song development, with juvenile birds acquiring acoustic structure and motor commands throughout this development (Briefer et al., 2013; Wilbrecht & Nottebohm, 2003). The process of song learning begins with listening to an adult tutor's song, which is followed by the juvenile producing a subsong: a rambling, low amplitude burst of song that over time becomes more similar to the songs performed by adults (Wilbrecht & Nottebohm,

2003). Subsong has been proposed to be similar to babbling in infants and its performance is a type of practice before the song is crystalized into its final mature form (Wilbrecht & Nottebohm, 2003).

Due to the similarity between the processes of learning birdsong and speech, songbirds have been proposed as a model for studying human vocal disorders (Doupe & Kuhl, 1999; Wilbrecht & Nottebohm, 2003). An example of this is *FOXP2*, a gene which has been implicated as an underlying cause of language development abnormalities in humans (Haesler et al., 2007; Teramitsu & White, 2006; Teramitsu et al., 2004). *FOXP2* regulates mechanisms which are common to both songbirds and humans and has similar expression in both species (Teramitsu et al., 2004). Because of this, songbirds have been used to study deficits associated with *FOXP2* using methods which would be unethical on human subjects and have helped researchers to understand how the gene contributes to human speech development (Haesler et al., 2007; Teramitsu & White, 2006; Teramitsu et al., 2004).

Along with the learning process, birds and humans also share similarities in the underlying neurobiology of their vocal behaviours (Abe & Watanabe, 2011; Jarvis, 2004; Wilbrecht & Nottebohm, 2003). Both human language and avian communication have specialized brain circuitry dedicated to the development and production of new sounds (Jarvis, 2004; Wilbrecht & Nottebohm, 2003). The vocal pathways of songbirds and mammals have similar connectivity and auditory pathways which allows them to integrate feedback into song production (Jarvis, 2004; Panaitof, 2012; Wilbrecht & Nottebohm, 2003). The similarity between the neurobiology of humans and birds makes them an excellent choice of model for studying human disorders involving disruptions in

these common pathways, as well as their potential treatments (Badwal et al., 2019; Brainard & Doupe, 2013; Cate et al., 2013; Jarvis, 2004; Panaitof, 2012; Wilbrecht & Nottebohm, 2003).

Songbirds have been used in studies on Parkinson's and autism disorders, using the well-characterized neural circuitry of certain bird species (e.g., the zebra finch; *Taeniopygia guttata*) as a model for vocal learning and production deficits (Badwal et al., 2019; Panaitof, 2012). The importance of song usage in bird behaviour paired with our understanding of avian brain pathways gives us an opportunity to explore the link between brain and behavior within bird species. Through study of their song, we may gain a better understanding of how relevant behaviours, such as that of aggression, are reflected in the bird's neural circuity, including pathways and connectivity.

Furthermore, having a better understanding of how birds employ and perceive their songs could have important implications for studying biodiversity of songbirds, such as following patterns of abundance and monitoring species (Shonefield & Bayne, 2017; Teixeira et al., 2019). For example, Rosenberg et al. (2019) were able to monitor 529 species of birds to evaluate population changes over time and identify biomes with higher or lower levels of species abundance. Recent studies have explored the use of autonomous recording units to sample avian acoustics for use in research, conservation efforts, and monitoring species abundance (Shonefield & Bayne, 2017). Bioacoustics (the study of sound produced by living organisms) can be used to measure a species' presence or absence, richness, abundance, and density, all of which are useful in planning and monitoring conservation outcomes (Teixeira et al., 2019).

Monitoring singing may also allow us to gain vital insight on habitat quality or reproductive success of target species, because the health of birds and the environment they reside in may influence their vocal behaviours (Teixeir et al., 2019). In one study, it was found that male Eurasian eagle owls (*Bubo bubo*) with the most abundant number of offspring and the largest proportion of rats in their diet sang earlier during the dusk chorus (Teixeira et al., 2019). Thus, knowing more about the vocal behaviours of different bird species can inform and improve their monitoring. Understanding vocal behaviours is a crucial step in monitoring conservation because they may provide relevant information for conservation efforts that could shape the planning of a conservation program (Shonefield & Bayne, 2017; Teixeira et al., 2019).

Whether to monitor biodiversity or link brain to behaviour, it is crucial to first understand how song may function in birds' two main biological drives, territorial defence and mate attraction. Identifying the importance of song in certain exhibited behaviours is the first step towards using birdsong for these various applications. Different from calls, songs are performed in most species by the males, and happen only during the breeding season (Catchpole & Slater, 1995; Marler, 2004). At the beginning of the breeding season males set up designated territories and use ~~bird~~song to communicate with each other (Broughton et al., 2010; Fedy & Stutchbury, 2004). ~~Bird~~song can be used in territorial defence, with birds responding quickly to intruders by changing what and how they sing in response to hearing another bird's song (Hughes et al., 1998; Searcy & Beecher, 2009; Vehrencamp et al., 2007).

To classify a behaviour as an aggressive signal, ~~the~~ three criteria laid out by Searcy and Beecher (2009) are often used. This includes the context criterion which

4

states that the signal must increase in aggressive contexts (e.g. territorial disputes), the predictive criterion which determines whether the signal predicts aggressive escalation by the signaler, and the response criterion which says that the receiver must respond to the signal. If a given behaviour satisfies both the predictive and response criterion (or better, all three) then it may be considered an aggressive signal (Searcy & Beecher, 2009).

Birds may change their singing in male-male interactions using song type matching which occurs when birds repeat the same song type back when responding to a rival's song. Another similar singing mechanism is frequency matching, when an individual reacts to a rival's song by repeating the same frequency back at them. Both song type matching and frequency matching have been proposed to be used as aggressive signals in some species (Hughes et al., 1998; Nielsen & Vehrencamp, 1995; Searcy & Beecher, 2009; Vehrencamp et al., 2007). However, results are mixed on whether or not these signals are actually a sign of aggression. Although occurrences of song type matching are above chance levels for numerous bird species, many studies have found it difficult to show strong support for the behaviour as a prediction of escalation (Searcy, Anderson et al., 2006; Searcy & Beecher, 2009).

This could be due to species possessing a hierarchical communication system, in which different signals are performed to indicate varying levels of threat from a rival (Akçay et al., 2014). For example, there has been evidence that some signals may not lead directly to a physical attack, instead acting as a less costly warning that may subsequently escalate to a stronger show of aggression before eventually resulting in an attack (Akçay et al., 2014). In a study by Akçay et al. (2014), it was found that matching in the song sparrow (*Melospiza melodia*) is likely an early stage aggressive signal, with

90% of birds who engaged in early song type matching eventually escalating and attacking their rival while the other 10% remained neutral. These findings suggest that birds do use song type matching as a signal of escalation above other social signalling functions, however, more studies examining song type matching as an early stage predictor are necessary to determine whether this holds true across multiple species or is specific to the song sparrow.

Birds may also interrupt rivals using song overlapping, in which the individual's song begins before the end of their rival's song (Naguib & Mennill, 2010). Evidence on whether or not overlapping acts as an aggressive signal is mixed, with some studies arguing that overlapping is a highly effective threat signal and others indicating that it may not be a signal at all (Searcy & Beecher, 2006 cf. Todt & Naguib, 2000). In a study done on the banded wren (*Thryophilus pleurostictus*), it was suggested that overlapping does play a defensive role in aggressive interactions (Vehrencamp et al., 2007). Similar findings were determined in a study on the great tit (*Parus major*) which showed an association between song overlapping and the singer occupying a position further away from the playback speaker (Langemann et al., 2000).

Another potentially aggressive signal is singing rate, meaning the speed at which birds produce concurrent songs (Cardoso et al., 2007; Linhart et al., 2013). There is evidence that the rate of syllable delivery provokes a response in both males and females of certain species and might act as an indicator of male quality (Ballentine et al., 2004; Cramer & Price, 2007; de Kort et al., 2009; Dubois et al., 2011; Illes et al., 2006). Linhart et al. (2013) found that male chiffchaffs (*Phylloscopus collybita*) responded to territorial intruders by increasing their syllable rate. Their study showed elevated responses in

males to playback recordings with increased singing rates but no change in response when the playback recording had a decreased singing rate. Therefore, increased singing rate satisfies the criteria laid out by Searcy and Beecher (2009), and acts as an aggressive signal during male-male interactions for this species (Cardoso et al., 2007; Linhart et al., 2013). Linhart et al. (2013) suggests that singing rate likely plays a larger role in aggressive signaling than in indicating male quality.

Similarly, changes in the rate of song type switching (which is described as when a bird switches between song types while singing) has been observed in aggressive situations (Nielsen & Vehrencamp, 1995; Searcy & Beecher, 2009). An increased frequency of song type switching in aggressive scenarios has been evidenced in multiple species including the song sparrow, the meadowlark (*Sturnella*), the western meadowlark (*Sturnella neglecta*), and the Carolina wren (*Thryothorus ludovicianus*; D'Agincourt & Falls, 1983; Falls & D'Agincourt, 1982; Peake et al., 2005; Simpson, 1985). However, the opposite has also been observed, with the red-winged blackbird (*Agelaius phoeniceus*) decreasing its frequency of switching when faced with a rival (Searcy & Yasukawa, 1990).

Along with altering their singing, birds may also respond to rivals by changing their song (Belinsky et al., 2015; Nice, 1943; Searcy & Beecher, 2009; Vehrencamp et al., 2007). One common example of this is a soft song, which is a lower amplitude song that has been shown to predict attack in species such as the song and swamp sparrows (*Melospiza georgiana*; Nice, 1943; Searcy & Beecher, 2009; Vehrencamp et al., 2007). Additionally, abridged songs have been observed in certain species, in which the introductory note is dropped in response to territorial playbacks (Belinsky et al., 2015).

7

Aside from aggressive responses, changes in song have also been suggested to play a role in the second major function of birdsong: mate attraction (Byers & Kroodsma, 2009). There is evidence that females of certain bird species react favourably to longer songs (e.g., the great reed warbler; *Acrocephalus arundinaceus*), larger song repertoires (e.g., the great tit), and a higher degree of stereotypy (or the repetitive use of song types, e.g., the zebra finch), indicating that there is some preference for certain features of song choice (Alger et al., 2015; Baker et al., 1986; Bensch & Hasselquist, 1992; Woolley & Doupe, 2008).

Although female preference for larger song repertoires are well studied, findings regarding their role in mate choice are mixed. Hasselquist et al. (1996) demonstrated that the size of a male's song repertoire was the best predictor of offspring survival, which would suggest that the size of a bird's song repertoire is associated with mate quality and that choosing males with larger song repertoires indirectly benefits females through survival of their young. As well, a study on zebra finches which experimentally altered the output of male songs suggests that females prefer normal song lengths compared to shortened ones (Tomaszycki & Adkins-Regan, 2005). However, in a study on female preferences in the house finch (*Haemorhous mexicanus*), females did not show any consistent preference for repertoire size (Nolan & Hill, 2004). In a review by Byers and Kroodsma (2009) who looked at 49 studies on the subject of female preference for repertoire size, it was found that half of the studies reviewed indicated a preference, while the other 50% indicated no significant preference.

It is also difficult to conclusively confirm the function of repertoire size in mate selection because of the constraints inherent in experiments centering on vocal

manipulation (Byers & Kroodsma, 2009; Tomaszycki & Adkins-Regan, 2005). There is currently no viable way to manipulate live vocals without gross disruption of song (Byers & Kroodsma, 2009; Tomaszycki & Adkins-Regan, 2005). Recordings taken of male birds often act as a stimulus, but this method is limited because it relies on observing the behaviours associated with choosing a mate, such as spending more time near a certain male singer, rather than following the actual mating process , and therefore may not be an entirely accurate way of gauging mate selection (Byers & Kroodsma, 2009). Because it is currently impossible to subtly alter live vocals, studies on female choice have been met with some controversy, with opposers to this theory arguing that there is no definitive evidence that repertoire size directly influences mate choice (Byers & Kroodsma, 2009).

However, even in a song as structurally simple as that of the black-capped chickadee (*Poecile atricapillus*), there is evidence that females may judge males based on aspects of their singing (Christie et al., 2004). Some studies suggest that structural differences in the chickadee song may reflect the fitness of a male by indicating his capability to cope with physiological constraints involved with sound production (Christie et al., 2004). If certain song structures are in some way costly to produce (e.g., to sing, to repeat, or to learn), that would make structure an honest indicator of male quality (Christie et al., 2004). In another study, in a different location, it was found that variation in relative amplitude of song could predict dominance status of black-capped chickadees, which marks it as another similar acoustic feature which might influence female choice (Hahn et al., 2013).

Another aspect of song that has been implicated in mate choice is complexity. Bengalese finch (*Lonchura striata domestica*) have been found to prefer mates who

perform complex songs over simple ones, and there is evidence that male canaries (*Serinus canaria domestica*) possess "sexy syllables" which are preferred by females (Leitner & Catchpole, 2004; Matsunaga & Okanoya, 2009). This perceived preference for more complex songs might be an indication that males who possess the ability to perform with higher complexity have a higher fitness than males who perform with less complexity (Byers et al., 2015). It is possible that song complexity may provide females with information on parental ability, condition, genetic quality, or age of the male singer (Ballentine et al., 2003). For example, juveniles who respond poorly to a lack of nutrition may develop variation in their song which could be perceived by females as an indication of indirect consequences for their offspring (Nowicki et al., 1998). In one study using food supplements to modify male condition, singing rate was implied to be an honest reflection of a male's current physiological condition (Nowicki et al., 1998). As well, past research supports a relationship between repertoire size, female choice, and various measures of reproductive success (Searcy & Yasukawa, 1996). However, a lack of critical information on how birds perceive the sequences of their conspecifics (i.e., members of the same species) makes it difficult to study the nuances of these preferences (Byers & Kroodsma, 2009).

Syntax in Birdsong

An additional essential characteristic of birdsong that may contribute to one or both of its functions is syntax, the internal set of guidelines that dictates the order that song types must follow to hold any sort of grammatical meaning (Doupe & Kuhl, 1999; Kershenbaum et al., 2016). Birdsong stands apart from other non-human communication due to its higher level of complexity, including syntax which was once thought to be

unique to humans (Abe & Watanabe, 2011; Cate & Okanoya, 2012; Mol et al., 2017). For example, the use of non-random but variable ordering of song types has been evidenced in multiple species of songbirds, including the common nightingale (*Luscinia megarhynchos*) and Cassin's vireo (*Vireo cassinii*; Sainburg et al., 2019). The level of predictability of those transitions differs depending on the species studied, with some bird species possessing highly predictable songs (e.g., the marsh wren; *Cistothorus palustris*) and others containing transitions that are less predictable with a higher degree of randomness, such as in the large-billed reed warbler (*Acrocephalus orinus*; Samotskaya et al., 2016).

Various styles of birdsong syntax have been observed across multiple species and songbirds can be grouped into one of three broader categories when it comes to song type variation in their song. Immediate variety encompasses those species who rarely or never sing the same song type twice in a row, meaning that there is little to no immediate repetition of song types. An example of a species which sings with immediate variety is the greenish warbler (*Phylloscopus trochiloides*), which switches immediately from one song type to the next throughout its song (Singh & Price, 2015). Eventual variety describes those that perform the same song type in a repetitive, predictable fashion before introducing a new song type. This includes the grey-hooded warbler (*Phylloscopus xanthoschistos*), who repeats one song type up to 20 times before switching to another song type (Singh & Price, 2015). No variety means that the species only performs one single song type repeated many times, as can be seen in species such as the Hutton's vireo (*Vireo huttoni*) and chipping sparrow (*Spizella passerina*; Hartshorne, 1973; Price, 2013).

There is evidence of birdsong possessing high-level dependencies, meaning that the song type performed depends on those that come before it (Hedley, 2016). Markov models have been used in this context to evaluate dependencies by determining a model that best fits the sequence and relating the complexity of the given model to the complexity of the bird's syntax (Hedley, 2016). Using Markov models, a study on Cassin's vireo found that the song types performed by this species depended not just on the song type sung immediately before, but also on the third or fourth preceding song type (Hedley, 2016).

On top of these dependencies, there has also been debate on whether or not birdsong possesses compositionality, which occurs when the meaning of a given combination depends on the meaning of its parts as well as the way that those parts are combined (Suzuki et al., 2018). The Japanese tit (*Parus minor*) is one species whose call fulfills the requirements of compositionality, suggesting that changes in the order of their call could result in a different meaning (Suzuki et al., 2018). However, critics of this theory suggest that there are factors outside of compositionality that could account for the observed vocal behaviours in the Japanese tit (Bolhuis et al., 2018). Other animals (e.g., non-human primates) are capable of using combinations of meaningful calls, but they are not compositional, which means that the order of those calls is not vital to their overall message (Suzuki et al., 2018). Although birdsong is undoubtedly more basic than human language, its potential use of compositionality could be useful in relating birdsong to speech.

The purpose of this complex syntax within birdsong, however, remains unclear. Some species (e.g., the Bengalese finch) have been shown to recognize a disruption in

12

typical song syntax, indicating that they rely on internal syntactic guidelines for communication (Abe & Watanabe, 2011; Yip, 2013). This capability of distinguishing between normal and abnormal syntax suggests that syntax does serve some function in communication, and possibly plays a role in one or both of the two major functions of birdsong: aggression and mate attraction (Kershenbaum et al., 2016; Molles & Vehrencamp, 2000; Osiejuk & Jakubowska, 2017). However, it is not yet clear how syntax is employed and perceived by conspecifics, or if the use of syntax holds any true meaning (Cate & Okanoya, 2012).

To assess the importance of song syntax as an aggressive signal, many researchers use playback experiments because they allow for an evaluation of male-male interactions in their natural environment (Hedley et al., 2017; Nielsen & Vehrencamp, 1995; Taylor et al., 2017). Playback experiments are particularly useful in examining this relationship because they allow for the manipulation of a rival song which makes it possible to derive causal relationships while maintaining a high degree of ecological validity (Hedley, et al., 2017; Nielsen & Vehrencamp, 1995; Taylor, Brumley, Hedley & Cody, 2017).

In a typical playback experiment, a recording of another male conspecific will be played somewhere within the bird's territory, eliciting a response. To assess the importance of certain aspects of song, researchers can alter the recording to reflect an atypical version of the song, including changes in the species' regular use of syntax. Physical and vocal reactions are monitored throughout the duration of the playback session and later analyzed for aggressive signals, which can then be compared between the typical and atypical playback sessions (Hedley et al., 2017; Nielsen & Vehrencamp, 1995; Taylor et al., 2017).

13

Playback research has been conducted to study the importance of syntax to communication in male-male interactions in Cassin's vireo (Hedley et al., 2017). Using a playback condition, in which a conspecific song is played back to the subject, Hedley et al. (2017) manipulated the recording by changing the syllable sequence of the regular song (i.e., the order of song types) and were able to discern that song syntax is an important and perhaps necessary aspect of male-male aggression and recognition between conspecifics. Evidence of sensitivity to syntax has also been shown to be present in the California thrasher (*Toxostoma redivivum*; Taylor et al., 2017). In a playback study done by Taylor et al. (2017), it was found that birds of this species responded more strongly to recordings that contained a male's natural syntax as opposed to ones that had been randomly generated, suggesting some degree of recognition was associated with proper syntax use.

However, other playback studies have shown the opposite results; in a study conducted on New York swamp sparrows, males responded more vigorously to a dialect of their song which contained syntax that differed from their own (Balaban, 1988). Although this increase in response was not expected, it could provide evidence that the order of song types affects the information content of a song, such as the strength of the aggressive signal. It has been suggested that song syntax could play a role in group recognition, and this theory was supported by the findings of Briefer, Rybak, and Aubin (2013) whose study on skylarks (*Alauda arvensis*) found an increase in aggression to modified syllable order that was similar to the response given when faced with the natural song of a stranger. This implies that changing the temporal order of song elements may

affect the encoded information, in this case being whether or not the intruder was part of a predetermined group (Briefer et al., 2013).

While there have been studies that have found both increases and decreases in response, some species of bird have been found to exhibit little to no difference at all in their response to changed syntax in the playback condition (Emlen, 1972; Holland et al., 2000; Pellerin, 1982; Nelson, 1988). This suggests that syntax may play little to no role in conspecific communication. However, considering the large amount of variation seen in singing behaviours, it is possible that syntax may function differently between species, which would explain the variation seen in current literature. These mixed results found amongst different species of songbirds highlights the need for further research on the use of syntax and how it is perceived.

Syntax could be used as an aggressive signal meant to convey a threat to other birds intruding on their territory. During an interaction with a rival, males have been shown to respond with a change in their internal syntactic structure, meaning that their choice of song type may be influenced by their rival's song (Liu et al., 2018; Osiejuk & Jakubowska, 2017). This shift in song order may reveal useful information on the properties of a species' syntax, and further research on male-male interactions between conspecifics could provide meaningful insight into communication mechanisms.

Syntax may also have implications for mate choice, which has been shown to be affected by other aspects of song (such as song structure), but there is little known evidence that syntax is specifically used for this purpose (Alger et al., 2015; Balaban, 1988; Kershenbaum et al., 2016). One study found that female serin birds (*Serinus serinus*) responded more often to repetitive syntax, and another found that male blue

grosbeaks (*Passerina caerulea*) produced a significantly larger number of song variants during the female's fertile period, meaning that the songs sung during the early breeding season contained more complex and consistent syntax (Ballentine et al., 2003). These findings imply that, at least in this species of bird, the complexity of song syntax did have functional significance and may be considered in female mate choice. It was suggested that song type order may serve to facilitate individual recognition between conspecifics which could be especially vital during mating periods (Ballentine et al., 2003). However, more research on female preferences is required to understand syntax's importance in mating behaviours (Cardoso & Mota, 2004; Ballentine et al., 2003).

Rather than being directly linked to the two major functions of birdsong (mate attraction and aggression), another explanation for the use of song syntax could be maximizing attention. Alternative song type choices, especially those within a varying frequency range, could serve to reduce sound competition, which could consist of competition from other bird species in the immediate area, other animals (e.g., frogs, mammals), or abiotic noises from the surrounding environment (e.g., waves, wind; Brumm & Slabbekoorn, 2005; Douglas & Conner, 1999; Kirschel at al., 2009). Common chaffinches (*Fringilla coelebs),* for example, have been shown to use different song types when singing near loud streams (Brumm & Slater, 2006). As well, Eastern meadowlarks (*Sturnella magna*) are known to adjust the timing of their singing to avoid competing sound from conspecifics (Knapton, 1987). It is possible that song syntax has evolved as a mechanism of making individuals better heard in a sound-intensive environment.
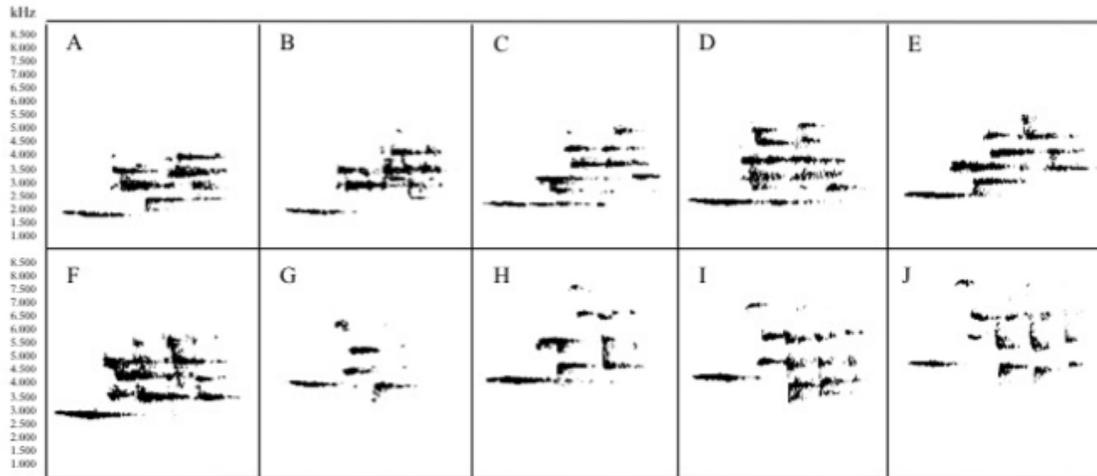
The Hermit Thrush

The hermit thrush (*Catharus guttatus*) is a common, migratory songbird found in many parts of Canada as well as the western and north-eastern United States (Dellinger et al., 2012). The breeding territories of the hermit thrush consist of hardwood forests as well as boreal and mountainous coniferous forests (Rivers & Kroodsma, 2000). Although the beauty of the hermit thrush song has attracted the attention of poets, there is currently a dearth of research, with very few studies examining the structure of their songs, organization of their song repertoires, or singing behaviour (Burroughs, 1871; Rivers & Kroodsma, 2000; Roach et al., 2012).

Song repertoires of the hermit thrush male are moderate in size and typically are composed of 6-12 song types (see figure 1), each consisting of an introductory note followed by a complex post-introductory portion (Roach et al., 2012; Rivers & Kroodsam, 2000). There is no evidence of song sharing in the hermit thrush, meaning that neighbouring males sing unique song types, although the general patterns of those song types (i.e. their structure) are similar (Roach et al., 2012; Rivers & Kroodsma, 2000). Past research in this area has supported the notion that the hermit thrush song does follow an internal syntactical code; song types have been shown to be partially non-random in order and are moderately predictable, meaning that certain song type sequences were preferred over others (Roach et al., 2012). Hermit thrush tend to cycle between song types that begin with introductory notes of higher (~4000hz) and lower (~3000hz) frequencies, and previous studies have shown hermit thrush song types to be delivered with immediate variety (i.e., the same song type is never repeated twice; Roach et al., 2012; Roach & Phillmore, 2017).

Figure 1.

Transitions matrix and song repertoire of an individual hermit thrush.

Note. Each block represents one song type with introductory note frequency measured in kHz.

My honours research supported past works by indicating that the hermit thrush does sing with some degree of order (Nesbitt, 2019). Consistency scores ranged from 0.30 to 0.82, indicating that there was a 30-82% accuracy in predicting the following song type in a singing bout, with chance levels at approximately 12.5% (Nesbitt, 2019). Along with song type order, the tendency to display an alternating pattern of high and low frequencies is an interesting facet of the hermit thrush's song structure. When studying hermit thrush vocals, it was found that all individuals cycled between high and low frequency song types throughout their singing bouts (Nesbitt, 2019). Furthermore, when categorized into high/low frequency groups (i.e., song types were placed into either a "high" or "low" group based on the frequency of the introductory note), song type consistency increased, indicating a more ordered song (Nesbitt, 2019).

Overall, it is not entirely clear if these patterns of hermit thrush song syntax serve any biological relevance in birdsong communication, and the mixed results found in current literature suggest that the function of syntax may differ depending on the species, meaning that different species may use syntax in different ways. Therefore, expanding the current knowledge on syntax use in a broad spectrum of species is vital. The presence of syntax use in the hermit thrush song indicates that it may serve a function in male-male aggression or mate attraction within this species.

There is some evidence that syntax use plays a role in hermit thrush mate attraction. It has been found that males alter their syntax over time, displaying more ordered songs earlier in the breeding season (Roach, Macleod, & Phillmore, in prep). Because of the comparatively little time males have in the breeding season to obtain a territory and breed, it is likely that singing earlier in the season increases their chances of attracting a mate over their competition (Catchpole, 1980). Therefore, a sharp decline in song consistency late in the breeding season suggests that syntax does function in mate attraction: to secure a female early in the mating process when more is at stake (Roach, Macloed, & Phillmore, in prep). If it is true that syntax has a function in mate attraction, it could also help to explain the alternating frequencies observed in hermit thrush song. Females of other species (e.g., canaries) have been shown to prefer more physically challenging songs which might be an incentive for hermit thrush to include both high and low frequency song types in their repertoire (Ballentine, Hyman et al., 2004).

Aside from mate attraction or territorial defence, another possible explanation for this behaviour is that it is performed to maximize attention. If there is noise interference at the same frequency that we see the characteristic gap occurring in hermit thrush song

(~3000 Hz), it is possible that the species has adapted its song to avoid this range in order to stand out in a highly sound competitive environment. This has been observed in other species, with birds singing in a restricted frequency range or moving up and down in their frequency use to communicate through diverse noise (Slabbekoorn & Smith, 2002).

Another explanation is that the change between differing frequencies functions in a similar way to song type switching, in which birds deliver song types in a bout before switching to another song type (Nielsen & Vehrencamp, 1995). Various explanations for song type switching have been proposed that could also hold true for frequency switching, including reducing habituation, reducing exhaustion of vocal musculature, and deceiving intruders (Falls & d'Agincourt, 1982; Krebs, 1976; Lambrechts & Dhondt, 1988).

Other closely related species to the hermit thrush may provide competitive noise that would drive the hermit thrush to avoid certain frequencies. This is supported by the finding that the gap in hermit thrush frequency coincides with frequency ranges of the black-capped chickadee and white-throated song sparrow (*Zonotrichia albicollis*), who are often found to inhabit the same environmental habitat as the hermit thrush (Nesbitt, McLean, & Roach, 2019). It is possible that the hermit thrush has evolved its song to avoid certain frequencies to be heard above other nearby bird species who sing within that frequency range. This would imply that syntax may serve an indirect role in the two major biological functions of birdsong (mate attraction and territorial defence) rather than a direct one.

The behavior of cycling up and down the frequency spectrum is not confined to only the hermit thrush, but is also seen in a closely related species, the veery (*Catharus*

fuscescen), and it has been suggested that the variety observed in song delivery may be the result of differences in the song's recipient, including motivation and context (Brennan & Jones, 2016). An example of a similar situation can be found in the blue-winged warbler (*Vermivora cyanoptera*) which is thought to employ two distinct songs in differing contexts (Ficken & Ficken, 1967; Gill & Murray, 1972). One study found that the warbler used one song type more often during the early breeding season (early June), and used the second song type exclusively in territorial situations until introducing it more often later in the season (late July; Kroodsma, 1988).

Although it could be true that syntax as a whole is used exclusively to maximize attention, it could also be the case that different elements of song order (i.e., order of specific song types vs. order of high/low frequency song types) could serve different functions in communication, meaning that the observed cycling high/low frequency pattern could play an altogether distinct role from that of song type consistency. It could also be true that the high and low song types themselves serve different purposes. If the two frequency groups are employed to accomplish equally important goals, then it would follow that birds would switch between them at a consistent pace to ensure that all needs are being met. For example, it has been found that male great tits tend to sing lower frequency songs more often when interacting with fertile mates, which suggests that low frequency song types are preferable to females (Halfwerk et al., 2011). However, high frequency song types are beneficial when trying to overcome competing noise sources (Halfwerk et al., 2011). Therefore, one possibility is that hermit thrush males may regularly use both high and low frequency song types to ensure that they are being heard over greater distances while impressing already nearby females.

Interestingly, hermit thrush repertoires appear to contain redundant song types (i.e., when an individual uses two unique song types in a very similar manner) which showed similarities in structure and frequency, indicating the possibility of redundant functions (Nesbitt, 2019). If this is the case, other hermit thrush may be perceiving redundant song types as being the same, which would mean that they convey identical information in conspecific communication (Nesbitt, 2019).

One possible explanation is that coding strategies which depend on elemental structures, such as syntax, must be tolerable to a certain degree of song degradation (i.e., when environmental factors attenuate sound transmission) to continue functioning properly. This means that the song types performed may be able to vary slightly without the listener perceiving any differences (Blumstein & Turner, 2005; Slabbekoorn et al., 2002; Holland et al., 2000). Because redundant song types are similar in structure and frequency, birds may be perceiving them as being the same song type rather than two separate entities. If true, this would affect future studies on hermit thrush syntax because it would change the way that we interpret different song types and their impact on the overall order of song.

Although it is unclear if the division of repertoires into high and low song types is related to any significant functions, it still raises questions about how males perceive the songs that they are listening to. In particular, whether or not birds hear the songs as representing a complete collection of song types or a smaller subset, such as high/low frequency categories (Roach et al., 2012). It has been suggested that hermit thrush may perceive all high song types and all low song types as two collective groups, rather than each song type as its own individual entity, which could have important implications for

song syntax because it dictates whether or not the order of discrete song types matter to overall function (Nesbitt, 2019).

Given the complex syntax demonstrated by the hermit thrush, it is likely that syntax does have some function in one, or both, of birds' two major biological functions: male-male aggression and mate attraction. The current study seeks to evaluate the use of syntax in male-male interactions through playback studies in a natural environment. Changes in behavior will be monitored in two sessions, one with a typical syntax stimulus and one with an atypical syntax stimulus in which song types were reordered to reduce stereotypy. Since hermit thrush song is not entirely random in the order of its song types and appears to be consistent in terms of cycling between high and low frequency song types, by changing the order of song types we can examine the impact of syntax in aggressive signalling between male hermit thrush. This method is similar to other syntax studies using playback experiments (Hedley et al., 2017; Nielsen & Vehrencamp, 1995; Taylor et al., 2017).

It is hypothesized that the hermit thrush will have a lessened physical response to the atypical playback sessions as compared to the typical, which would indicate that syntax is a necessary component of effectively conveying territorial aggression. As a secondary objective, vocal responses will be recorded throughout the playback sessions to evaluate the song for aggressive signals. It is hypothesized that there will be differences in the syntax use of male hermit thrush when faced with a rival song, including frequency type matching and song overlapping, as well as the use of low-amplitude soft song.

Method

A playback study using within-subjects design was employed to assess the responses of hermit thrush males to conspecific songs with typical vs. atypical syntax. The playback sessions were counterbalanced across subjects, with half of the individuals receiving the typical stimulus during the first playback session and the other half receiving the typical stimulus during the second playback session. The playback sessions were conducted a few days apart (except in some cases where weather or the subject's activity did not permit), with enough time between sessions to reduce the risk of the first playback session influencing the second, while also minimizing the chance that the bird's breeding status would change between one session and the next. Birds were located through visual or auditory cues to ensure that playback occurred within the limits of their territory to maximize the bird's attention to playback stimuli. The paired sessions were performed at a similar time of day in the same marked location. The territories of each subject were located within the same geographic region to minimize structural variation in song.

Playback Stimuli

Typical stimuli consisted of recordings of male hermit thrush spontaneously singing in their natural habitat using characteristic syntax. These recordings were taken from a collection of hermit thrush songs recorded in 2012 in the Halifax Regional Municipality which allowed for use of playback songs that had a similar structure for the geographic region of hermit thrush but no risk of being recognized as a current neighbor (Roach & Phillmore, 2017). A typical stimulus consisted of ~45 songs taken directly

24

from a recorded sequence of spontaneous singing recorded using a Marantz PMD 670 solid-state digital recorder with a Sennheiser ME66 directional microphone, with the only edits being the occasional addition or deletion of silence between song types to achieve the desired rate. Playback stimuli were chosen through spectrographic analysis based on the clarity of the recording, minimal background noise, the presence of only one male hermit thrush within the territory, and high consistency scores (i.e., more ordered song). Songs with a higher degree of order were chosen specifically to ensure that typical stimuli were capturing the necessary elements of syntax that were of interest in the current study. The two stimuli were identical in terms of the total number of songs, the number of times each song types occurred, and the timing of those song types (i.e., the amount of space between one song type and the next was kept constant). The only difference between typical and atypical stimuli was the order of the song types within the sequence (see figure 2).

Figure 2.

Typical vs Atypical Syntax Sequence
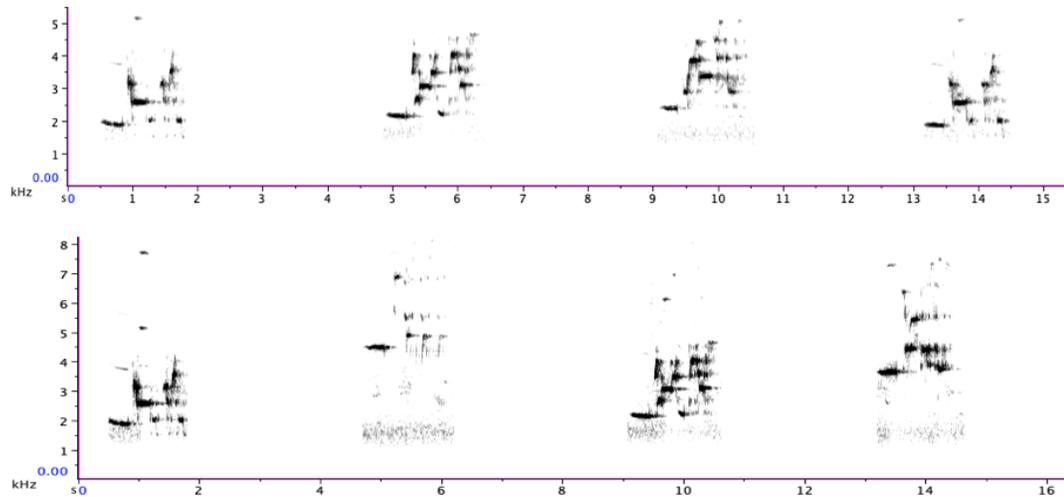
Note. This image depicts a comparison of the first four song types in the atypical syntax stimulus (top) compared to the typical syntax stimulus (bottom).

Sequences were filtered in Audacity to remove background noise using a high pass filter (1500hz). The same filtering was done to both typical and atypical stimuli. Recordings were kept to a maximum of three minutes of singing and were created using an audio editing software (Audacity 2.1.1.0). The length of the recordings was chosen to be long enough to elicit a reaction in the focal bird without causing extended stress, similar to what has been used in previous studies (Hedley, et al., 2017; Hyman, 2003; Roach, 2016).

Atypical stimulus consisted of recordings which were altered by cutting and pasting song types in a sound editing software to remove the order/predictability by making all transitions equally likely to occur. These were designed by randomly altering the order of song types of each normal recording. The atypical stimulus was created using the same song types ordered in a semi-random way with the goal of producing sequences that rarely repeat the same transitions. This creates a song with a very low consistency

26

score that still exhibits immediate variety, and in doing so disrupts the regular up and down frequency cycling. The average consistency score for typical sessions was .728 ± .11 which was reduced to .320 ± .03 in the atypical sessions after manipulation. Up and down frequency cycling was also reduced after manipulation, as is demonstrated in figure 3.

Figure 3.

High/Low Frequency Cycling in Typical and Atypical Stimuli
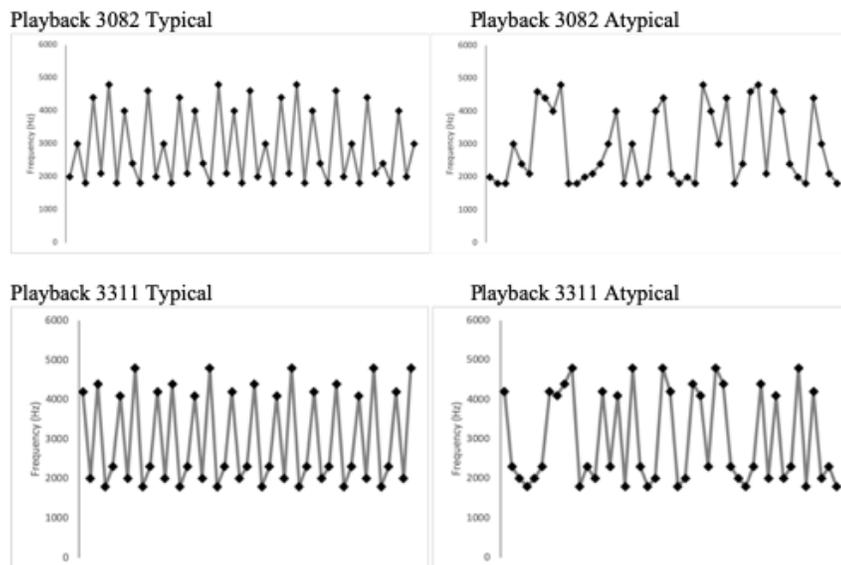
Note. The figure shows a comparison between typical and atypical stimuli of frequency cycling throughout a song.

Playback stimuli were uploaded to an iPhone 7 and broadcasted through a speaker. Unique recordings were played for each bird in a given area to minimize the possibility that neighbouring individuals had previously encountered the playback stimulus. Due to technical difficulties, the speaker was switched from a Sony SRS-X2 Bluetooth speaker to a Sony SRS-XB12 wireless speaker partway through the study.

Playback output can be assessed spectrographically by visual examination to ensure that no critical element of the song was lost in broadcast.

Data Collection

Data were collected throughout the 2019 breeding season (May 11-June 30) within the Halifax Regional Municipality. Recordings were taken at various hours of the day, collected using a Marantz PMD661 MKIII recorder with a Sennheiser ME66 directional microphone and a Zoom H4n pro digital recorder with internal microphone. The majority of these recordings were collected at dawn (6 AM – 9 AM) and a few collected at dusk (around 7 PM), but the time of day was always matched between paired sessions. Playback locations were marked using tags on trees and GPS to keep track of individuals' territories which are consistent throughout the breeding season. Individuals were identified based on their location within the same territory and, due to lack of song type sharing between hermit thrush neighbours, could be confirmed by their song types (Rivers & Kroodsma, 2000; Roach et al., 2012; Roach, Macleod, & Phillmore, in prep).

When a male bird was found singing on his territory, pre-playback recordings of the subject's spontaneous singing were collected. Playback sessions then commenced. Ropes were used to mark off an arena within the bird's territory, measuring 8m in each direction from the speaker producing the playback stimulus. The volume of the speaker remained consistent, and was measured by a Tacklife SLM01 decimeter, both in the lab and before each session in the field, to have an amplitude of approximately 80dB measured at a distance of 1m as was used in previous playback studies (Hedley et al., 2017; Roach, 2016).

28

Playback sessions consisted of the three-minute playback recording and three minutes of observing post-playback response. Throughout the session and the following three minutes, researchers narrated the physical responses of the bird through an Olympus VN-541PC handheld recorder from a discreet location just outside the arena. Notes were made when birds entered the arena, swooped through the arena, or landed at any distance within the arena. Distance from the speaker was recorded at all times that the bird was positioned within the arena. When possible, spontaneous singing was also recorded after playback. As well, vocal responses were recorded throughout the playback session using a Marantz PMD661 MKIII recorder with a Sennheiser ME66 directional microphone.

Physical Behaviour

To measure physical behaviours, narration of the bird's physical responses to the playback stimulus were transcribed. The researcher transcribing the narration into data was blind to the individuals' identities. Measurements consisted of distances from the speaker and the number of times the bird swooped through the arena, broken down into six variables as used in previous studies: (1) average distance from the speaker, (2) closest distance to the speaker, (3) amount of time spent within a 5m radius of the speaker, (4) number of times the bird swooped within 5m of the speaker, (5) latency to approach a distance of 5m from the speaker, and (6) latency to the first flight that passed within 5m of the speaker (Hyman, 2003; Nielsen & Vehrencamp, 1995; Roach, 2016). In cases where the bird did not enter or swoop over the arena, the total length of the playback session (180 seconds) was used for latency-related variables, and the limit of

29

the arena (8m) was used for distance-related variables. Other potentially aggressive behaviours (i.e., positioning of body and wings) were noted in the narration.

Vocal Behaviour

A spectrographic analysis was used to measure birds' vocal responses to the playback stimulus and was conducted using RavenPro 1.4 interactive sound analysis software. Large files (i.e., greater than 150 MB) were broken into smaller durations using the program Audacity and subsequently imported into RavenPro. Spectrograms generated in RavenPro 1.4 (Hann window size 1600 FFT) were adjusted for contrast and brightness to generate a clear image. Within each recording, songs were sorted into structurally distinct song types through visual appraisal and comparison of the spectrogram. This method of classification is well-established in birdsong research and has been found to be superior to computer algorithms at identifying song type patterns (Kershenbaum et al., 2011), and previous studies on hermit thrush song have also used this method (Roach et al., 2012; Roach & Phillmore, 2017). Song repertoires were constructed using spontaneous singing collected from the individual prior to the playback session.

Overlapping was measured spectrographically by identifying songs which were performed by the focal subject before the end of the playback song. The rate of overlapping was found by calculating the proportion of songs which overlapped playback songs. To determine the likelihood of overlapping occurring by chance, Ficken's (1974) method was employed, in which the observed rate of overlapping was compared with the expected rate of overlapping that would occur if the bird was singing without taking into consideration the timing of the playback stimulus. According to this method, expected

rate was calculated for each playback stimulus by dividing the number of seconds that the bird was engaged in singing by the total number of seconds to calculate the probability of the bird singing, where v represents the total amount of time during which the bird is singing, and $\bar{v}$ is the total amount of recorded silent periods:

$$p(v) = v/(v + \bar{v})$$

Frequency matching occurs when individuals respond with song types that are similar in frequency to the song type last delivered by a conspecific (Searcy & Beecher, 2009). To account for frequency matching happening by chance, an expected rate of frequency matching was calculated using the proportion of high/low song types present within the song, thus representing the probability of each category of song type (high or low) naturally occurring. The current study considered frequency matching in terms of "high" and "low" song types which can be determined through assessment of the hermit thrush song repertoire. Songs that begin before the conclusion of the preceding playback song were excluded, and songs that failed to begin immediately following the playback song were excluded, to ensure that the focal bird did in fact hear the entire playback song before responding.

Matching rate was defined as the proportion of eligible song types (those which qualified as being in the same high/low bracket) that matched with the preceding playback's song type. Expected rate was defined as the probability of high/low song types being used, calculated as the proportion of each song type being used during spontaneous singing. The expected rate highlights how often each unique song type is generally sung by the bird, outside of the playback condition. The overall expected rate

was calculated as the average of the expected probabilities of the different song types used throughout the playback session.

The three chosen categories of vocal responses were first measured independently of each other. To then compare results, overlapping and frequency matching rates were normalized using an odd's ratio:

Normalized rates > 1 represent an above chance level of overlapping/matching, while rates < 1 represent a below chance level of overlapping/matching.

If syntax does play a role in male-male competition, then territorial males should perform stronger physical signals of aggression towards typical stimuli compared to atypical stimuli. Specifically, I would predict that average distance from the speaker, closest distance to the speaker, latency to approach a distance of 5m from the speaker, and latency to the first flight that passed within 5m of the speaker should be lower, and that the amount of time spent within a 5m radius of the speaker and number of times the bird swooped within 5m of the speaker should be greater when responding to a typical stimulus versus an atypical stimulus. To test these predictions, I first conducted a principal component analysis on the six variables listed above in the program R 3.5.1. Principal component analyses are useful for examining variation in a wide dataset (Wold et al., 1987). The computed principal component values were then compared using a t-test or Wilcoxon signed rank test depending on the distribution. Paired comparison tests were used to analyze the vocal responses. For count data (e.g., number of swoops across the arena), as well as continuous variables with non-normally distributed data, the Wilcoxon signed rank test was used. For continuous variables with a normal distribution,

32

a paired samples t-test was used. Pearson correlations were used to assess any association between the physical and vocal responses to playback stimulus.

The Shapiro-Wilk test was used to assess normality for each analysis. For paired tests, a t-test was used in the case of a normal distribution and a Wilcoxon signed-rank test was used in the case of a non-normal distribution. For between-subjects tests, an independent t-test was used for normal distributions and a Mann-Whitney U test was used for non-normal distributions. All tests were evaluated at an $\alpha = 0.05$ level.

Results

Among the 16 individuals collected, there were ten successful paired sessions, making a total of 10 birds with 20 recorded playback sessions for the within-subjects analysis. Along with the paired sessions, there were also individuals who had either the typical or atypical session but not both. Due to the presence of birds with incomplete paired sessions, between-subjects data analysis was also conducted which treated each playback session as an independent event. These birds were included in the between-subjects analysis because they met the requirement of a single successful session. Therefore, the between-subjects analysis had a sample size of 15. All birds were located within the Halifax regional municipality and Dartmouth.

Physical Responses

To assess whether birds responded differently to typical vs. atypical syntax, the six physical variables were compared between each session. Along with examining each variable independently, a principal component analysis (PCA) was used to reduce the model by grouping correlated variables. This was done both to reduce dimensionality and

33

observe any highly correlated variables. Two components with eigenvalues greater than one resulted, grouping average distance, time within 5m, latency to time within 5m, and closest approach into component one (PC1). Component two (PC2) consisted of flights within 5m and latency to flights within 5m (see Table 1). Combined, PC1 and PC2 accounted for 86.37% of total variance.

Table 1. Factor loadings for principal components with eigenvalues greater than one.

Variable	PC1	PC2
Time5m	-.944	.140
AvgDis	.940	-.173
LatencyTime5m	.888	.272
ClosestApp	.879	.122
Flights5m	.194	-.917
LatencyFlights5m	.137	.901

Note. A cutoff of .300 was used for factor loadings included in the table.

The two PCs were compared for differences between the typical and atypical sessions using a paired test. PC1 (which encompassed average distance, time spent within 5m of the speaker, latency to a landing within 5m of the speaker, and closest approach) was found to be non-significant (paired t-test: $t(9) = -0.09$ $p = .932$). The second principal component (which encompassed flights within 5m of the speaker and latency to flights within 5m of the speaker) was also found to be non-significant (paired t-test: $t(9) = -0.60$, $p = .561$). These results indicate that the aggressive response was the same to both stimulus types.

Due to the findings being non-significant, each of the variables was also assessed individually to ensure that no relationships were masked by the PCA. Average distance was found to be non-significant (Wilcoxon signed-rank test: $z = -0.53$ $p = .594$), number of flights was non-significant with (paired t-test: $t = 0.51$, $p = .620$), latency of flights was non-significant (paired t-test: $t = 0.86$, $p = .413$), time spent within 5m of the speaker was non-significant (Wilcoxon signed-rank test: $z = -0.36$, $p = .719$), latency of time spent within 5m of the speaker was non-significant (paired t-test: $t = 0.35$, $p = .738$), and closest approach was non-significant (Wilcoxon signed-rank test: $z = 0.28$, $p = .779$). Thus, all of the individual variables were found to be nonsignificant, suggesting that there was no difference in aggressive response based on stimulus type.

The between-subjects analysis was then conducted in a similar manner. The difference between the typical and atypical stimulus types for PC1, $F(13) = 0.68$, $p = .424$, and PC2, $F(13) = 1.05$ $p = .324$, were both found to be non-significant. When examining individual variables, latency of time within 5m was found to be non-significant, $F(13) = 0.19$, $p = .671$; flights within 5m was non-significant, $F(13) = 3.42$, $p = .087$; latency of flights within 5m was non-significant, $F(13) = 0.01$, $p = .911$; closest approach was non-significant, $z = -0.26$, $p = .792$; average distance was non-significant, $z = -0.99$ $p = .325$; and time within 5m of the speaker was non-significant, $z = -0.93$, $p = .353$. All tests were found to be non-significant, suggesting that aggressive response did not differ based on playback condition across the different birds.

Whether comparing aggression within subjects for individuals who completed both a typical and atypical session or comparing aggression amongst all typical and

atypical sessions, there were no differences found in the aggressive response to typical versus atypical syntax.

Vocal Responses

Overlapping rate was calculated by comparing expected number of overlapping song types to the observed rate of overlapping song types. When assessing aggressive vocal responses, all sessions were pooled together without regard to playback stimulus type. There was a significant difference (Wilcoxon signed-rank test: $z = -3.69, p < .001$) indicating that birds actively avoided overlapping the playback stimuli. Only one individual had overlapping rates markedly higher than chance level (see Figure 4).

Figure 4.

Rates of Overlapping
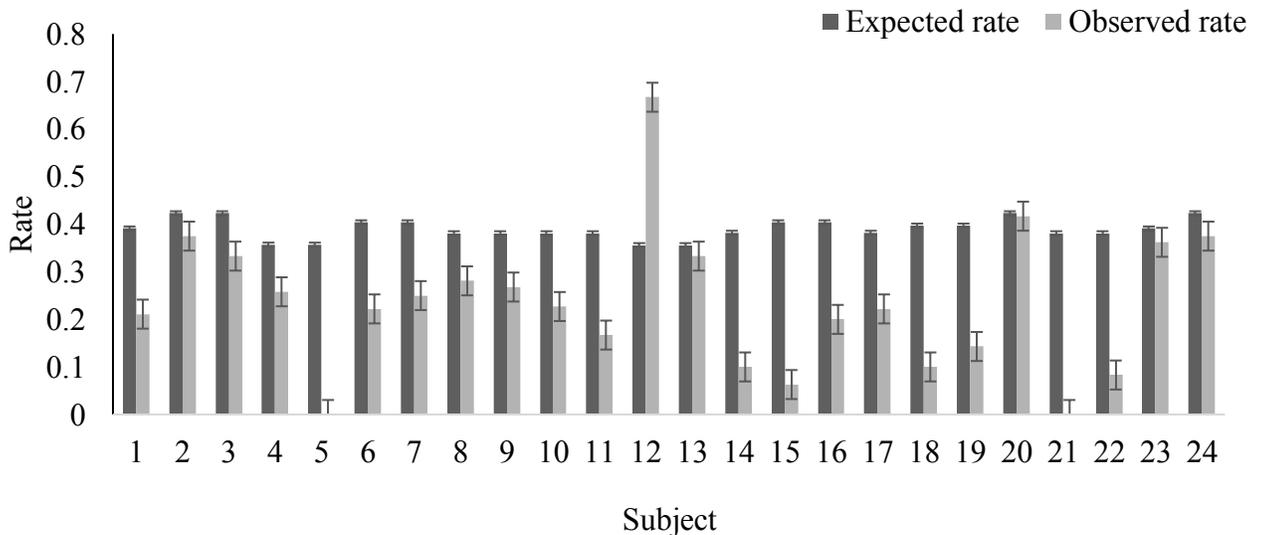
Note. This figure shows the expected and observed overlapping rates for each subject.

To assess whether there was an association between overlapping and physical aggression, a correlation was run between the normalized overlap rate (calculated as

36

observed rate divided by expected rate) and each of the two principal components for physical responses. This would tell us if the rate of overlapping increased or decreased with measures of physical aggression. Kendall's tau was used because the data were not normally distributed. There was no significant correlation between PC1 ($\tau = .10$ $p = .487$) or PC2 ($\tau = -.03$, $p = .843$) with overlapping rate. This indicates that there was no association between the strength of the physical response and the rate of overlapping.

To determine if there was a difference in overlapping rates when presented with typical versus atypical stimuli, t-tests were used. Between-subjects differences was found to be non-significant (independent t-test: $t(22) = -0.88$, $p = .414$). Likewise, within-subjects differences across the two stimulus types was found to be non-significant (paired t-test: $t = -0.90$, $p = .409$). Thus, as with physical response, overlapping was not associated with stimulus type.

Frequency matching, which is when birds alter their singing to match the frequency rates of a rival's song, was determined by evaluating the difference between the observed and expected occurrence. Advanced matching was also evaluated using the same methods.

In the case of regular matching, where birds respond to the playback song with a song type that matches in frequency range, birds matched significantly less than what would be expected by chance (Wilcoxon signed-rank: $z = -2.31$, $p = 0.021$). When examining advanced matching, where birds precede the playback song with a song type that matches in frequency range, it was found that birds did not significantly differ from what would be expected by chance (Wilcoxon signed-rank: $z = -0.76$, $p = 0.446$). The

data shows that birds matched the frequency of the playback stimulus song at a lower than chance level when considering regular matching (see Figure 5).

Figure 5.

Rates of Frequency Matching
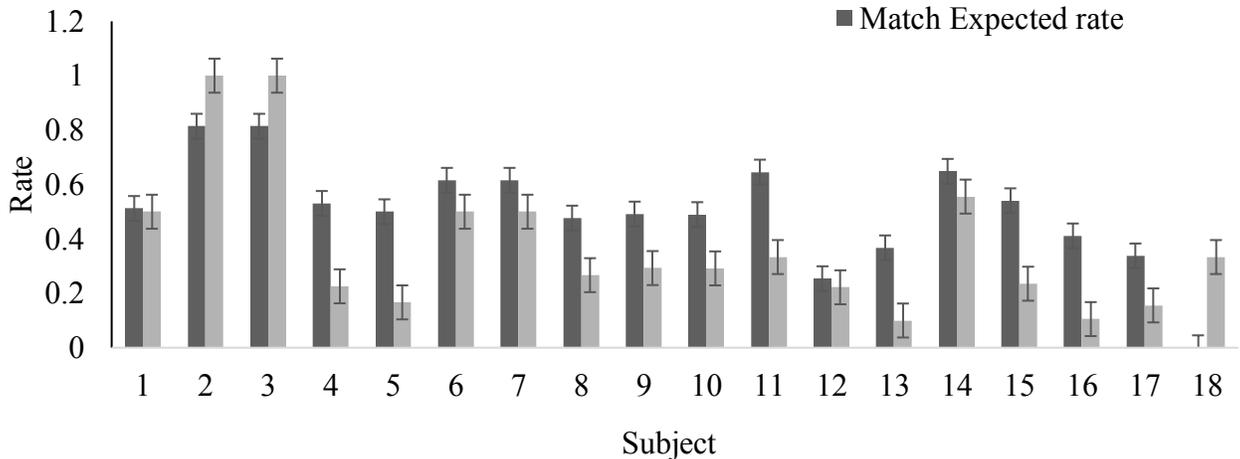
Note. This figure shows the expected and observed frequency matching rates for each subject. Subject 18 did not possess any recorded high frequency song types within its song repertoire giving it an expected rate of 0.

Once again, the use of physical aggressive signals (PC1 and PC2) were correlated with vocal aggressive signals, in this case being rate of frequency matching. PC1 was not correlated with either regular matching ($\tau = .13$, $p = .595$) nor advanced matching ($\tau = -.18$, $p = .470$). Similarly, PC2 was not correlated with either regular matching ($\tau = .31$, $p = .207$) nor advanced matching ($\tau = .01$, $p = .966$). There were no significant correlations between physical signals of aggression and vocal signals of aggression, indicating that the bird's physical response was not related to their use of frequency matching.

A between-subjects and within-subjects test were used to evaluate the impact of playback stimulus (typical vs atypical). The results show that neither the regular matching rate ($z = -0.40$, $p = .690$) nor advanced matching rate ($z = -0.04$, $p = .965$) differed across typical and atypical stimulus types. This suggests that playback stimulus did not affect the rate of matching across individuals. A within-subjects analysis was also used to examine differences between playback conditions. Regular matching did not differ between playback stimuli (Wilcoxon signed-rank: $z = -0.37$, $p = .715$), nor did advanced matching (Wilcoxon signed-rank: $z = -1.10$, $p = .273$). This indicates that the playback condition did not affect the rate of matching, meaning that birds reacted in the same way to both atypical and typical versions of their song.

Novel Vocalizations

One striking difference between singing during playback was the occurrence of abridged songs. A song was classified as being abridged when the introductory note at the beginning of each song is dropped (see figure 6). Abridged songs were not observed in spontaneous singing but on average 28.8% of songs performed during playback sessions were abridged, and 83% of sessions (15 of 18 total sessions) included at least one abridged song. There was a significant negative correlation, $\tau = -.39$, $p = .025$, between the percentage of abridged song types across completed sessions and PC1, the measure of physical aggression which encompassed average distance, time within 5m, latency to time within 5m, and closest approach. This indicates that birds who showed more signs of aggression during playback used fewer abridged songs in their singing. However, there was no association between the percentage of abridged songs and PC2

which included the measures flights within 5m and latency to flights within 5m, $\tau = -.21$, $p = .238$.

Figure 6.

Abridged Song Type
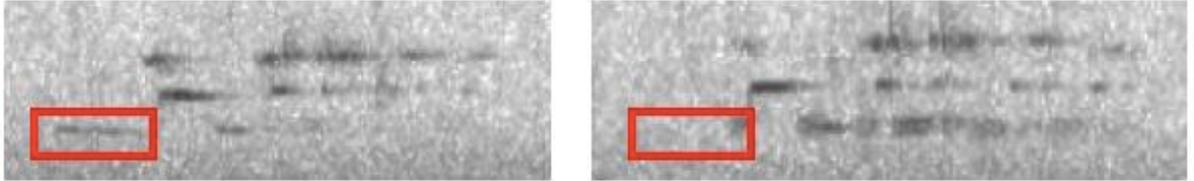
Note. The figure depicts an example of a regular song type (left) compared to an abridged version of that song type (right).

As well, many of the songs observed during playback did not match songs from the bird's broadcast repertoire (which ranged in size from 8 to 14 unique song types) as documented during spontaneous singing. These song types which were performed during playback but not during spontaneous singing were classified as unidentified song types. Recordings of spontaneous singing ranged in the number of songs performed with a minimum of 20 songs within a recording and a maximum of 157 songs. On average, 22.5% of song types performed during playback were unidentified, and 50% of sessions included at least one unidentified song type. Of the unidentified song types, 31% were abridged. The use of unidentified song types was not significantly correlated with either PC1, $\tau = -.02, p = .935$ or PC2, $\tau = .20, p = .290$. The emergence of unidentified song types during playback sessions suggests the possible existence of song types exclusively used when interacting with other birds, which could have implications on a bird's response to an intruding rival.

Discussion

The goal of the current study was to determine whether changes in syntax affected the aggressive response of hermit thrush when faced with a territory intrusion. In both within and between-subjects analyses there was no difference in physical responses to the two stimuli, suggesting that syntax does not play a role in conveying aggression in the hermit thrush species. These findings are consistent with the works of Emlen (1972), Holland et al. (2000), Pellerin (1982), and Nelson (1988) who examined syntax in other species and found that birds did not react differently in playback sessions using altered syntax. However, it remains inconsistent with research on other species that has shown a heightened response to typical syntax in aggressive situations (Hedley et al., 2017; Taylor et al., 2017), and those which suggested the opposite behaviour with birds reacting more aggressively in response to altered syntax (Balaban, 1988).

Based on the mixed results of previous research and what was found in the current study, it is possible that the use of syntax differs between species and that it may serve a different purpose depending on the population examined. Based on the wide range of variation between species in other aspects of song, this would not be surprising. For example, the structure of birdsong can be anywhere from very simple (e.g., including a few whistles) to complex (e.g., including a long set of notes and phrases; Alger et al., 2015; Gammon et al., 2005; Kroodsma & Parker, 1979; Podos et al., 1992). As well, the size of birdsong repertoires ranges widely, with species such as the black-capped chickadee (*Poecile atricapillus*) producing only one song type while the brown thrasher (*Toxostoma rufum*) contains repertoires composed of up to 1,800 different song types (Gammon et al., 2005; Kroodsma & Parker, 1979).

Hermit thrush do perform their song types in a non-random order, as evidenced by above chance levels of predictability and consistency in their songs (Roach et al., 2012). As well, hermit thrush display alternating frequencies in their song bouts, moving up and down the frequency scale as the song is performed (Roach et al., 2012). These behaviours indicate that hermit thrush song does possess syntax, meaning that their song is bound by a set of rules. For example, hermit thrush never sing the same song type twice in a row, meaning that one particular song type is never followed by that same song type. If syntax is not used by hermit thrush as a signal of aggression, it raises questions on why this behaviour occurs. Therefore, the next step is to evaluate potential explanations for the existence of syntax in hermit thrush song other than its role in aggressive contexts, which was not supported by the current study.

Although the hermit thrush does not appear to use syntax as a signal of aggression, it is possible that syntax gives males an advantage in some other evolutionarily relevant way, such as through mate attraction, which is the other main function of birdsong. Although there are few studies on the use of syntax to attract mates, other aspects of song structure have been implicated in mate choice which makes syntax a worthy avenue of future research (Ballentine et al., 2003; Christie et al., 2004; Hahn et al., 2013; Leitner & Catchpole, 2004; Matsunaga & Okanoya, 2009; Nowicki et al., 1998; Searcy & Yasukawa, 1996). For example, repertoire size has been shown to affect female choice in certain species, with studies showing links between male repertoire size and offspring survival rates (Hasselquist et al., 1996), and others showing female preference for songs that are longer over experimentally shortened ones (Tomaszycki & Adkins-Regan, 2005).

Though research is limited, syntax itself has been found to be associated with mate choice in certain species, although the method by which it affects a female's choice is still unknown. For example, Serin birds have been shown to sing with a higher syntax consistency during the female's fertile period, suggesting that mate choice may be influenced by using syntax (Ballentine et al., 2003).

Similarly, hermit thrush in particular have been found to display songs with more ordered and predictable song types sequences earlier in the breeding season which suggests that the use of syntax may be connected to attracting a mate (Roach, Macleod, & Phillmore, in prep). If a higher degree of syntax is preferable to females, it follows that males would place more of a focus on ordered song earlier in the breeding season when competition for females is highest. It would also make sense that overall males would care less about syntax later in the breeding season because by that point it is likely that many have already accomplished the goal of finding a mate and therefore would be less likely to spend energy on maintaining a highly ordered song. Given this information, it is possible that syntax may be used by the hermit thrush as a mechanism for attracting mates rather than warding off rivals, as was hypothesized in the current study.

Future research focused on the female response to differing syntax stimuli may serve to make this clearer. One possible avenue for this research is to study female hermit thrush in a laboratory environment to evaluate their responses to differing syntax stimuli and identify mating behaviours. Similar studies have been successfully performed on other species to evaluate aspects of mate choice by placing male birds with altered or regular vocals on either side of a female's cage and recording how much time the female spent in proximity to each male (Tomaszycki & Adkins-Regan, 2005).

Another potential explanation for the development of complex syntax in the hermit thrush species is that, rather than playing a direct role in the two main functions of birdsong, it plays an indirect role by helping them to be heard over other surrounding noise, thus maximizing attention from both mates and rivals. In nature, a bird's territory is subject to a wide array of surrounding noise, including that of other bird species, animals which share similar territories, and abiotic sounds such as that of rivers, wind, or urban noise (Brumm & Slabbekoorn, 2005; Douglas & Conner, 1999; Kirschel at al., 2009). Some bird species have been found to change their song in order to avoid acoustic interference, meaning that they sing at louder volumes, varying frequencies, or different times of day to avoid overlapping with other sounds in their environment (Brumm & Slabbekoorn, 2005; Douglas & Conner, 1999; Kirschel at al., 2009). An example of this is seen in the eastern willet (*Tringa semipalmata*), a bird species which nests in coastal environments and prefers high frequency song types (Douglas & Conner, 1999). In most environments high frequencies are to be avoided because they degrade more rapidly, however near the coast there is a high degree of low frequency ambient noises which means that species who habit those areas benefit from singing at frequencies which may be better heard over the surrounding noise (Douglas & Conner, 1999).

Hermit thrush songs alternate between high and low frequency song types (Nesbitt, 2019; Roach et al., 2012) which could reduce sound competition from other species or environmental noise. Alternating between many song types allows for a greater range of frequencies which would give birds a better chance at standing out compared to other sound-competing species who may not have as large a repertoire to draw from. By avoiding the frequencies of neighboring species' songs, birds can be better heard by

44

conspecifics and maximize signal transmission (Knapton, 1987; Slabbekoorn & Smith, 2002). In this case, it is possible that rather than having a direct role in aggression or mate attraction, syntax may function to increase signal efficiency thus ensuring that the signal reaches the receiver. If hermit thrush are indeed using syntax as a method of being heard over other sounds, then the order in which they sing may depend on the syntax of surrounding bird species that sing at similar times of day. In this case, the use of syntax would not differ in aggressive contexts but instead would differ based on the common noises in their environments.

One study which looked at the frequency ranges of the black-capped chickadee and white throated song sparrow found that their songs occupied a characteristic frequency gap found in hermit thrush song (~3000 Hz) supporting the idea that songbirds who share similar environments have evolved to sing at differing sound frequencies to avoid being drowned out by competing noise (Roach et al., in prep). This method of cycling up and down in frequency use is not exclusive to the hermit thrush; both the veery and ruddy-capped nightingale thrush (Catharus frantzii) follow a similar up and down pattern with their song type frequencies (Brennan & Jones, 2016; Ortiz-Ramírez et al., 2016). Another study by Luther (2009) showed that birds in Amazonian forests divide acoustic space between species that interact acoustically at similar times and places, supporting the idea that species do alter their singing in response to noise interference by other birds. Therefore, it may be the case that syntax has evolved in the hermit thrush to avoid their songs being masked in areas with a lot of competing noise. Ongoing work in our lab, in which researchers are exposing male hermit thrush to different noise

frequencies and examining changes in song structure and syntax, may elucidate this prospect.

Future studies may seek to evaluate the frequencies of other noises common to hermit thrush breeding grounds, such as those of cohabiting species. Expanding our knowledge of hermit thrush singing behaviours in the context of cohabiting birds can allow for a better understanding of how the different songs interact and give a fuller picture of the influences affecting the evolutionary development of the hermit thrush's song types. As well, short term adaptations in song can be studied by examining the use of syntax in response to more recent human noises, such as traffic noises. By evaluating the song frequencies of other species commonly found in hermit thrush habitats, as well as surrounding abiotic noises, we can gain a better idea of how these sounds interact, therefore paving a path toward a better understanding of the use of syntax in this context.

A 2017 study on the hermit thrush species by Roach and Phillmore showed that their song structure differed significantly between three major geographic groups. Most notably, eastern and western birds varied considerably in the structure of their introductory note, with eastern birds showing a larger range of introductory note frequencies than western birds (Roach & Phillmore, 2017). It was suggested that sound transmission may play a role in the differences in structure (Roach & Phillmore, 2017). A more recent study by Roach et al. (in prep) found that California hermit thrush had significantly higher stereotypy scores compared to eastern hermit thrush residing in New Brunswick and Ontario. This data showed that western birds sang in a more ordered manner than eastern birds (Roach et al., in prep). Thus, given what we know about hermit thrush and their geographical differences in song, it would be interesting to examine how

syntax impacts aggressive scenarios in other subspecies of hermit thrush to see if the importance of syntax depends on location.

This could be done by performing a similar experiment in a different geographical region on another subspecies of hermit thrush to compare with the results of the current study. If syntax is being used as a mechanism of increasing attention there would likely be differences in the level of syntax use between hermit thrush subspecies located in different habitats (Roach & Phillmore, 2017). If future studies show that hermit thrush located in different regions use syntax differently, it would provide support for the theory that syntax is used for maximizing attention on their song. This can be further supported by examining the use of frequency cycling between the two regions; although the birds in Roach et al. (in prep)'s study differed in the predictability of their song types, both followed the same up and down frequency pattern that is typical of the hermit thrush. One way to examine the possibility of syntax being used to maximize attention would be to perform a similar experiment as the current study in California to evaluate differences in syntax use in aggressive situations between eastern and western birds. Another potential route of study would be to examine the role of syntax in other closely related species who exhibit the same frequency cycling that is observed in the hermit thrush, such as the veery. Studying differences and similarities in syntax use within these species could yield interesting results.

Aside from the possibility that syntax is used for other functions, a different explanation could be that another aspect of syntax which was not captured by the current study affected the way that birds reacted to playback stimuli. According to a study by Pellerin (1982), the silences which follow each song type may play an important role in

the syntax of the overall song. In their study, corn buntings failed to recognize dialects of their song which included randomized silences, indicating that it is not only the syntax of the song elements but of the periods between song types which matters in vocal recognition (Pellerin, 1982). In the current study, silences between song types were controlled for during creation of the altered syntax recordings. A possible future avenue of research would be to examine the importance of these silent periods by doing playback experiments which focus on temporal changes between song types. If the period of time between songs is important in hermit thrush recognition, it could explain why hermit thrush still showed an aggravated response to stimuli with altered syntax; they may have been able to recognize enough of the syntax through these silent periods to still familiarize the song as coming from a rival.

It could also be the case that changes in other vocal elements aside from syntax are more important in aggressive contexts. The current study manipulated syntax by changing the order of the individual song types, but there are other ways that syntax can be altered that may reveal important aspects of the species' song. For example, songbirds may weigh information gathered from vocal features, meaning that certain aspects of song may hold greater importance in recognition and signaling than others. Nelson (1988) found that field sparrows were more likely to not recognize a song if certain crucial features were disrupted, including the structure of the song phrase and its frequency. It could be the case that syntax does relay some information on the rival's aggravated state but not enough to dissuade the target bird from responding when the syntax is disrupted. If other features of song are more important in conveying aggressive

information to the bird, then syntax itself may not be enough to cause notable changes in the responding bird's behaviour.

A second objective of the current study was evaluating the use of vocal signals as a method of conveying aggression in response to differing syntax stimuli. This was done by examining the bird's use of singing behaviours that have been documented in other species as potential signals of aggression. Overlapping and frequency matching are two such vocal signals which have been found to occur at higher than chance levels in some species during aggressive situations (Akçay et al., 2014; Langemann et al., 2000; Naguib & Mennill, Nielsen & Vehrencamp, 1995; 2010; Vehrencamp et al., 2007). Overlapping, which is defined as an individual beginning their song before the end of their rival's song, has been suggested to be a threat signal by certain species (Naguib & Mennill, 2010; Searcy & Beecher, 2006). The results of this study showed that the observed rate of overlapping was significantly lower than chance, demonstrating that birds did change their singing in response to a rival song. This, along with overlapping not being correlated with measures of physical aggression, suggests that overlapping is not used as a signal of aggression because the rate of overlapping decreased in aggressive contexts.

Birds actively avoided overlapping during playback condition which could be an indication of an attempt to de-escalate and avoid a fight. This is consistent with the works of Vehrencamp et al. (2007) who examined overlapping in banded wrens during playback conditions. Their study showed that high levels of overlapping was associated with an earlier retreat from the playback speaker, signifying that overlapping did play a role in de-escalation (Vehrencamp et al. 2007). This behaviour could also explain the lack of physical aggression displayed by some of the birds during playback condition. If a bird is

feeling threatened it is possible that they may choose to avoid instigating a physical fight by maintaining distance with the aggressor. However, it should be noted that there was no correlation between the strength of the physical response and the rate of overlapping, meaning that the rate of overlapping was not associated with the degree of physical aggressive signaling. There is no strong evidence that individuals who avoided overlapping also avoided physically aggressive responses. However, future studies may seek to explore the possibility of avoidance of overlapping acting as a de-escalation technique by focusing on the relationship between overlapping rates and physical signals such as retreating from the speaker as was done in Vehrencamp et al.'s (2007) study.

An alternative explanation for this behaviour is that birds avoid overlapping to decrease interference of their song, thus increasing the efficiency of signal transmission. In this case, it would make sense that hermit thrush avoid overlapping both in and outside of aggressive contexts in order to ensure that their message is being heard. This aligns well with the notion that hermit thrush use differing syntax as a means of avoiding acoustic interference, highlighting the idea that birds arrange their songs through various measures to ensure that their message is being heard by others of the same species. The use of overlapping to avoid being masked by other singers is consistent with observations within our lab which showed an avoidance of overlapping during natural countersinging, indicating that hermit thrush avoid overlapping even in non-aggressive situations. These results are supported by other works using playback studies which show an avoidance of overlapping in multiple species including the Eurasian wren (*Troglodytes troglodytes*) and long-tailed manakins (*Chiroxiphia linearis*; Maynard et al., 2012; Yang et al., 2013). It is possible that overlapping does not act as a signal of aggression but instead an

avoidance of overlapping ensures that their song is not drowned out by competitive noise. One way to examine this idea would be through an altered form of the traditional playback study, in which another species' song or even abiotic noise is used in place of a rival conspecific. If the subject continues to practice the observed avoidance of overlapping for various types of noise, it suggests that the behaviour is a response to being masked by competing sound rather than a signal of aggression.

When examining frequency matching it was found that matching occurred at lower than chance levels during playback. Frequency matching has been suggested to be a signal of aggression in other species, acting in a similar manner to the closely related song type matching which has been shown to occur above chance levels during aggression contexts for many species (Hughes et al., 1998; Nielsen & Vehrencamp, 1995; Searcy & Beecher, 2009; Vehrencamp et al., 2007). Although song type matching has been found in other species to be more likely in aggressive contexts, there is little evidence that individuals respond with measures of physical aggression when song type matching occurs (Searcy & Beecher, 2009), which was consistent with the findings of the current study; frequency matching was not correlated with measures of physical aggression. Our results indicate that birds avoided matching the frequency of their rival's latest song type when faced with a territorial intrusion.

Active avoidance of song type matching has been documented in concurrent research on the hermit thrush, as well as past research on the wood thrush, a related species (Whitney, 1991). It has been suggested that this behaviour may be another effort to reduce sound interference, similar to the proposed explanation for song overlapping (DeMerchant & Roach, in prep). Birds may be attempting to increase the efficiency of

51

their signal transmission by singing at opposite frequencies to that of the rival's preceding song type, thus avoiding being masked by another bird's song.

Aside from avoiding acoustic interference, another explanation could be that avoiding song type matching is a means of de-escalating the situation rather than instigating a physical fight. Searcy and Beecher (2009) suggest that song type matching may act as a lower level aggressor in a hierarchy of threat signals, meaning that the act of matching predicts the next level of aggressive signaling rather than predicting a physical fight. In this case, song type matching may be avoided to prevent the situation from progressing to more threatening signals. The results are consistent with the avoidance of matching acting as a de-escalation technique, as the avoidance of frequency matching provides evidence that birds are seeking to minimize the situation and avoid a fight. This would make sense from a survival standpoint as it is likely beneficial for both individuals to solve the conflict without engaging in physical fighting which is made possible by having many opportunities to de-escalate the situation before it reaches the point of physical aggression.

Another interesting finding of the current study was the hermit thrush's use of abridged songs. Abridged songs are versions of songs found in spontaneous singing in which the introductory note has been dropped. This vocal behaviour has been seen in concurrent research on the hermit thrush by our lab and appears to be used exclusively in situations where a bird is responding to a rival (DeMerchant & Roach, in prep). These vocalizations are not unique to the hermit thrush but thus far have only ever been recorded in one closely related species, the veery (*Catharus fuscescens*; Belinsky et al. 2015). In this study, Belinsky et al. (2015) found a correlation between the lack of

introductory note and the use of low amplitude soft song, a quieter version of a birds'

normal song which occurs more frequently in aggressive contexts. They also found that

abridged songs met Searcy and Beecher (2009)'s requirements for the context criterion

by showing that the veery used abridged songs and soft song to a significantly higher

degree in aggressive situations than spontaneous singing (Belinsky et al. 2015). Taken

together, these results suggest that abridged songs may be used as a form of aggressive

signaling, though it is important to note that in both Belinsky et al. (2015)'s study and the

current study there was no evidence that abridged songs met the other two criteria of

aggressive signals, and that Belinsky et al. did not find evidence supporting abridged

songs as an aggressive signal. Another possible explanation for an increase in the use of

abridged songs during aggressive situations is that the shortened versions of the regular

song types are a means of energy conservation. That is, it may be the case that birds use

abridged songs to save their strength when a physical altercation may be imminent.

However, more research on the subject is necessary to draw any conclusions.

To understand the use of abridged songs as a form of aggression, it is vital to

examine the role introductory notes play in communication. It has been suggested that the

whistled component of songs may have a function in long range communication because

they can better withstand sound degradation incited by the surrounding environment

(Dabelsteen & Pederson 1993, Dabelsteen et al., 1993). This means that introductory

notes may play a larger role in conspecific recognition over greater distances while the

post-introductory portion of the song plays a role in closer communications including

individual recognition (Dabelsteen & Pederson 1993, Dabelsteen et al., 1993). This aligns

with what is seen in the field; introductory notes may be dropped in aggressive contexts

because the bird is more focused on the individual within its territory and therefore places emphasis on the parts of its song which concern close-range functions. This would also explain why abridged songs seem to be more common in aggressive contexts without meeting the other two criteria for aggressive signaling. It could be the case that abridged songs are not in themselves aggressive signals but are simply not needed given the close-range nature of the interaction. Future studies may seek to examine the use of abridged songs in aggressive contexts by performing playback studies in which the songs are altered to include abridged songs rather than the regular songs performed during spontaneous singing. In doing this, researchers can evaluate whether the response to singing changes when more abridged songs are included in the song.

This study also found a notable amount of unidentified song types which were classified as songs that did not occur during spontaneous singing. Although it is possible that some of these unidentified song types are typical repertoire songs which were not captured during spontaneous singing, this is unlikely for most cases given the number of spontaneous songs recorded for each bird. One possible explanation for the emergence of new song types in aggressive contexts is that these songs exist only at low-amplitudes, making them a form of soft song. Soft songs are generally less complex vocalizations performed at a low volume which are used in close proximity situations (Reichard & Welklin, 2015). These lower amplitude songs have been documented in a variety of species and contexts but are poorly understood in terms of their function (Reichard & Welklin, 2015).

Soft song has been suggested to be used by other species as a signal of aggression and has been linked to structural differences in song when compared to normal broadcast

singing (Anderson et al., 2008; Nice, 1943; Searcy & Beecher, 2009; Vehrencamp et al., 2007). Although the current study did not focus on collecting data on soft song, it should be noted that field observations of soft song were common throughout playback, meaning that field researchers recognized the songs performed as being quieter during the playback period than before or after the stimulus was played. Future studies may seek to further examine the role of soft song in hermit thrush communication by evaluating whether it meets Searcy and Beecher (2009)'s three criteria for aggressive behaviour, as well as by examining the structure of soft songs and their relationship with the normal song repertoire.

Taken as a whole, the vocal behaviours of the hermit thrush appear to have a commonality, that being their potential use in signal efficacy. The results of the current study suggest that one of the main purposes for hermit thrush's song variation is to maximize attention and transmit their signal to a greater audience. Although song likely does play a role in aggressive situations, it makes sense that the most important outcome would be the ability for that song to be heard. Given the results of the current study it is possible that soft song and abridged songs may play a role in aggressive signaling but the other considered features likely function to increase transmission efficiency.

Limitations

One limitation of the current study is the sample size of $n = 10$. The smaller sample may have affected significance levels of the results due to a lack of power. However, playback studies with similarly sized samples have been done on other species which showed significant results. For example, a playback study by Taylor et al. (2017)

on the California thrasher possessed a sample of $n = 9$. Within-subjects analysis was also done to mitigate this limitation, by increasing the number of individual sessions examined. Looking at each session as its own event rather than one half of a pair allowed for a larger sample, making it more likely to pick up any discrepancies in significance due to power.

Another limitation of any playback study is the necessity of choosing how to manipulate syntax, which can cover a broad range of singing behaviours. Changing the order of the song types both decreased the predictability of the song and abolished the distinct up and down frequency cycling used by the hermit thrush, thus eliminating two aspects of singing behaviour that are characteristic of the species.

Conclusion

Future research on the role of vocal behaviours in birdsong may benefit from a focus on signal transmission and the factors that affect its efficiency. The hermit thrush remains a good candidate to study these factors due to the complexity of its song and the size of its repertoire. The song repertoire of the hermit thrush is not so large as to create difficulties in examination of the song but is large enough to allow for more complex vocal behaviours such as the use of song syntax. Hermit thrush also share commonalities with other thrush species which allows for future studies focused on those other species. As well, geographical differences between hermit thrush subspecies offers an opportunity to evaluate evolutionary differences in song structure based on location.

The results of this study provided valuable insight into the use of aggressive vocal behaviours in the hermit thrush species. Moving forward, it would be beneficial to

explore the role of a potential hierarchical systems using playback studies in which the aggressive signals being studied are escalated throughout the session. This could lead to a better understanding of how the hierarchical system functions in hermit thrush communication as well as provide knowledge into which methods of aggressive signaling are considered more or less threatening. Future studies may also seek to further evaluate the relationship between vocal and physical responses to rivals in order to gain a better understanding of how these methods may be employed by hermit thrush in maintaining their territories. By focusing more heavily on the interactions between physical and vocal aggression, researchers may be able to better comprehend the roles they play in escalation between rivals.

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CURRICULUM VITAE

Morgan Elizabeth Nesbitt

University of Western Ontario: 2015-2017

University of New Brunswick: 2017-2020

    Bachelor of Science, majoring in Bio-Psychology

    Master of Arts, majoring in Experimental Psychology

Publications:

None

Conference Presentations:

Science Atlantic Undergraduate Research Conference 2019