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# FUNCTIONS OF VOCAL MIMICRY IN THE COMPLEX SONG OF THE EUROPEAN STARLING, *STURNUS VULGARIS*

by

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# FUNCTIONS OF VOCAL MIMICRY IN THE COMPLEX SONG OF THE EUROPEAN STARLING, *STURNUS VULGARIS*

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Vocal learning is an ability that has only evolved in a handful of taxa. Songbirds learn their songs, and some species have flexible learning in which they not only incorporate species-specific sounds, but heterospecific and/or environmental sounds as well. The functions of vocal mimicry are still unknown for many species and studying mimicry can teach us about the variation within the song learning process. In this thesis, I focused on five hypotheses on how mimicry could function in sexual selection. The repertoire size hypothesis suggests that selection for larger repertoire sizes allows mimicry to occur because imitation can increase repertoire size. The permissive learning hypothesis states that heightened song complexity requires a relaxed song template, which may allow passive use of mimicry. The learning and performance hypothesis suggests that learning ability and song or performance quality are honest signals of a singer’s quality and that listeners may focus on mimicry to assess individuals. The fourth and fifth hypotheses, which have received very little attention, are the structural function and acoustic function hypotheses, which suggest that mimicry has an as-yet-unknown structural or acoustic role in song, respectively. In these cases, mimetic accuracy does not matter; rather imitations and species-specific vocalizations are used in different ways. I explored these hypotheses using European starling (*Sturnus vulgaris*) song. Instead of testing the evolutionary functions of mimicry directly, I concentrated on the structural mechanics of mimicry in song. This approach allowed me to indirectly test whether mimetic and nonmimetic song components have the same functional effect. Chapter I is an overview of the more than 300 songbird species that are vocal mimics and shows that mimicry evolved repeatedly throughout the evolution of the songbird clade. The next three chapters are a detailed case study of the vocal mimicry of European starlings. In chapters II through IV, I use a combination of structural and acoustic analyses to emphasize the ways in which mimicry functions in starling song. I show that mimicry is treated differently from species-specific sounds, although in subtle, structural ways, and it remains unclear how important the inclusion of mimicry is to listeners.

# Dedication

I dedicate this thesis to Dr. Mary Bomberger Brown. She was a fabulous mentor, role model, and friend, and loved watching starlings.

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# INTRODUCTION

Young songbirds must listen to the songs of adults, practice their imitation of these songs, and eventually produce a characteristic song of their own. A mentally-challenging ability, song learning takes many forms and has led to great diversity and complexity in the songs of extant species (Brenowitz and Beecher 2005). Species vary in how permissive or discriminatory they are about what sounds constitute species-specific song. Some species have very flexible learning that allows them to imitate heterospecific and/or environmental sounds and incorporate these into their species-specific song. For the purposes of this thesis, these *vocal mimics* are all species that imitate or “appropriate” the sounds of other species (avian or nonavian) and/or inanimate objects, and use these sounds in their calls or songs (Dobkin 1979).

Vocal mimicry is intriguing because it is not obvious why some species engage in imitation. Indeed, while the functions of mimicry are known for some species, the reasons for vocal imitation by many others are still unknown. Several reviews have proposed a variety of functional and causal hypotheses for mimicry (e.g. Baylis 1982, Kelley et al. 2008, Dalziell et al. 2014) and it is becoming increasingly clear that mimicry functions in different ways for different species. As such, studying mimicry in individual species can teach us much about the diverse song learning processes in the songbird clade.

## *Sexual Selection Hypotheses for Mimicry*

This thesis will focus on five hypotheses for how mimicry functions in song and sexual selection. First, the ***repertoire size hypothesis*** suggests that large repertoires are selected for (Beecher and Brenowitz 2005), which may drive individuals to use mimicry to increase their repertoire size (Kelley et al. 2008, Dalziell et al. 2014). In this hypothesis, repertoire size is either an honest signal of male quality, or a sexually-selected ornament (Mountjoy and Lemon 1997). Mimicry can potentially supplement song repertoire. As such, one could have one of two expectations. First, individuals may achieve large repertoires by using a disproportionally large amount of mimicry in their songs. Alternatively, individuals who are incapable of producing large repertoires may use mimicry to increase their repertoire size. Some studies found that female starlings (*Sturnus vulgaris*) prefer males with larger repertoires (Mountjoy and Lemon 1996, Eens et al. 1991), although other studies did not (Gentner and Hulse 2000). Thus, it is still unclear whether repertoire size indicates quality in starlings (Mountjoy 1994, Mountjoy and Lemon 1997). Cuthill and Hindmarsh (1985) and Hindmarsh (1986) suggested starlings do not use mimicry to increase repertoire size, and therefore concluded that mimicry has no function in starling song.

The idea that mimicry has no functional effect brings us to the second hypothesis. The *learning mistakes hypothesis* states that species with complex songs must have a relaxed song template that focuses on structure or song sequence and not on song content (e.g. Kelley et al. 2008, Dalziell et al. 2014, Cuthill and Hindmarsh 1985). In this case, individuals may incorporate sounds from the surrounding soundscape because there is no selection against imitation as long as structural song rules are upheld (Hindmarsh 1986, Aubin and Bremond 1983, Bremond 1968, Fletcher and Smith 1978). Because the inclusion of mimicry in this scenario is neutral and not maladaptive, I will refer to it as the ***permissive learning hypothesis***. Both the repertoire size and permissive learning hypotheses assume that mimicked components are treated no differently from species-specific song components (e.g. Hindmarsh 1986). However, early studies were limited in scope and often only addressed mimicry indirectly. Hypotheses three, four, and five focus on alternative ways in which mimicry could have a sexual function in song.

The ***learning and performance hypothesis*** is that learning ability and subsequent song quality or singing performance are honest signals of an individual's quality. Adverse conditions early in life decrease immune function and quality of adults, which are often reflected in song learning ability and the physiological singing capabilities of an individual (e.g. Nowicki and Searcy 2004, Duffy and Ball 2002, Spencer et al. 2004). Furthermore, male vocal performance may affect territory size or female stimulation (Nottebohm 1972). As such, in species that mimic, mimetic accuracy – how well an imitated sound matches the sound produced by the model – and/or the use of many imitated sounds could allow assessment of individuals. Males vary in mimetic ability (Riegert and Juzlova 2017, Zann and Dunstan 2008) and physiological constraints limit what can be imitated (Gammon 2013, Zollinger and Suthers 2004, Dalziell et al. 2014, Podos et al. 2009). Therefore, either mimetic accuracy could serve as an honest indicator of male quality (Coleman et al. 2007) or mimicry is cognitively challenging and therefore mimetic repertoire size matters (Boogert et al. 2011, Dalziell et al. 2014, Dalziell and Magrath 2012). Male song sparrows (*Melospiza melodia*) that imitate many different models and do so accurately are preferred over singers that cannot (Beecher and Brenowitz 2005). Mating success was positively correlated with duration and quality of mimicry in the satin bowerbird (*Ptilonorhynchus violaceus*), while mimicry did not increase repertoire size (Loffredo and Borgia 1986).

The fourth hypothesis, which I have named the ***structural function hypothesis***, is that mimicry serves a structural function different from that of species-specific sounds. For example, mimicry could be used to diversify song structure or emphasize important components in song.

Finally, the ***acoustic function hypothesis*** is that mimicry serves a different acoustic function than that of species-specific sounds. For example, mimetic components could expand the acoustic range of song (such as in Northern mockingbirds, *Mimus polyglottos*, Gammon and Lyon 2017), or may introduce novel sounds (sexy or high performance syllables) that are difficult to produce and may therefore be preferred by listeners (Vallet and Kreutzer 1995, Podos 1996, Podos 1997, Ballentine et al. 2004, Dalziell et al. 2014). In both cases, mimicry could effectively add interest or complexity to songs, which may attract or stimulate females better than simpler songs (e.g. Kroodsma 1976).

Both the structural and acoustic function hypotheses differ from the learning and performance hypothesis in that accuracy does not matter. Mimetic quality is less important than the emergence of a song quality normally rare or absent from species-specific song. These alternative functions have not been considered in most studies of mimicry.

### *Starling Background*

To explore these hypotheses, I focused on the European starling, which is an ideal species for studies of song learning. Starlings are hardy opportunists native to Europe and Asia and found across North America. There are many of them (at least 150 million in the USA alone) and they are highly gregarious, forming large foraging and roosting flocks in the nonbreeding season, and breeding colonies in the spring (e.g. Hausberger 1997). Males sing year-round from chosen nest cavities, which in America are holes in buildings and trees in urban parks and neighborhoods, allowing a researcher easy access to nests and recordings. Males are not shy and will broadcast sing for hours regardless of human presence. Starlings have two song types – whistle and warbling song – that serve different functions. Whistle song is used predominantly for social cohesion and tolerance, as well as intrasexual interactions (Hausberger 1997), while warbling song functions mainly in mate choice and reproductive stimulation of paired females (Eens et al. 1991). The presence of two disparate song types, as well as the complex sociality and the elaborate song of the starling, provide opportunities to address a variety of questions about song learning and mimicry.

Whistle song is composed of simple, one-to-two note whistles separated by several seconds of silence. There are five universal *species-specific themes* that vary locally, with populations having distinct dialects (Adret-Hausberger 1986, Adret-Hausberger and Güttinger 1984, Adret-Hausberger 1984, Hausberger 1997) that are stable across years (Adret-Hausberger et al. 1990) and recognizable to conspecifics (Adret-Hausberger 1982). Different themes are used in different social contexts (Adret-Hausberger 1989, Hausberger 1997, Henry 1998): proportions sung of each theme vary based on population (Adret-Hausberger 1984), flock and roost size (Adret-Hausberger 1982), level of sociality (Adret-Hausberger 1988), whether the population is captive or wild (Henry 1998), and season (Hausberger et al. 1995). Whistle dialects develop at breeding colonies and are thought to maintain social structure in large nonbreeding roosts

(Hausberger et al. 2008). In addition to the five themes, individuals sing *individual themes* unique to each singer, which may function as vocal signatures and may include mimicry (Adret-Hausberger and Güttinger 1984).

The structure of warbling song is very different from whistle song. Warbling occurs in bouts of continuous song lasting about 30 seconds (Eens et al. 1989), separated by silence. A song bout is composed of four sections that are each made up of motifs (Eens et al. 1989, Gentner and Hulse 1998, Eens et al. 1991, Mountjoy and Lemon 1995, Hindmarsh 1984). A motif is a set of one to ten notes repeated as a discrete unit. A male's repertoire size is the number of unique motifs he sings (e.g. Eens et al. 1989). Motifs are created through a mixture of improvisation, modification, and appropriation of sounds (Adret-Hausberger et al. 1989). Starlings are open-ended learners, which means that each male can add to or revise his repertoire from year to year and repertoire size may therefore indicate age and experience (Adret-Hausberger et al. 1989).

Starling motifs are highly variable and very different from each other (Adret-Hausberger and Jenkins 1988) but all have a quality distinctly starling (Adret-Hausberger et al. 1989). The first song section is whistle motifs, which may overlap with those used in whistle song. The second is composed of variable motifs, which are diverse, complex, and have a large frequency range. A variable motif is generally repeated a specific number of times, sometimes with minor variation, before the next motif is sung (Adret-Hausberger and Jenkins 1988, Adret-Hausberger et al. 1990, Eens et al. 1989). Most of an individual's mimetic repertoire is incorporated in the variable motifs (Eens et al. 1989, Eens et al. 1991). A third section, the rattle motifs, are characterized by rapid repetitions of clicking sounds and other notes. As the third section is not very distinct from the second, I combined the two into “variable” motifs. Finally, a song bout ends with repeated terminal motifs of high frequency (e.g. Adret-Hausberger and Jenkins 1988, Böhner and Todt 1996). Not all types of motifs are included in every song bout; often song is interrupted before terminal motifs are sung (e.g. Eens et al. 1989, Eens et al. 1991, Mountjoy and Lemon 1995). The quality and structure of motifs is distinct, such that a motif can easily be placed into the appropriate section of a song bout (Mountjoy and Lemon 1995). Furthermore, while no two warbling song bouts are identical (Adret-Hausberger 1989), differences between individuals are obvious, as motifs are unique to an individual (Adret-Hausberger et al. 1989, Hausberger et al. 1995), and each has stereotyped sequences of motifs (Mountjoy and Lemon 1995). Thus, song content is unique to an individual, but the overall structure or arrangement is nonrandom and follows species-specific rules (Adret-Hausberger et al. 1989, Hausberger et al. 1995, Adret-Hausberger et al. 1990, Gentner and Hulse 2000). These rules are similar for both female and male warbling song, although females use song differently from males and only sing in the fall (Henry and Hausberger 2001).

The focus of this thesis is the function/s of mimicry within the warbling song of male starlings. Male warbling song (henceforth simply “warbling song” or “song”) predominantly functions in mate attraction (Hindmarsh 1984, Cuthill and Hindmarsh 1985, Eens et al. 1989, Hausberger et al. 1991, Eens et al. 1991) and female reproductive stimulation (Hausberger et al. 1995, Eens et al. 1991), although motifs may also be useful for individual recognition (Adret-Hausberger and Jenkins 1988, Adret-Hausberger et al. 1990, Gentner and Hulse 2000, Gentner and Hulse 1998, but see Knudsen et al. 2010). Various findings support these conclusions. Male singing output increased nine-fold when females were present but did not change when another male was introduced (Eens et al. 1990). Males direct warbling song at females (Eens et al. 1989), especially when soliciting extra-pair copulations (Eens et al. 1991). While playback of warbling song attracts females and males (Mountjoy 1994, Hausberger 1997), males do not respond vocally (Hausberger 1997). The only territorial, male-male interactions observed at nest boxes involved whistle song rather than warbling (*pers. obs.*). As such, warbling does not appear to be used aggressively. Finally, song bouts have less sequence variation during the breeding season (Adret-Hausberger and Jenkins 1988) and singing decreases after pairing (Hindmarsh 1984), which both demonstrate the sexual importance of song. Therefore, for the purposes of this thesis, song will be considered a sexual signal.

This thesis addresses the repertoire size, permissive learning, structural and acoustic function hypotheses, and briefly touches upon the learning and production hypothesis. Instead of testing the evolutionary functions of mimicry directly, I concentrated on the structural mechanics of how mimicry is used in song. This approach allowed me to indirectly test whether mimetic and nonmimetic song components have a similar function.

### *Chapter Overview*

In chapter I, I take several steps back and give an overview of the evolutionary history of vocal mimicry in songbirds. I introduce song learning and vocal mimicry and explain what is known about mimicry by songbirds. I discuss how the evolution of vocal mimicry can be considered the emergence of permissiveness in learning and use phylogenetic tools to determine when mimicry evolved in songbirds. I also look at differences in the proportion of mimetic species across continents. I found that more than 300 species are vocal mimics and mimicry evolved repeatedly throughout the evolution of the songbird clade. This first chapter is meant as an extended introduction to mimicry to prepare the reader for chapter II through IV, which are a detailed case study of the use of vocal mimicry in song by European starlings.

Chapter II gives necessary background information about what starling song is like, along with what sounds are mimicked and how mimicked sounds are incorporated into song. I also detail the extensive individual variation in song and mimicry. I focus on two sexual selection hypotheses for vocal mimicry: the repertoire size hypothesis and permissive learning hypothesis. I compare the relationships between repertoire size and mimetic and nonmimetic song components to determine whether mimicry is used to supplement song repertoire. I found that mimicry is not directly used to supplement song repertoire. While these findings are congruent with the permissive learning hypothesis, they also suggest that mimicry may function in different, as-yet-unknown, ways.

Chapter III is an exploration of song structural complexity using network tools. Here, I focus on the structural function hypothesis by determining whether mimicry facilitates song structure. I describe starling song structure and compare mimetic to nonmimetic song components in two ways. First, I determine whether mimicry is used preferentially at points of structural diversity within song sequences. Then I explore whether there is a difference in how often mimetic and nonmimetic components are repeated, as repetition is an important structural feature of starling song. I found that mimetic song components are used differently from nonmimetic ones, in unexpected ways. Mimicry was used less often at structurally diverse sequences in song, but mimetic components were repeated more often than nonmimetic ones. These findings indicate that mimicry is important in starling song, and that mimetic components are not simply mistakenly incorporated.

The fourth and final chapter focuses on the potential acoustic functions of mimicry in song. Chapter IV is by necessity slightly more theoretical in that I do not experimentally test the learning and performance or acoustic function hypotheses. However, I use quantitative acoustic measurements to determine differences between mimetic and nonmimetic motifs. Furthermore, I compare the acoustic contrast in song sequences to learn whether mimicry expands sound diversity. I found that mimicry does widen acoustic parameters of starling song. However, sequences of mimetic motifs in song had less acoustic contrast than did nonmimetic sequences. As such, although mimicry has a functional effect, the syntactical rules governing European starling song constrain how mimicry can be used.

My work uses novel techniques to expand our understanding of song structure, as well as the relationship between structure and mimicry. I show that mimicry is treated differently from species-specific sounds, although this is in subtle, structural ways, and it remains unclear how important the inclusion of mimicry is to listeners. Mimicry can function with more subtlety than previously considered. My thesis also demonstrates that the European starling is an excellent model for addressing questions about the functions of mimicry, as well as structural questions about song construction and composition.

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# CHAPTER I: EVOLUTIONARY ORIGINS OF VOCAL MIMICRY IN OSCINE SONGBIRDS[1]

## Abstract

Vocal learning is an important behavior in songbirds, which learn their song. Some songbird species learn heterospecific sounds as well as conspecific vocalizations. The emergence of vocal mimicry is necessarily tied to the evolution of vocal learning, as mimicry requires the ability to acquire sounds through learning. I compiled a database of known vocal mimics and conservatively restricted the sample to 293 species from 40 families. I then traced the evolutionary history of vocal mimicry across the avian phylogeny using ancestral trait reconstruction using a complete dataset of oscine passerines from three continents (North America, Europe, and Australia). I found that the common ancestor to oscine songbirds was unlikely to be a vocal mimic, suggesting that song learning evolved with mechanisms to constrain learning to conspecific models. Mimicry then evolved repeatedly within the songbird clade, either through relaxation of constraints on conspecific learning or through selection for active vocal mimicry. Vocal mimicry is likely ancestral in only a handful of clades and I detected many instances of independent origins of mimicry. My analysis underscores the lability of vocal mimicry in songbirds and also highlights the evolutionary flexibility of song learning mechanisms.

## Introduction

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Acoustic communication often plays a role in species recognition in animals (e.g. Emlen 1972, Claridge 1985, Hauber et al. 2001, Seddon 2005, Percy et al. 2006). For many species, acoustic signals are genetically encoded; individuals can produce species-specific sounds without the need for learning (Jang and Gerhardt 2006, Jarvis 2006, Janek and Slater 2000). In others, species-specific vocalizations are learned by first perceiving acoustic information and then practicing imitating these acquired sounds (Marler 1976). Such *vocal learning* is a behavior found in select mammals (humans, bats, cetaceans, and elephants; e.g. Jarvis 2006, Crockford et al. 2004, Prat et al. 2015) and birds (hummingbirds, parrots, and songbirds; e.g. Bolhuis and Gahr 2006). Within birds, this ability evolved independently multiple times (Tyack 2007, Jarvis 2007, Slater 1989).

Roughly half of the world's avian species are oscine passerines (songbirds) that learn their song. In many species, young birds listen to the songs of adults to gain an acoustic template, fine-tune their imitation by comparing their practice songs to the template, and eventually produce a characteristic song of their own (much simplified; see Marler 1970a&b, Konishi 1965, Marler 1976, Soha 2017). However, there is striking variation in the oscine learning program (e.g. Nottebohm 1972, Soha 2017). Brenowitz and Beecher (2005) identified five dimensions of variation that cause complexity in song learning: timing of learning, number of songs learned, fidelity of imitation, type of exposure, and level of constraint to species-specific models. The last dimension, level of constraint, ranges from species that learn only species-specific song components (highly constrained) to species that incorporate heterospecific and environmental sounds (unconstrained). In other words, a species can be discriminatory or permissive about what sounds it learns and incorporates into vocalizations.

Some highly permissive species, termed *vocal mimics*, readily learn not only species-specific sounds but also sounds produced by other species or inanimate objects (Marshall 1950, Kaplan 2003, Kelley et al. 2008). There are many potential functions and definitions of vocal mimicry, which have been the focus of study (reviewed in Marshall 1950, Dobkin 1979, Baylis 1982, Hindmarsh 1986, Kelley et al. 2008, Dalziell et al. 2015, Jamie 2017; see also Dalziell and Welbergen 2016). However, little is known about the roots of mimetic ability in songbirds. Here, we focus on the evolutionary origins of the predilection to mimic heterospecific sounds, combined with the ability to imitate them ('descriptive definition' of vocal mimicry; Baylis 1982).

The emergence of vocal mimicry is necessarily tied to the evolution of vocal learning, as mimicry requires the ability to acquire sounds through learning. Therefore, we assume that vocal mimicry could not have evolved before vocal learning. However, there are two broad scenarios in which vocal mimicry could have arisen relative to the emergence of vocal learning. First, if vocal learning evolved due to selection for increased song repertoire (e.g. Nottebohm and Liu 2010), mimicry could have evolved as a mechanism to acquire more song components or as a byproduct of a broad acoustic template. The ability to mimic heterospecific sounds could then have been lost in lineages that evolved a narrow predisposition to learn only conspecific sounds. In this case, we would expect mimicry to align with the emergence of vocal learning and to be ancestral to all songbirds. Second, in an alternative scenario, vocal learning may have originally evolved with a strong bias toward acquisition of strictly species-specific sounds. Over time, the perceptual window for sound acquisition could have become more permissive in some lineages, allowing vocal mimicry. The emergence of permissiveness in song learning could have arisen through relaxation of selection for narrow predispositions during song learning, or through strong selection for newly acquired functions (Dalziell et al. 2015).

To determine which of these two scenarios was more likely, I traced the evolutionary history of vocal mimicry across the avian phylogeny using ancestral trait reconstruction. First, I compiled a database of known mimetic species to better understand global patterns of mimicry. Second, I focused on the phylogenetic pattern of the emergence of mimicry. By tracing the history of vocal mimicry on the songbird phylogeny, I determined when the trait is likely to have emerged. Third, I used my phylogenetic approach to suggest the types of questions about mimicry that should be tackled in the future.

## Methods

### *Definition of vocal mimicry*

For the purposes of this study, I use a broad definition of vocal mimicry, which encompasses imitation of all types of non-conspecific sounds: other animals, anthropogenic (e.g. dog whistle, chainsaw) and environmental (e.g. water drip, leaves rustling) noises. I chose this general definition to allow analysis of the evolution of the ability to learn and produce ‘mimicked’ sounds. While information on vocalizations is available for many species, determining the functions of mimicry requires careful experimental studies that have only been conducted on a few species.

### *Compiling the database*

Data were compiled from a variety of primary and secondary sources. A preliminary search was done on Google Scholar. Then I expanded the search to various websites using search terms “mimic- “, “imitate- “, and “copy- “. Field guides and handbooks, including all volumes of the Handbook of the Birds of the World, were browsed manually for mention of vocal imitation or copying behavior. Sources without peer-review were verified whenever possible with an extensive search for corroborative scientific publications on each species on Google Scholar. If an account could not be verified, the species in question was not included in analysis. Scientific and common names were standardized using the IOC Bird List version 5.4 (Gill and Donsker 2015).

For every account of a mimetic species, presence and extent of vocal imitation were recorded. Each species was given a vocal imitation score of 0 (absence) or 1 (presence) based upon documentation of observed mimetic ability. If no data were found to suggest presence of vocal imitation ability, the species was given a score of 0 (as in Garamszegi et al. 2007) in all database analysis (but see ***Phylogenetic analysis***). Accounts for more than 100 mimic species gave no details of the extent of mimetic ability, and these species were therefore not included as mimics.

When running analysis on my database, I only included what I term ‘flexible mimics’. Flexible mimics are species that imitate a wide variety of sounds, often having plastic repertoires and an extended period of song learning. In these species, mimetic ability is found in most individuals. I disregarded accounts of mimicry in brood parasites that learn the calls or songs of their host species (17 species of *Vidua* finches; e.g. DaCosta and Sorenson 2014). Although brood parasites are flexible in which species they imitate (Langmore et al. 2008, Madden and Davies 2006), in this case, they have merely shifted their learning template from a conspecific to heterospecific tutor, and do not imitate a wider range of sounds (Kelley et al. 2008). Other species removed from analysis were species of which an individual or small number of individuals imitated a heterospecific in presumably unnatural scenarios, such as when brought together in captivity (e.g. bullfinches, zebra finches). Any accounts of a single individual imitating heterospecific song were also excluded, as this imitation most likely resulted from a learning mistake. In total, I excluded roughly 250 species from analysis.

### *Database analysis*

I calculated proportions of mimetic species within avian families and across geographic regions using the full database of 293 flexible mimic species. I was especially interested in patterns of mimicry within families, and determined whether mimics were clumped within, or dispersed throughout, a family. As I used published accounts of mimicking species, I expected under-sampling of certain regions (Asia, Africa, South America) compared to other well-studied regions (North America, Europe, and Australia). To investigate this further, I compared the proportion of mimetic oscine species in each region. I used bird checklists from Avibase (excluding all accidental and introduced species) as the source for the total number of resident oscine species to allow comparison between regions (Lepage 2017).

### *Phylogenetic analysis*

To determine the ancestral state (mimetic or non-mimetic) of oscine passerines, I conducted a phylogenetic analysis using the compiled database. To remain conservative in my analysis and account for potential unknown mimic species, I only used oscines from North America, Europe, and Australia. I assumed the song of all oscine species from these regions has been described, as birds in these areas have been relatively well-studied, and species not known to mimic could be confidently classified as 'non-mimetic'. This assumption was supported by the relatively high proportion of known mimics on these continents. This restricted my sample to 817 species, 130 of which were mimics, for core analyses. Vocal imitation scores were mapped onto phylogenetic trees taken from the global phylogeny of birds accompanying Jetz et al. (2012). The tree source was Hackett All Species: a set of 1000 trees with 9993 operational taxonomic units (OTUs) each. The discrete character of absence or presence of mimicry was mapped onto the phylogeny as a basic binary value. I then reconstructed the ancestral state for the basal ancestor of all species in the phylogeny. I reconstructed discrete ancestral states using the ER model, which estimates the marginal ancestral states based upon Bayesian likelihood. Stochastic character mapping was used to estimate the number of state changes across the phylogeny. All analyses were done on all 1000 trees using the R package *phytools v. 0.5-38* (Revell 2012).

To test the robustness of my result, I also ran ancestral state reconstruction on 1000 trees with 3550 species. In this analysis, I included all flexible mimics from all geographic regions and labeled any other species as nonmimetic (mimicry absent). As such, some of the species classified as nonmimetic were most likely capable of mimicry. I compared the probability of mimicry being ancestral to oscines from both sets of analyses.

## Results

### *Database analysis*

Of the roughly 5,004 extant avian species and 115 families in the suborder Passeri (songbirds), 293 species (5.8%) from 40 families (34%) were classified as flexible mimics (Suppl. Table 1.1). Songbird families vary greatly in mimetic ability and number of mimicking species (Figure 1.1a&b). Of the 40 songbird families with at least one mimic, mimicry is rare (i.e., proportion of flexible mimics ≤ .10) in 26 families, or 65%. In six songbird families, roughly half the species have some level of mimetic ability (Artamidae, Dicruridae, Mimidae, Nicatoridae, Ptiliogonatidae, and Regulidae). In these cases, mimicry is spread across a family such that mimetic and nonmimetic species are often each other's closest living relatives. Finally, mimicry is widespread and ubiquitous in three families (Atrichornithidae, Menuridae, Ptilonorhynchidae).

*Supplemental Table 1.1 Full database of global flexible mimics. (PDF, 178 KB)*

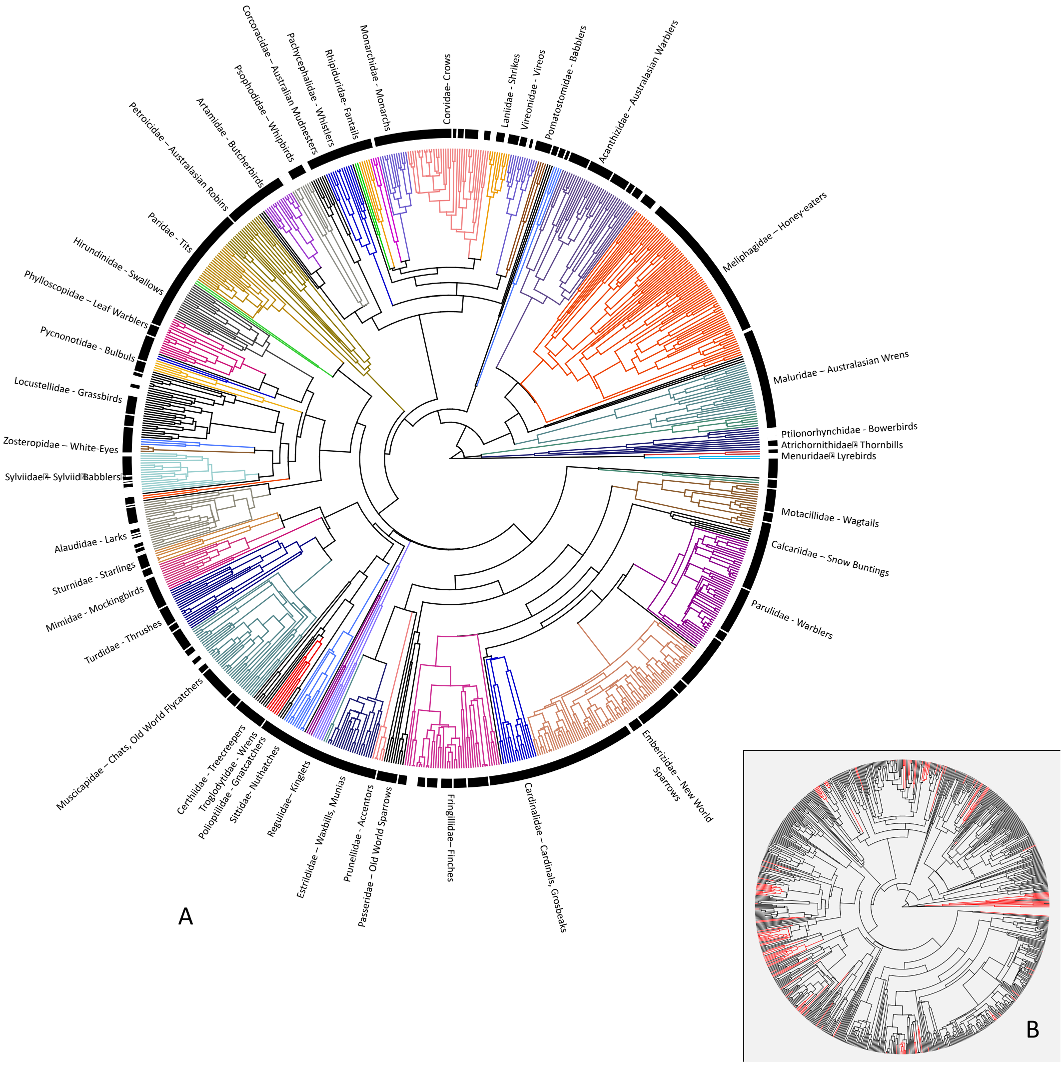

*Figure 1.1 Phylogeny of songbirds from North America, Europe, and Australia. a) Presence of mimicry is represented by white marks. Families are individually-colored and labeled for ease of reference. b) Mimetic ability is represented in red. Vocal mimicry evolved independently at least 86 times and was lost at least 25 times.*

The proportion of oscine species capable of mimicry varied regionally as well. In the well-studied regions, roughly 15% of oscine species were mimetic (Table 1.1; North

America: 14.2%, Europe: 18.6%, Australia: 13.6%). The result for Australia is identical to what Marshall (1950) found 70 years ago. In contrast, only about 5% of oscines in other regions were mimetic (Asia: 5.1%, Africa: 6.8%, South America: 3.0%, Central America: 2.3%).

*Table 1.1 Proportion of known mimics on each continent.*

| **Region** | **Known oscine mimics** | **Total oscine species** | **Proportion** |
|---|---:|---:|---:|
| US + Canada | 53 | 374 | **0.142** |
| Europe | 40 | 215 | **0.186** |
| Australia + New Zealand | 53 | 389 | **0.136** |
| Asia | 102 | 2004 | 0.051 |
| Africa | 98 | 1442 | 0.068 |
| South America | 25 | 821 | 0.030 |
| Central America | 12 | 531 | 0.023 |

### *Phylogenetic analysis*

Based on phylogenetic analysis constrained to species found on my three focal continents (North America, Europe and Australia), the most recent common ancestor of all songbirds most likely did not have mimetic ability (probability of presence = 0.167 ± .039). This was not substantially different from my estimate of ancestral mimetic ability based on the global database of mimics from all continents (probability of presence = 0.185 ± 0.003).

Based on the focal dataset, I estimate that vocal mimicry evolved independently at least 86 times across bird taxa (Figure 1.1b), and was lost about 25 times. The ancestors of two songbird families – Mimidae and Menuridae – were very likely vocal mimics (probability > 0.75; Table 1.2). In Atrichornithidae, Corvidae, and Ptilonorhynchidae, it is unclear whether mimicry was ancestral or not (probability ≈ 0.5). Four families had a small likelihood of ancestral mimicry (Artamidae, Laniidae, Polioptilidae, Sturnidae;

close to 0.1), while all other oscine families did not have ancestors capable of mimicry (probability << 0.01, Suppl. Table 1.2).

*Table 1.2. Probabilities of the presence of vocal mimicry in the ancestor of select songbird families.*

| **Family** | **Probability mimicry was present in ancestor** | **Number of species included** | **Total number of species** | **Proportion of family in analysis** |
|---|---|---|---|---|
| Artamidae | **0.111666** ± 0.0634 | 14 | 24 | **0.58** |
| Atrichornithidae | **0.539222** ± 0.1183 | 2 | 2 | **1.00** |
| Corvidae | **0.545074** ± 0.1706 | 35 | 130 | **0.27** |
| Laniidae | **0.173934** ± 0.0755 | 9 | 33 | **0.27** |
| Menuridae | **0.888148** ± 0.1323 | 2 | 2 | **1.00** |
| Mimidae | **0.939697** ± 0.0173 | 10 | 34 | **0.29** |
| Polioptilidae | **0.113447** ± 0.0182 | 3 | 18 | 0.17 |
| Ptilonorhynchidae | **0.545074** ± 0.1706 | 10 | 20 | **0.50** |
| Sturnidae | **0.180287** ± 0.0311 | 6 | 123 | 0.05 |

*Supplemental Table 1.2. Probabilities of the presence of vocal mimicry in the ancestor of every songbird family in analysis. (PDF 63 KB)*

## Discussion

Mimetic ability is likely not ancestral to songbirds. Vocal mimicry has evolved numerous times and is currently widespread among extant species. One-third of songbird families contain at least one species that mimics, and the majority of species in some families is mimetic, indicating that mimicry may serve an important function in some clades. My phylogenetic analysis indicates that mimicry may have emerged at the base of some families, multiple times within other families, or never emerged in still other families. Mimicry appears to have been ancestral in two families (Mimidae and Menuridae), with probabilities of presence greater than 0.75. These families include well-studied species in which functions of mimicry have been investigated. For example, the male northern mockingbird, *Mimus polyglottos*, uses mimicked notes to expand the frequency bandwith of its song by around 40%, which may be particularly attractive to females (Gammon and Lyon 2017). In superb lyrebirds, *Menura novaehollandiae,* mimetic accuracy seems to be important, and may be used by females to choose between males (Dalziell and Magrath 2012).

Although my dataset includes birds from most continents, regions with a long history of birdsong publication – North America, Europe, Australia – were overrepresented compared to South America, Africa, and Asia. Roughly 15% of oscine species in well-studied regions are mimetic (Table 1.1; for Australia, see also: Marshall 1950). This is different from my conservative estimate of 5.8% of global oscine species as flexible mimics. If vocal mimicry is evenly distributed across all continents, I suspect that many avian vocal mimics have not been recognized or studied, primarily on the continents excluded from my phylogenetic analysis (i.e., South America, Africa and Asia). Some avian families found exclusively in less-studied regions may include mimetic species we know nothing about.

To partially address the problem of the potentially large number of uncharacterized mimetic species on some continents, I limited my core phylogenetic analysis to the well-studied regions (North America, Europe, and Australia). However, this sampling scheme by necessity reduces the robustness of ancestral state estimation at the family level due to under-sampling of species in some families. Therefore, my estimates are limited based upon the proportion of species of each family included in analysis, and the quantitative estimates of ancestral states should be taken with caution.

The effect of under-sampling depends on the family and the proportion of species existing on the three focal continents. For example, my analysis indicates relatively high probabilities of ancestral mimicry in corvids and mimids, even though only 27% and 29% of species were included in my phylogenetic analysis, respectively. These families are well-known for their mimetic ability, and it is therefore unsurprising that mimicry may very well have been an ancestral trait. In other cases, the severe underrepresentation of families may have led to a low estimate of the presence of ancestral mimicry. For example, the family Sturnidae, represented by 6 of 123 species in my analysis, includes many well-known mimetic Asian mynah species that were excluded from analysis (Suppl. Table 1.1), or mimetic species that have not been described in the literature (Micronesian starling; Haldre Rogers, *pers. comm.*). Thus, a more detailed family-level analysis with better sampling may reveal that vocal mimicry is in fact ancestral to *Sturnidae*. Other families in which mimicry may be more widespread than estimated include Artamidae and Polioptilidae (with proportions ≈ 0.1), as well as Alaudidae and Vireonidae (with proportions ≈ 0.0 in my analysis).

Underrepresentation of some families could also have led to exaggerated estimates of mimicry. For example, while some species of shrike (family Laniidae) are renowned for their mimicry, other species may have no mimetic ability. It is possible that my limited sample of shrikes may have included a disproportionately large number of mimics, and this could have inflated the estimate.

My phylogenetic analysis indicates that vocal mimicry is likely not ancestral to oscine songbirds. As song learning probably evolved at some point early in the evolution of oscines (Nottebohm 1972, Nottebohm and Liu 2010), this implies that mimetic ability did not evolve concurrently with the origin of song learning. Instead, my analysis supports the hypothesis that the ancestral songbird had a restricted song template that excluded non-species-specific sounds. Vocal flexibility may have been limited by constraints on template acquisition facilitating the learning of only conspecific sounds, and/or by restrictive sound production mechanisms. These restrictions and constraints on vocal mimicry would have lessened repeatedly and independently within the songbird clade.

Given my results, the question becomes why and how restrictions on sensory recognition (song template) and/or sound production (syringeal function) became relaxed in some lineages. Here, I propose two hypotheses. In the first hypothetical scenario, species-specificity in both song recognition and production slowly relaxed over time in the absence of selection. At some point after song learning evolved, mimicry became possible and the imitation of heterospecific sounds became commonplace in many species, eventually gaining functional significance. Alternatively, permissiveness in imitation may have undergone repeated positive selection after the evolution of song learning. A proposed mechanism driving the evolution of vocal learning is mate choice based on song complexity or novelty (Nottebohm 1972, Jarvis 2004) as females of many species appear to prefer males singing more complex repertoires (e.g., canaries, Draganoiu et al. 2002; starlings, Mountjoy and Lemon 1996, Gentner and Hulse 2000; chaffinches, Leitao et al. 2005), and learning enhances complexity (Nottebohm 1972, Jarvis 2006). Similarly, Laiolo et al. (2011) suggest that mimicry increases song complexity and serves as an honest signal. As such, selection for vocal repertoire complexity or plasticity in vocal performance may have led to a less restricted song learning template. As imitation became increasingly plastic, vocal learning would have broadened to include mimicry. Of the mimicking species used in my analysis, more than 90% are likely using mimicry solely in song. It therefore seems likely that sexual selection played a role in the emergence of mimicry.

Regardless of the presence or absence of selection pressures that led to mimicry, the trait is certainly very labile. Although flexibility in song template and production are both required, the imitation of heterospecific sounds emerged frequently, suggesting that many nonmimetic species are very close to attaining this ability. This is intriguing as it remains unclear what prevents nonmimetic oscines from mimicking heterospecific sounds. However, answering further questions about the emergence of mimicry requires comparative data of mimetic and nonmimetic species, as well as the careful study of the song of mimetic species. Only then can we begin to tackle detailed questions about the evolution of mimicry and its functions.

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See published paper for Appendix I with a list of relevant recordings.

# CHAPTER II: HOW EUROPEAN STARLINGS INCORPORATE MIMICRY INTO SONG

## Abstract

Passerine (songbird) song learning systems take many forms and variation in learning ability is reflected in differential reproductive success. Over 300 species are capable of vocal mimicry, the learning and incorporation of heterospecific sounds into communication. It is still unclear why many of these species include mimicry in song. The repertoire size hypothesis suggests that selection for large repertoire size causes individuals to use imitation to supplement their repertoires. Another hypothesis, the permissive learning hypothesis, is that complex song requires a broader song learning template, thereby allowing accidental and passive acquisition of sounds from the soundscape. I used European starling (*Sturnus vulgaris*) song to test these hypotheses and determine whether mimetic sounds were incorporated into song in the same way as nonmimetic ones. I first determined how much variation existed between males in both mimetic and nonmimetic repertoire composition. I then determined how mimicry was incorporated into song units and whether males used mimicry to increase repertoire size. I found that a large amount of variation existed in how much, and what is, mimicked by males. Males copied an average of 12 different models; some sounds were imitated by all males, some only by one male. Some used mimicry extensively while others barely mimicked. Mimicked sounds were incorporated into song motifs in four distinct positions – as an entire motif, embedded into species-specific sounds, at the beginning, or at the end. Different heterospecific sounds were preferentially used in different positions within motifs. Finally, mimicry did not directly increase repertoire size; instead, increase in

repertoire size led to a greater number of mimicked motifs due to the larger overall number of motifs. Our findings align with the expectations from the permissive learning hypothesis, although it is unclear whether heterospecific sounds function in other ways not addressed here. Further study of the incorporation of mimicry in starling song is necessary to understand how mimicry functions in this species.

## Introduction

Animal communication systems are diverse, ranging from simple cues to complex, multi-modal signals. Vocal learning, whereby individuals imitate acquired signals and modify them based on social feedback, has evolved in several taxa. Individuals of the 5,000 oscine passerine (songbird) species must learn *song*, an acoustic signal used in reproductive contexts. Songbird song learning systems take many forms (Brenowitz and Beecher 2005), and individual variation in learning ability is reflected in differential reproductive success. Within songbirds, over 300 species have greater flexibility in what they learn and incorporate heterospecific sounds into species-specific communication (Goller and Shizuka 2018). Studying these *vocal mimics* can provide unique insights into which sounds are acquired by song learning and how they are incorporated into song.

Mimicking species vary in what they imitate and how they learn mimetic sounds. As songbird species are physiologically-constrained in what sounds they are capable of reproducing (Zollinger and Suthers 2004), some species imitate sounds that resemble species-specific vocalizations (Riegert and Juzlova 2017, Gammon 2014). Other species preferentially imitate alarm calls (icterine warbler, *Hippolais icterina*, Riegert and Juzlova 2017) or simple vocalizations (Robin chat, *Cossypha spp.*, Ferguson et al. 2002;

European starling, *Sturnus vulgaris*, Hindmarsh 1984, 1986), although this is not true for all mimics. Similarly, it is still unclear whether mimics learn imitated sounds directly from conspecifics (Baylis 1982, Hindmarsh 1984), directly from heterospecific models - as in spotted bowerbirds (*Chlamydera maculata*, Kelley and Healy 2010), Albert's lyrebirds (*Menura alberti*, Putland et al. 2006, Kelley et al. 2008), and icterine warblers (Riegert and Juzlova 2017) - or both (Adret-Hausberger et al. 1990). In this chapter, I focus on what is imitated to draw conclusions about how mimicry is used in birdsong.

Potential functions of vocal mimicry have only been studied in a handful of species. We know that individuals of some species use mimicry in their *calls* - simple vocalizations with nonsexual functions - to steal food (fork-tailed drongos, *Dicrurus adsimilis*, Flower 2011), voice alarm (Brown thornbills, *Acanthiza pusilla*, Igic and Magrath 2013; Steller's jays, *Cyanocitta stelleri*, Billings et al. 2017; phainopepla, *Phainopepla nitens*, Chu 2001; great bowerbird, *Chlamydera nuchalis*, Frith and Frith 1990), attract prey (shrike *Lanius spp*., Heinroth and Heinroth 1958, Atkinson 1997), or attract heterospecific flock-mates (greater racket-tailed drongo, *Dicrurus paradiseus*, Goodale and Kotagama 2006). However, the functions of mimicry in song are more difficult to understand.

Excellent reviews have been published suggesting various functional hypotheses for mimicry in song (see Kelley et al. 2008, Dalziell et al. 2014, Dobkin 1979, Garamszegi et al. 2007). Some hypotheses suggest that mimicry plays a role in a nonsexual context. For example, in studies of spotted bowerbird mimicry, Kelley and Healy (2010, 2011, 2012) found that neither conspecifics or heterospecifics were attracted to mimicry and individuals were 30 times more likely to mimic during nest disturbance than at any other time. The authors hypothesized that spotted bowerbirds learn mimicry when they are alarmed and repeat these sounds during future alarming situations (Kelley and Healy 2012), similar to what Dalziell and Welbergen (2016) proposed for superb lyrebirds (*Menura novaehollandiae*). However, other nonsexual selection hypotheses have received little support and most mimicking species do not appear to use mimicry in this way (Garamszegi et al. 2007).

Hypotheses on sexual selection as the ultimate motivation of vocal mimicry have found more support. This chapter will address two of the main sexual selection hypotheses: the repertoire size and permissive learning hypotheses. The repertoire size hypothesis suggests that larger repertoire size is preferred by females, and mimicry therefore occurs because it allows an individual to expand their repertoire (Dalziell et al. 2014, Kelley et al. 2008). In this case, mimicry, *per se*, is not what is being selected for, but it may increase an individual's repertoire size and therefore yield higher reproductive fitness. The permissive learning hypothesis suggests that species with complex songs must have a relaxed song learning template and therefore sometimes imitate sounds from the local soundscape on accident (Riegert and Juzlova 2017, Kelley et al. 2008). In this situation, mimicking heterospecifics is neither beneficial nor detrimental. A study on European songbirds concluded that mimicry in most species is simply a side effect of song learning and is therefore occurring passively (Garamszegi et al. 2007). However, they did find positive correlations between vocal mimicry and large brain size, song continuity, and age-dependent expression of repertoire size (Garamszegi et al. 2007), so it appears the answer is not so straightforward. In either of these hypotheses, mimetic sounds should be treated the same as species-specific ones (Hindmarsh 1984, 1986, Baylis 1982).

Mimicry provides a unique opportunity to track song learning. Tracing mimicked sounds within song is often easier than following the development and retention of species-specific sounds from early life. We can focus on the distinction between mimetic and nonmimetic categories instead of on a continuum of conspecific sounds. How different species learn songs, and to what extent song traits are genetically encoded, is highly variable and poorly understood (Love et al. 2019). However, a young songbird generally has innate predilections, apparently ancestral to the songbird lineage (Goller and Shizuka 2018), that limit its vocalizations to species-specific sounds (Marler 1976). In mimetic species, mimicked song components are not constrained by an individual's predisposition to learn and produce conspecific sounds. If all sounds are treated the same by a mimicking species, the genetic constraints on song learning must be relaxed to include heterospecific sounds. This unrestricted sound selection, in which mimetic and nonmimetic sounds are incorporated in the same manner, is an expectation from both the repertoire size and permissive learning hypotheses. Alternatively, males may acquire and incorporate mimicked sounds very differently from how they utilize species-specific components. We know little about how individuals compare in their use of mimicry, or what effect mimicry has on the development of species-specific song. As even closely related species may have markedly different learning programs (Love et al. 2019), studying mimicry may allow a clearer understanding of what occurs during song learning. In this study, I compared mimetic and nonmimetic components of European starling song to learn about the relationship between mimicry and repertoire size.

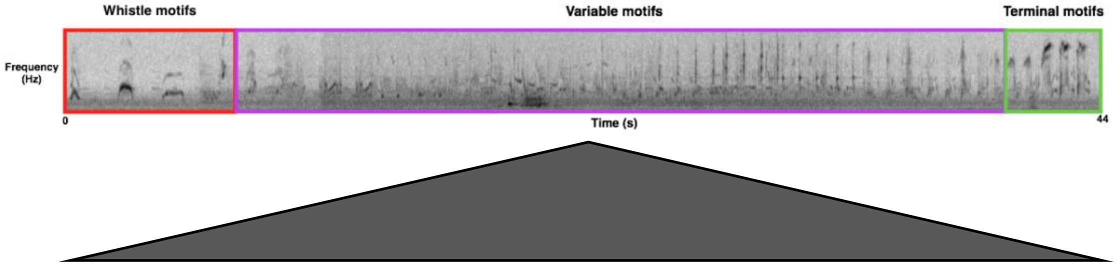
In starlings, the significance of repertoire size is not fully understood. While males with larger repertoires were healthier (Mountjoy and Lemon 1996), better at novel foraging tasks (Boogert et al. 2008), were dominant and had higher immune responses (Spencer et al. 2003), female response to large repertoires was mixed. Mountjoy and Lemon found that females preferred males with larger, more complex repertoires (1991, 1996) and Boogert et al. (2008) suggested repertoire size is an honest indicator of quality. However, in a different study, female starlings did not favor large repertoires, instead making decisions based on transition stereotypy (Gentner and Hulse 2000). If the repertoire size hypothesis is true for starlings, and large repertoires are important, males may use mimicry to supplement song repertoires. If this is the case, the assumption is that either males with relatively small or males with relatively large repertoires use proportionally more mimicry than males with intermediate repertoire sizes.

European starlings are talented mimics that copy a wide range of avian and nonavian sounds (e.g. Thomson 1922, Chisholm 1932, Tretzel 1965, Hindmarsh 1984, 1986). Starlings use a combination of invention, modification, and imitation to create their songs. Males that imitate the same sounds incorporate them differently into song (Adret-Hausberger and Jenkins 1988). Indirect findings from some studies of starling song led to the conclusion that mimetic sounds are used interchangeably with species-specific sounds (e.g. Eens et al. 1989) and that mimicry serves no specialized function (Hausberger 1997). Other authors suggested that mimicry increases repertoire diversity and facilitates individual recognition (Adret-Hausberger and Jenkins 1988, Adret-Hausberger et al. 1989, Hausberger et al. 1995, Gentner and Hulse 2000, but see Knudsen et al. 2010). Furthermore, there are other ways in which mimicry could function in song that have not been addressed. It is therefore still unclear to what extent mimicry matters for starlings and a first step is understanding exactly how mimicry relates to repertoire size. This study is the first step in paring down potential functions of mimicry under the umbrella of sexual selection.

I analyzed wild European starling song to address three questions about individual variation and mimicry. First, how does song content vary among males? I expected songs to vary in content (e.g. motif composition and the types of sounds used) but to adhere to the structure of the species-specific song template. While previous studies have documented individual variation, populations differ in the sounds used, and I wanted to determine the song variation in my population. Second, how are mimetic sounds incorporated into starling song? To answer this question, I compared mimetic and nonmimetic motifs, and categorized the position of mimicry within song units. I wanted to understand how individuals in the study population were incorporating mimicry. Third, does mimicry increase repertoire size? If so, how? While both the repertoire size and permissive learning hypotheses suggest a correlation between mimicry and repertoire size, this has not been directly tested in starlings. If repertoire size is supplemented with mimicry (repertoire size hypothesis), I had two mutually exclusive expectations. First, individuals with smaller repertoires could use proportionally more mimicry than birds with larger repertoires. In this case, singers with few nonmimetic motifs would be increasing their repertoire by using more mimicry. Alternatively, males with the largest repertoires achieve this, in part, by using proportionally more mimicry. In turn, the permissive learning hypothesis suggests that either (1) there is no relationship between repertoire size and mimicry and the proportion of mimetic sounds should remain the same regardless of repertoire size, or (2) individuals with larger repertoires should use more mimicry, as they potentially incorporate a greater diversity of sounds. Alternatively, any of these scenarios could indicate a different function of mimicry beyond repertoire size (e.g. structural, honest signal, etc…), which would require further research.

## Methods

European starlings have two song types: whistle song and warbling song. Whistle song is composed of high-pitched whistles used for social identity and group cohesion in flocks (e.g. Hausberger et al. 2008, Hausberger 1997). Warbling song is used in mate attraction and female stimulation (e.g. Hindmarsh 1984, Cuthill and Hindmarsh 1985, Hausberger et al. 1991), and is the focus of this study. Song is composed of *motifs*. Each motif is a set of one to ten *notes* (discrete sounds that are the building blocks of birdsong and music) repeated as a discrete unit. Motifs are analogous to words and notes are the letters that compose each motif. A male's repertoire size is the number of unique motifs he sings (e.g. Eens et al. 1989). Warbling song has a clear organizational structure of three sections containing different types of motifs (Figure 2.1). A song bout begins with several introductory *whistle motifs*, followed by a series of rambling, repeated, *variable motifs*, and concludes with a series of high-frequency, loud *terminal motifs* (e.g. Adret-Hausberger and Güttinger 1984, Eens et al. 1989, Gentner and Hulse 1998, Gentner and Hulse 2000). Some authors divide variable motifs into variable and rattle motifs, but as these two sections are not always distinct, I chose to combine them.



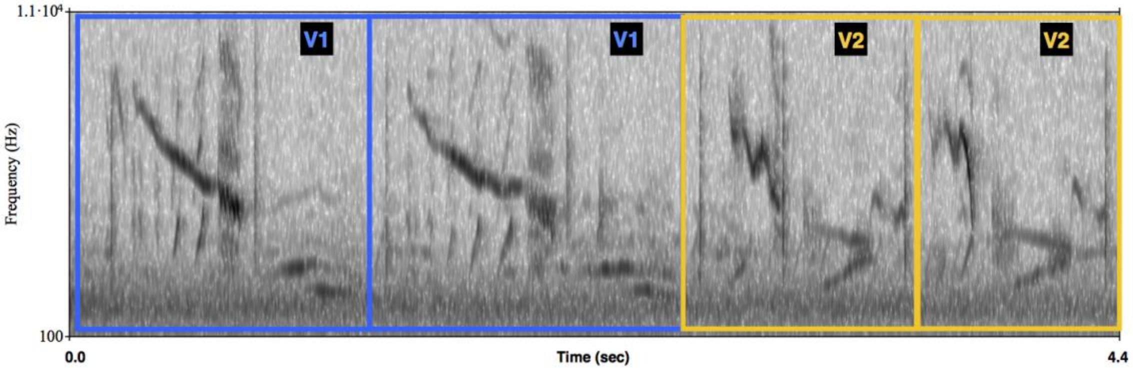


*Figure 2.1. Spectrogram of a 44-second warbling song bout. Each song bout is generally composed of three components: introductory whistle motifs, variable motifs, and terminal motifs. Song bouts may begin with variable motifs or truncate before terminal motifs. V1 and V2 are examples of discrete units of song (motifs) that are repeated multiple times before the song transitions to the next motif.*

I recorded male starlings broadcast-singing outside their nest holes in Lincoln, Nebraska, using a Sennheiser omnidirectional microphone (ME 66 shotgun) and Marantz solid state recorder (PMD 661). I used nest site and vocal characteristics to identify individuals (as was confirmed in Hindmarsh 1984, Hausberger et al. 1991, Eens et al. 1991, Adret-Hausberger 1982, Adret-Hausberger 1984). Song sampling occurred in the spring of three consecutive years: one male (2017), 11 males (2018), and seven males (2019). During this time, males sing incessantly before their first brood. Recording of each male occurred over consecutive days as weather permitted, such that I finished recording one male before moving on to the next. Most recordings were done in the morning from 0800 to 1100. Focal males were distributed across the city, with nest cavities separated by at least 20 meters. In this analysis, I included recordings from 19 males for which I had at least 30 full song bouts. I chose 30 bouts because this was the most conservative suggestion from previous studies to sample a male's full song repertoire (150 motifs, Adret-Hausberger et al. 1989; 15 song bouts, Böhner and Todt

1996; 15 minutes or 30 bouts, Hindmarsh 1984), and American individuals appear to have larger repertoires than European individuals (Europe: 17-55 motifs, Hausberger 1997; USA: 60-80 motifs, Chaiken et al. 1993, Hausberger 1997; Figure 2.2). Full song bouts were interspersed with abbreviated whistle and terminal motif sequences, which were also recorded.

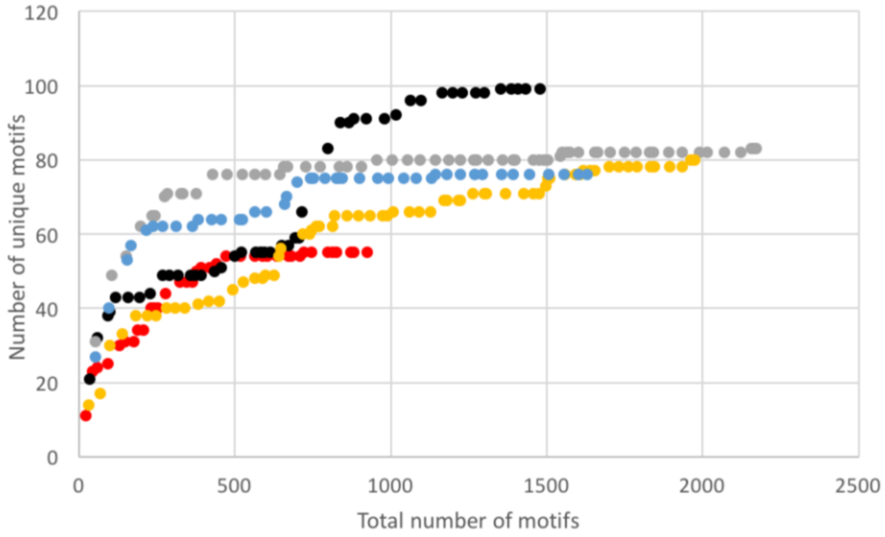


*Figure 2.2. Cumulative motif curve for the sampling of the song repertoire of five individuals. The asymptote indicates a majority of the repertoire was sampled.*

I used Praat (v. 6.0.23; Boersma and Weenink 2019) to view spectrograms of song. Using the annotation tool, I labeled all motifs in recordings by comparing them visually and acoustically, and compiled a vocabulary of motifs for each male (such as in Eens et al. 1989, Gentner and Hulse 1998, Palmero et al. 2012, Palmero et al. 2014). All motifs recorded – whether full song bout or abbreviated sequence – were annotated and incorporated into a male's repertoire vocabulary. To ensure consistency in classification, I annotated all songs.

I further classified motifs as mimetic or nonmimetic. A motif was considered mimetic if it contained at least one mimicked sound. I acoustically determined mimetic sounds and visually confirmed the similarity by comparing them to spectrograms of suspected models (Hindmarsh 1984, Igic and Magrath 2013, Ferguson et al. 2002). Starlings are accurate mimics and models could be identified by an experienced birder (MG) with 94.5% repeatability (consistent reclassification of 205 out of a subset of 217 motifs). All individuals generally imitated the same vocalization type from a given model (House sparrow: 80 of 84 imitations were of chirp; American robin: 80 of 89 imitations were of call) and I lumped all imitations by model for analysis.

I also determined how each mimicked sound was incorporated into a motif. There were four position categories (Figure 2.3): at beginning (mimicked sound added to start of motif), at end (mimicked sound added as final note in motif), entire (mimicked sound is full motif), and integral (mimicked sound is embedded in motif and cannot be easily excised from other notes). I compared incorporation of mimetic sounds between males.

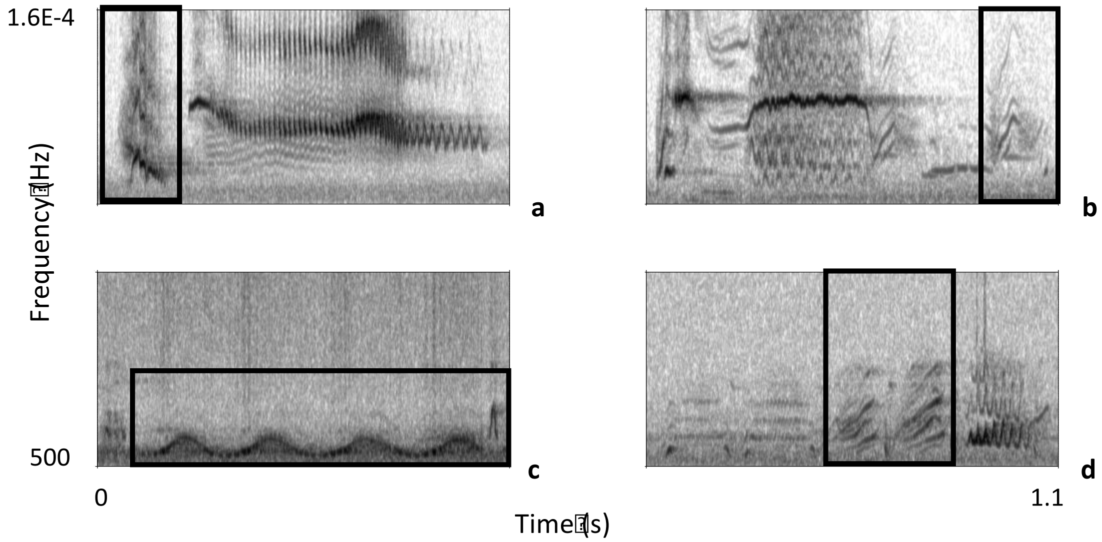


*Figure 2.3. Spectrographic examples of the four positions of mimicked sounds. Mimicry was included at the beginning (a; house sparrow), at the end (b; house sparrow), as the entire motif (c; ambulance siren), or integrated into the motif (d; northern flicker).*

*Statistical Analysis*

### *Variation in song composition*

I compared the number of mimetic and nonmimetic motifs in each male's repertoire using a Wilcoxon signed-rank test. I then investigated the differences in the proportion of nonmimetic and mimetic whistle, variable, and terminal motifs. I did this with a generalized linear-mixed model using the package *lme4* in R (v. 1.2-13, Bates et al. 2014) and posthoc Tukey tests. I also did a follow-up chi-squared test to compare the number of mimetic and nonmimetic variable motifs.

### *Mimetic sounds*

I used several linear regression analyses to determine the relationship between number of models and number of uses per model, number of mimetic sounds and number of models, and to determine whether number of males using a model and the number of uses of that model were related. I used a second linear-mixed model to compare positioning of mimetic sounds with male as random effect. I investigated mimetic sound positioning between males and between models using single factor ANOVA in R, followed by posthoc Tukey tests.

### *Mimicry and repertoire size*

I used linear regression to look at the relationships between repertoire size and number of mimetic motifs or nonmimetic motifs, number of models, and proportion of mimicry. Spearman's rho was calculated to determine whether mimetic and nonmimetic motif number were correlated. After these analyses, I did a follow-up linear regression to determine whether males with smaller repertoires were using the rarest models (those used in three or fewer motifs) more than males with larger repertoires.

## Results

### *Variation in song composition*

A total of 15,000 recorded motifs from 600 song bouts were classified into 1,326 unique motifs: 773 as nonmimetic and 553 as mimetic. Mean repertoire size per male was 70 motifs (range: 34 to 127). The mean for nonmimetic motifs was 39 (range: 19 to 78) and 31 (range: 4 to 56) for mimetic motifs. All males sang song bouts composed of whistle, variable, and terminal motifs, though in different proportions. On average, 26% (range: 11 to 40%) of motifs were whistles, 54% (range: 36 – 75%) were variable, and 20% (range: 9 to 43%) were terminal motifs.

Repertoires were, on average, 56% nonmimetic (range: 30 to 88%). Male repertoires contained significantly more nonmimetic motifs than mimetic ones (41 versus 29; $p = 0.005$, Z-value = -2.79, W-value = 21.5), although there was a lot of variation (Figure 2.4a). Some males had more mimetic than nonmimetic motifs, and two males had an equal number of the two categories.

The proportion of motifs in the three song sections differed for nonmimetic and mimetic motifs. The mean nonmimetic motif proportional breakdown was 0.3 whistle, 0.45 variable, and 0.25 terminal. The mimetic breakdown was less uniform across sections, with means of 0.22 whistle, 0.62 variable, and 0.16 terminal. The differences in the proportions between nonmimetic and mimetic categories were significant for all three song sections ($p < 0.001$). Whistle and terminal sections contained a significantly higher proportion of the nonmimetic repertoire than of the mimetic repertoire ($p < 0.01$ for both). This pattern was true for number of nonmimetic whistle and terminal motifs as well (whistle motifs: df = 18, t-stat = 5.85, $p < 0.001$; terminal motifs: df = 18, t-stat = 4.9, $p < 0.001$; Figure 2.4b). In contrast, the proportion of mimetic motifs was higher than that of nonmimetic motifs within the variable section of song ($p < 0.005$), although there was no difference in the number of variable motifs between the two categories ($p = 0.49$; 367 nonmimetic versus 370 mimetic). There was a lot of individual variation in the breakdown of a male's repertoire into the six types. Not all males included mimicry in all three song sections.

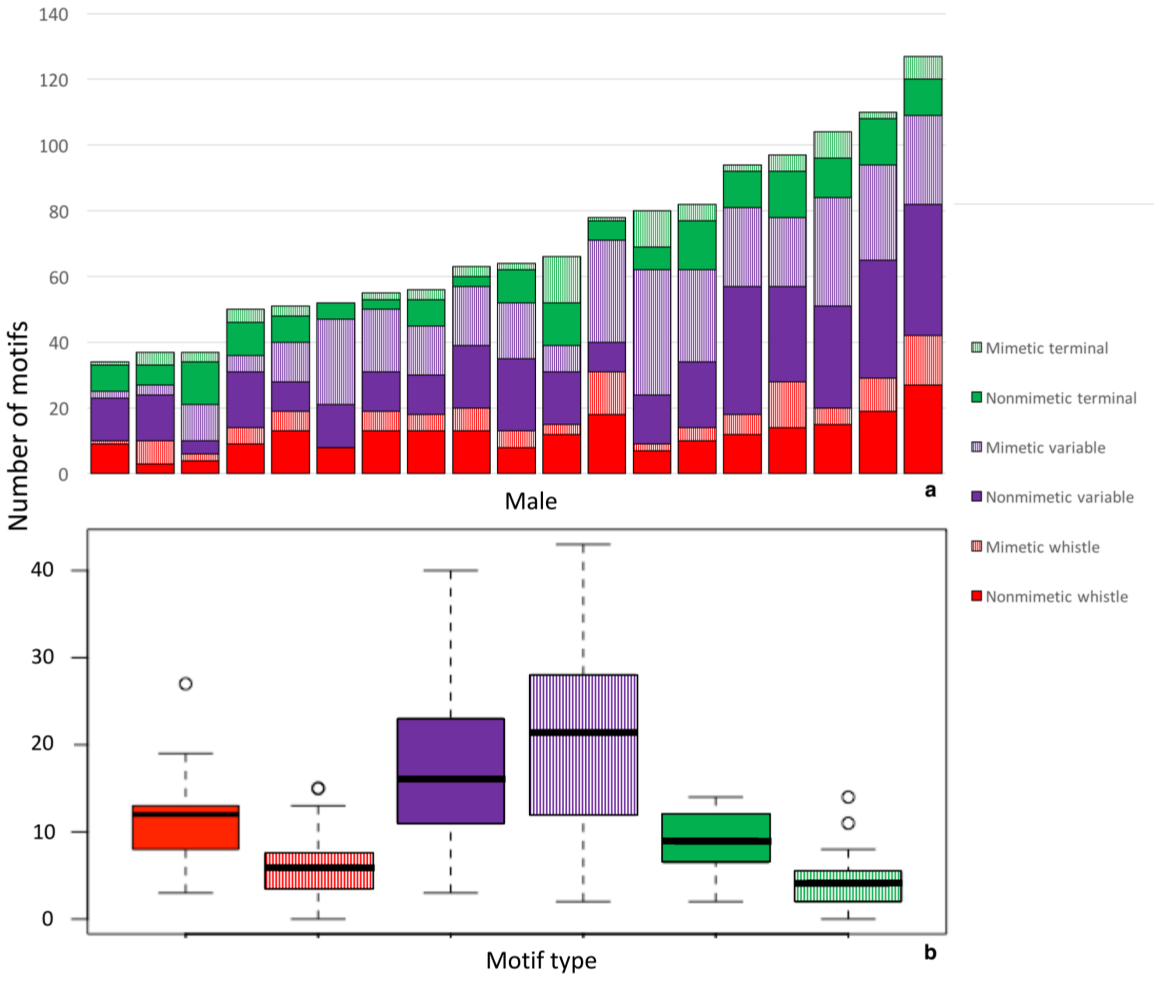


*Figure 2.4. a) Individual variation in the number of the six motif types (nonmimetic and mimetic whistle, variable, and terminal motifs), arranged by increasing repertoire size.*

*Breakdown of song varied between males, and not all males had all six types in their repertoire. Some males had more nonmimetic than mimetic motifs, while the opposite was true for other males, and two males had an equal number of nonmimetic and mimetic motifs. b) Boxplot of the number of nonmimetic and mimetic whistle, variable, and terminal motifs. There were significantly more nonmimetic whistle and terminal motifs than mimetic ones. There was no significant difference in number of variable motifs between the categories.*

*Mimetic sounds*

There was a lot of variation across individuals in the number of models used, as well as the average number of uses of a specific model. Males imitated an average of 12 models (range: 4 – 22). The average number of motifs that included a specific model, calculated as a mean based on the males imitating that model, was 2.7 motifs per male (range: 1 – 5.6). Males used an average of 32.2 mimetic sounds in their song (range: 4 – 51). There was no relationship between the number of models a male imitated and the number of unique mimetic motifs that contained that model (p = 0.92, F = 0.011, t-stat = -0.1, Figure 2.5).

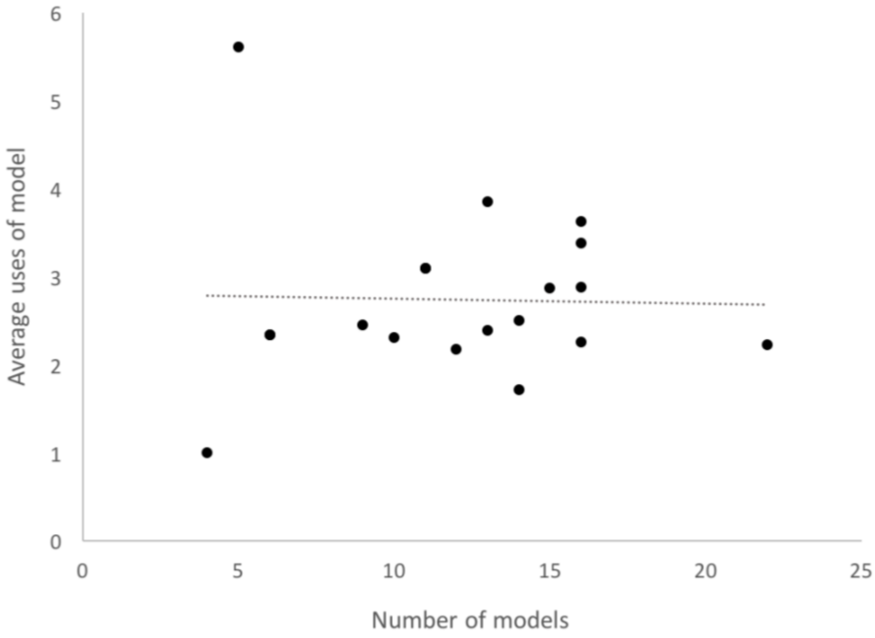


*Figure 2.5. Relationship between number of models used by a male and the average uses of each model. Each point represents values for one male. Average uses ranged widely (1*

*to 5.6), as did number of models (4 to 22). There was no significant trend in the relationship.*

Certain models were incorporated into motifs by all or nearly all males and these models were used more often by each male (Figure 2.6, Table 2.1). For example, males used house sparrow 7.7 times (range 1 – 20; n = 19) and American robin 6.7 times (range 0 – 13; n = 18). Some models were used by relatively few males (Common nighthawk, White-breasted nuthatch) or by only one male (Brown thrasher, human, walk signal). There was a positive relationship between number of models and number of mimetic sounds used by a male ($p < 0.001$, $R_2 = 0.63$, t-stat = 5.4). Furthermore, as number of males imitating a model increased, the number of times that model was incorporated into motifs increased exponentially ($R_2 = 0.85$). This was driven by a significant positive relationship between number of males using a model and the mean number of uses of that model; popular models were used more by all individuals ($p < 0.001$, F = 91.25, t-stat = 9.55; Figure 2.6).

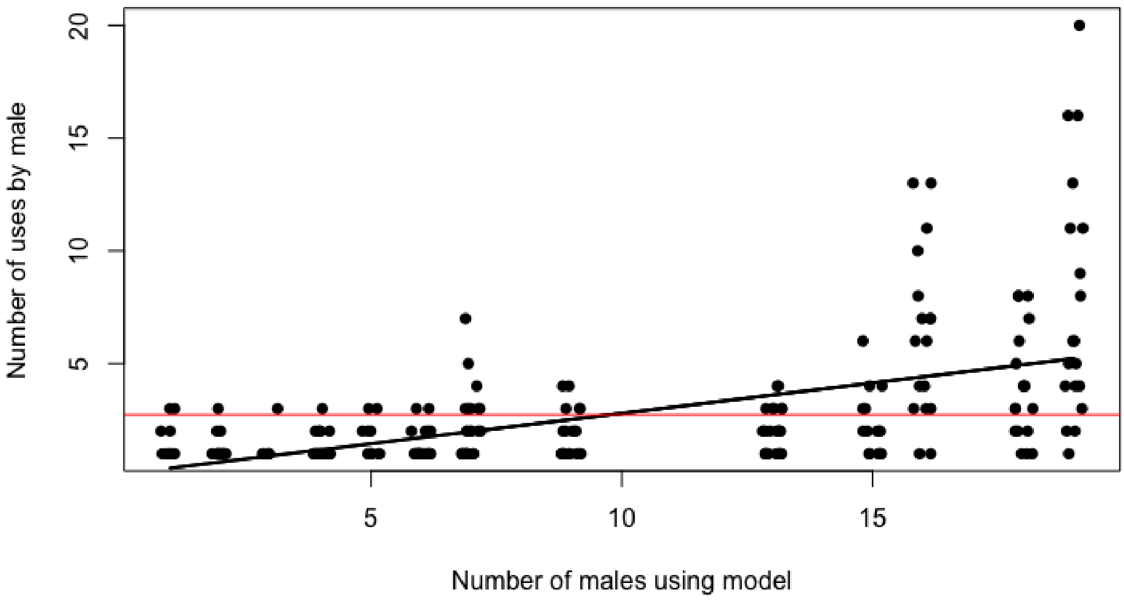


*Figure 2.6. Positive relationship between number of males using a model and the number of uses of that model by every individual. The red line indicates the average number of uses of a model by an individual. This relationship was highly significant ($p < 0.001$, $R_2 = 0.28$). Both number of uses of a model and the number of males using a model were highly variable; however, all males used popular models more often. House sparrow was used by every male an average of 7.7 times. Other models were used only once by a single male (recess bell, Cedar waxwing) and others were used repeatedly by one male (human) or two males (House finch).*

*Table 2.1. Models imitated by males in this study. Table also indicates the number of motifs the model was used in ("motifs"), number of males using this model ("males"), and in how many motifs that model appeared in per male ("average uses per male").*

| model | motifs | males | average use per male (of males using) |
|---|---|---|---|
| recess bell | 1 | 1 | 1 |
| CEDW | 1 | 1 | 1 |
| Unk.Sparrow | 1 | 1 | 1 |
| walk signal | 1 | 1 | 1 |
| EATO | 2 | 2 | 1 |
| RWBL | 2 | 2 | 1 |
| WTSP | 2 | 2 | 1 |
| EABL | 3 | 3 | 1 |
| MALL | 23 | 7 | 1.21 |
| siren | 5 | 4 | 1.25 |
| WBNU | 8 | 6 | 1.33 |
| RTHA | 8 | 5 | 1.6 |
| GRCA | 5 | 3 | 1.67 |
| NOCA | 7 | 4 | 1.75 |
| Unk.Gull | 11 | 6 | 1.83 |
| motor | 13 | 7 | 1.86 |
| NOFL | 25 | 13 | 1.92 |
| COGR | 2 | 1 | 2 |
| EUCD | 2 | 1 | 2 |
| mechanical | 2 | 1 | 2 |
| RBWO | 4 | 2 | 2 |
| Unk.Frog | 8 | 4 | 2 |
| BHCO | 10 | 5 | 2 |
| CONI | 12 | 6 | 2 |
| KILL | 18 | 9 | 2 |
| EAME | 26 | 13 | 2 |
| BCCH | 19 | 9 | 2.11 |
| CANG | 9 | 4 | 2.25 |
| AMGO | 36 | 15 | 2.4 |
| AMCR | 19 | 7 | 2.71 |
| BRTH | 3 | 1 | 3 |
| human | 3 | 1 | 3 |
| BLJA | 72 | 18 | 4 |
| HOFI | 9 | 2 | 4.5 |
| AMRO | 106 | 16 | 6.69 |
| HOSP | 146 | 19 | 7.68 |

Mimetic sounds were incorporated into a motif in four ways. Mimicked sounds were used at the beginning (13) or ending (116) of a motif, as the entire motif (153), or embedded into it ("integral", 342). An integral position was significantly most common (df = 54, t-value = 9.51, p < 0.001), while sounds used as entire motifs or motif endings were equally common (z-value = 1.12, p = 0.68). On average, males were twice as likely to embed mimicry within a motif (integral motifs) than to use a mimicked sound as the entire motif. Only half of the males used mimicry at the beginning of motifs, and this position was significantly less common than any other position ($p < 0.003$). Males did not significantly differ in their use of mimetic sounds in these four positions (df = 18, F = 0.75, p = 0.74). However, models were used preferentially in different positions within a motif (df = 35, F = 2.71, $p < 0.001$; Figure 2.7). For example, House sparrow and American robin made up 80% and 78% of the mimicked sounds used at the beginning or ending of a motif, respectively. Sounds from a larger variety of models were integral to motifs, while different models were used as entire motifs (Eastern meadowlark, Blue jay, American goldfinch, Killdeer, ambulance siren).

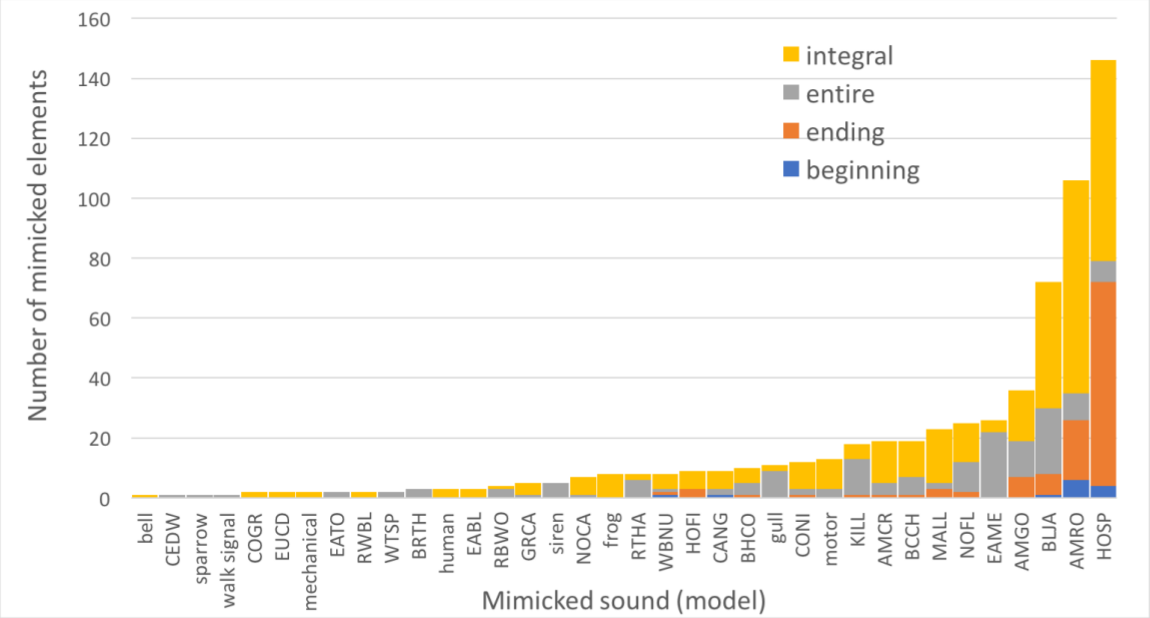


*Figure 2.7. Number of mimicked sounds and positioning of these sounds for all models. Models are arranged based on number of males imitating that model (from 1 to 19). House sparrow and American robin were most common and were used in all four positions within motifs. Most mimicked sounds were not used at the beginning of motifs. Ambulance siren and Eastern meadowlark were often used as entire motifs. Abbreviations, following the four-letter bird banding codes (Pyle and DeSante 2003), are as follows: bell (school recess bell), BRTH (Brown thrasher), CEDW (Cedar waxwing), COGR (Common grackle), EUCD (Eurasian collared-dove), human (faint human conversation), mechanical (mechanical sound), sparrow (unknown sparrow chip), walk*

*signal (crosswalk walk signal), EATO (Eastern towhee), HOFI (House finch), RBWO (Red-bellied woodpecker), RWBL (Red-winged blackbird), WTSP (White-throated sparrow), EABL (Eastern bluebird), GRCA (Gray catbird), CANG (Canada goose), frog (unknown frog species), NOCA (Northern cardinal), siren (ambulance siren), BHCO (Brown-headed cowbird), RTHA (Red-tailed hawk), CONI (Common nighthawk), gull (unknown gull species), WBNU (White-breasted nuthatch), AMCR (American crow), MALL (Mallard), motor (motorized plane), BCCH (Black-capped chickadee), KILL (Killdeer), EAME (Eastern meadowlark), NOFL (Northern flicker), AMGO (American goldfinch), AMRO (American robin), BLJA (Blue jay), HOSP (House sparrow).*

### *Mimicry and repertoire size*

Repertoire size was positively correlated with number of mimetic motifs ($p < 0.001$, $R_2 = 0.72$, t-stat = 6.6; Figure 2.8) and number of models ($p = 0.007$, $R_2 = 0.35$, $f = 9.32$). However, nonmimetic motifs showed this same correlation ($p < 0.001$, $R_2 = 0.82$, t-stat = 8.96). Number of mimetic and nonmimetic motifs were also positively, but weakly, correlated ($r_s = 0.518$, $p = 0.02$). Males with large repertoires did not use proportionally more mimicry (linear regression: $p = 0.43$, $R_2 = 0.04$, t-stat = 0.815). Two males with intermediate repertoire size had the largest proportion of mimicry in their repertoires. Individual repertoire size was not significantly related to the number of rare models used by that male ($p = 0.43$, $R_2 = 0.04$, t-stat = 0.8) or the number of motifs incorporating these rare models each male sang ($p = 0.41$, $R_2 = 0.04$, t-stat = 0.84).

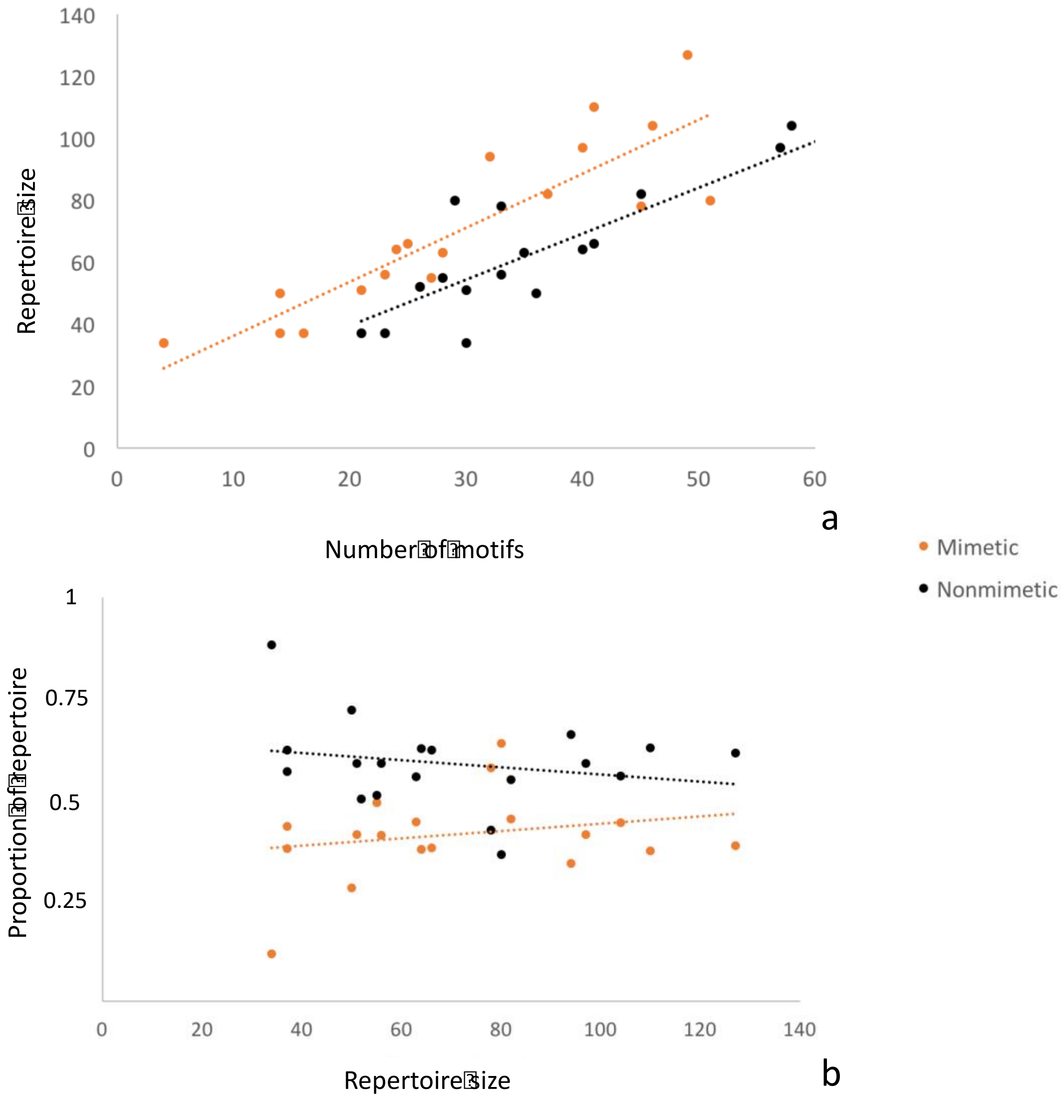


*Figure 2.8. a) Repertoire size is positively correlated with number of mimetic and nonmimetic motifs. The lines are parallel, indicating that the two relationships are congruent: birds with more mimetic motifs and nonmimetic motifs have significantly larger repertoires. b) Nonsignificant relationships between repertoire size and proportion of repertoire that is mimetic or nonmimetic. Males with larger repertoires do not use proportionally more mimicry.*

## Discussion

### *Variation in song composition*

Male starlings are highly variable in *what* they sing but follow universal rules in *how* they sing. All individuals sang the standard three sections - whistle, variable, terminal motifs - of song, incorporating the most mimicry in the variable motifs (as found in Eens et al. 1989, Eens et al. 1991). However, the proportions of mimetic and nonmimetic whistle, variable, and terminal motifs, as well as the amount of mimicry, varied across males. There were also significant differences in the whistle-variable-terminal motif breakdown between mimetic and nonmimetic categories across males. As mimicry was included in 12% to 70% of a male's repertoire, and usage of mimicry varied, mimetic sounds may help distinguish individuals (e.g. Gentner and Hulse 2000).

### *Mimetic sounds*

There was clear variation in the extent to which mimicry was incorporated by individuals into song. While there were individual differences in the number of models used as well as the number of times each model was integrated into motifs, there was no overall relationship between the two. Males that only imitated several models did not use these more often than males using many models. However, differences in the number of times a model was used (e.g. House sparrow was used ubiquitously, a recess bell was not) indicate that different mimicked sounds are treated differently in constructing motifs. Usage of mimicked sounds from a specific model increased with the number of males copying that model. One possible explanation for these observations is that social interaction, and the "popularity" of certain mimicked sounds, may influence incorporation of mimicked sounds. Once a sound is mimicked by many males, it may be shared between conspecifics and become ubiquitous in the population. Indeed, there is some evidence that starlings may selectively incorporate models to match the songs of neighboring males (Hindmarsh 1984). Males could listen to the mimicry of neighbors and imitate the same models, or even imitate directly from neighbors. Similarly, starlings may use the distinction between familiar and unfamiliar motifs to recognize individuals (Gentner and Hulse 2000), and mimicry could help facilitate this process. The fact that female starlings also mimic (Pavlova et al. 2005) supports the idea that mimicry facilitates individual recognition (but see Knudsen et al. 2010).

Alternatively, starlings may have innate biases or species-specific constraints on what types of sounds are imitated and how to incorporate mimicry into song. For example, imitated sounds from certain models were incorporated into motifs in the same way by all males. Males appeared to use mimicked sounds in a song section with motifs that were structurally similar, such as a siren as a whistle motif, or a house sparrow chirp to replace the clicks between variable motifs. Males also showed the same trends in how they incorporated mimetic sounds into motifs, strongly favoring integral positioning. Although there was some variation (only a subset of males added mimicry to the beginning of motifs), positioning does not seem to be as flexible as what sounds are mimicked. Similarly, which of a model's sounds were imitated remained consistent across males. For a male to diversify his song, he would therefore have to imitate models that other males do not, such as the males that incorporated human speech, a recess bell, and a walk signal into their songs.

Starlings may be flexible in what they imitate and how often they use the same sounds, but not in how they construct motifs. Two main factors in the incorporation of sounds were the number of times a mimetic sound was used and the number of models a male imitated. Most males with a relatively large number of mimetic motifs imitated many models and used each model multiple times. However, some males achieved a large mimetic repertoire by either imitating many models and not using them often, or by repeatedly using a limited set of models. Some males did neither well. Across males, there was a tenfold difference in number of mimetic motifs. Variation in model and mimetic sound usage indicate that individuals can achieve large mimetic repertoires in different ways. Similarly, the range in mimetic diversity indicates that males are not all equally good at imitation or at embedding mimicked sounds into motifs.

Individuals incorporated a mean number of 12 models into their songs. This is nearly twice the number of models per individual reported in a previous study of starlings in Europe (mean of seven models/male; Hindmarsh 1984). It remains unclear how males learn mimicked sounds and how they choose which sounds to incorporate. Males appear to preferentially imitate short, clear notes and often imitate abundant species (Hindmarsh 1984). The combination of these two factors may explain imitation of many models, but does not explain why some abundant species with simple songs of tonal frequency sweeps (such as the Northern cardinal) were not imitated by most males. It also does not explain why several simple, clear sounds commonly heard throughout starling habitat, such as a crosswalk signal, were only imitated by one male. The species mimicked by most males (House sparrow, American robin) were common and encountered by all males in the study. However, other species equally common in the area (e.g. Common grackle, Northern cardinal) were only imitated by a few males. Clearly, exposure to potential models was not the only influence on the incorporation of mimicry into song.

### *Mimicry and repertoire size*

In this study, repertoire size was highly variable (spanning a fourfold difference in size). Males using more mimicry had larger repertoires. However, individuals with large repertoires incorporated more mimetic motifs simply because they used more motifs overall, not because their songs had proportionally more mimicry. The two males with the highest proportion of mimetic motifs had repertoires of intermediate size. Thus, increased mimicry did not directly cause increased repertoire size, but increase in repertoire size may incidentally lead to increased use of mimicked motifs. Furthermore, males with the smallest repertoires did not supplement their song by preferentially imitating rarely-used models. These results contradict the expectations from the repertoire size hypothesis and support the permissive learning hypothesis. All evidence from this study suggests that mimicked sounds are used the same way as species-specific ones in terms of repertoire size. The next two chapters will focus on determining whether mimetic and nonmimetic motifs are serving the same structural and acoustic functions in song.

### *Significance*

Many pieces in the mimicry puzzle are still missing. This study demonstrates that the flexible song learning and mimicry of the European starling is related to larger repertoires, but that mimicry does not directly increase repertoire size. Although many studies have focused on the repertoire size hypothesis as an explanation for mimicry (Kelley et al. 2008, Dalziell et al. 2014), directed studies may unravel intricacies within this learning process. Not only could mimicry have multiple functions, but there are many ways in which mimicry could be used to diversify song. It will be interesting to learn whether mimicry (1) serves a role in other song factors, such as song structure or song quality, and/or (2) allows males to sing more acoustically diverse motifs. For example, northern mockingbirds use mimicry to increase the maximum frequency of their song (Gammon and Lyon 2017), which may be attractive to females, and incorporating mimetic sounds could allow starlings to similarly alter the acoustic quality of their songs. Mimicry could also have a social function, such as through facilitation of individual recognition (Adret-Hausberger and Jenkins 1988, Adret-Hausberger et al. 1989, Hausberger et al. 1995), and this could have important implications for a species as social as the starling.

By studying how mimicry is used by individuals and species, we can expand our knowledge of the diversity of song learning systems. By studying mimicry, we can begin to understand how birds learn to sing, and what effects mimicry may have on the song development of a species. Vocal mimics are scattered throughout the songbird phylogeny and provide a unique system for studying learning (Goller and Shizuka 2018). As most studies of song learning have focused on a small number of model species (zebra finch, *Taenopygia guttata*; white-crowned sparrow, *Zonotrichia leucophrys*), it is important to study species with more elaborate songs to understand the full scope of the song-learning continuum.

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# CHAPTER III: SONG STRUCTURE AND VOCAL MIMICRY IN EUROPEAN STARLINGS

## Abstract

Song is a form of communication crucial to territorial defense and mate attraction in songbirds. While song complexity varies widely, even species with elaborate songs have genetic constraints on song development that facilitate the formation of species-specific song structure. Past studies have focused on one measure of song complexity - song repertoire size - as a correlate of reproductive success; however, other song factors may be more important. Species-specific structural rules may allow conspecifics to more easily observe differences in the songs of individuals, thereby quickly and reliably assessing potential mates and competitors. I used a network approach to describe the song of the European starling (*Sturnus vulgaris*) and to explore how song learning, specifically vocal mimicry, leads to variation in a complex song. This chapter addresses the structural function hypothesis, which suggests a subtle function of mimicry in *song structure* (the arrangement of song components and connections between them). I measured structural diversity within song bouts by quantifying transitions to/from motifs, as well as repetition of motifs and bout linearity. I then compared mimetic and nonmimetic motifs to determine whether mimicry served a specific role in song structure. I found that starlings sang fewer mimetic motifs at points of structural diversity within song bouts, but repeated mimetic motifs more often than nonmimetic ones. My results indicate that mimicked sounds may function differently in song structure than species-specific sounds, and that variation in song structure could provide important information to conspecifics. Studying the relationship between mimicry and the structural properties of complex songs may

allow us to understand the interaction between song development, mimicry, and reproductive fitness.

## Introduction

Vocal communication is integral to the behavior and sociality of many animal species. In songbirds, *song* is a form of communication crucial to territorial defense and mate attraction. The structural complexity of song varies widely across species, from simple, stereotyped arrangements of several notes, to elaborate, variable hour-long displays of hundreds of notes (Brenowitz and Beecher 2005). Even among species with elaborate songs, constraints on song learning and development exist to facilitate emergence of appropriate song architecture (Marler 1997). However, our understanding of structure and syntax is limited, and it is still unclear how certain singing behaviors, such as vocal mimicry, affect or alter the structural properties of complex songs.

Attempts have been made to compare song complexity of individuals within and across species. A longstanding assumption is that males with relatively complex songs are more reproductively successful than males with simpler songs (e.g. Soma and Garamszegi 2011). The most common measure of complexity in birdsong is repertoire size, although its usefulness as a metric has been mixed. Some studies have found a relationship between repertoire size and fitness (Reid et al. 2005), immune function (Pfaff et al. 2007), and cultural membership in a population (Creanza et al. 2016). However, other studies have found no indication that individuals pay attention to differences in repertoire size (Gentner and Hulse 2000a&b). These mixed results indicate that, although repertoire size variation is correlated with other individual differences in some species, other song factors may be more important (Soma and Garamszegi 2011, Creanza et al. 2016).

There are other reasons why repertoire size may fall short as a useful measure of song complexity. First, repertoire size can be difficult to estimate accurately, especially in species that have relatively large repertoires (willow warbler, *Phylloscopus trochilus*, Gil and Slater 2000; Cassin's vireo, *Vireo cassinii*, Hedley 2016). Unless the songs of many individuals are sampled to determine a good minimum sample size, repertoire size may be greatly under- or over-estimated, making the metric unreliable as a point of comparison. For example, if a male uses different parts of his repertoire on consecutive days, recording over one day may not yield full repertoire size. Second, it is difficult to quantify repertoire size in species with a vast number of song components (brown thrasher, Kroodsma and Parker 1977). Individuals may mix and match song components, or continuously improvise, generating a huge (potentially infinite) number of motifs. Third, repertoire is measured in various ways, which makes comparison difficult. For example, repertoire size could be reported as the number of unique motifs (Gil and Slater 2000), notes (Catchpole and Slater 1995), strings of motifs or phrases (Hedley 2016), or song types (Verner 1975). This variation makes interspecific comparisons challenging. Fourth, and most biologically important, females do not appear to listen to the full repertoire of courting males before making a choice (Gentner and Hulse 2000a). Males of some species sing songs that last several minutes, and females paying attention to repertoire size would need to spend considerable time listening before making a choice. Instead, females may focus on song metrics other than repertoire size, such as accuracy of learning (Creanza et al. 2016), structural stereotypy (Gentner and Hulse 2000a&b), diversity, or a combination of factors (Soma and Garamszegi 2011).

There is a growing understanding that variation in song structure may encode information recognized by conspecifics. Pattern of song structure, or *syntax*, is the specific arrangement of song components and the transitions between them (Lachlan et al. 2013). General rules governing syntax of the song of a species appear to be innate, and therefore genetically regulated. Juvenile zebra finches tutored with randomized sequences arranged motifs in the same way, and used the same strings of sequences, as juveniles tutored by adult males (James and Sakata 2017). Similarly, many transitions between motifs were shared by males (Marsh wren, *Cistothorus palustris*, Verner 1975; Pacific wren, *Troglodytes pacificus*, Kroodsma 1980). There is also evidence that song structure and bout length vary based on social context and purpose (House finch, *Haemorhous mexicanus*, Ciaburri and Williams 2019) and with age (European starling, *Sturnus vulgaris*, Adret-Hausberger et al. 1990). Song structure may therefore encode information for listeners (Hedley 2016) and a balance of stereotypy and diversity in song is thought to be ideal for communication (Zipf's law, Briefer et al. 2010, Palmero et al. 2012, Palmero et al. 2014).

Even apparently complex songs with many components (i.e., large repertoire size) and much individual variation follow a few simple patterns in song structure. Common structural rules may be shared by singers of a species even when there is large variation in repertoire size (Gil and Slater 2000, Sasahara et al. 2012) and in the note types sung (Payne 1979). Species-specific structural rules allow conspecifics to quickly and reliably assess potential mates or competitors. One widespread rule is that transitions are nonrandom such that certain song units appear more often together than apart (e.g. European starling, Gentner and Hulse 2000a&b; Canary, *Serinus canaria*, Cohen et al. 2019; House finch, Ciaburri and Williams 2019; California thrasher, *Toxostoma redivivum*, Cody et al. 2016, Sasahara et al. 2012; House wren, *Troglodytes aedon*, Deslandes et al. 2014; Willow warbler, Gil and Slater 2000; Pacific wren, Kroodsma 1980; Common nightingale, *Luscinia megarhynchos*, Weiss et al. 2014; Bengalese finch, *Lonchura striata domestica*, Okanoya 2004; Marsh wren, Verner 1975; Hermit thrush, *Catharus guttatus*, Roach et al. 2012; Spectacled warbler, *Sylvia conspicillata*, Palmero et al. 2012; Zebra finch, James and Sakata 2017; Cassin's vireo, Hedley 2016; Indigobird species, *Vidua spp.*, Payne 1979, Watts and Strogatz 1998). Another rule is that a small subset of the song units in an individual's repertoire is used preferentially, while other units are rare (Palmero et al. 2012, Deslandes et al. 2014). This "core repertoire" (Gil and Slater 2000) may be composed of song units with particular qualities, such as a favored frequency or bandwidth (Draganoiu et al. 2002), which set those song units apart. Males of some species emphasize their core repertoire by repeating one song unit several times before moving to the next (Willow warbler, Gil and Slater 2000; European starling, Böhner and Todt 1996). In some species, certain phrases are always sung in sequence (stereotyped), while others are not (canary, Cohen et al. 2019; California thrasher, Sasahara et al. 2012).

Recent studies have successfully used network analysis to describe variation in the structural functions of song components within complex songs. For example, specific song components in nightingale song are points of convergence or divergence in the song pathway (Weiss et al. 2014), and in both California thrashers (Cody et al. 2016) and canaries (Cohen et al. 2019), phrases are sung at specific locations within a song bout. In nightingales, the song components with an unequal number of converging and diverging paths were the ones shared by males (Weiss et al. 2014), suggesting that specific components or positions in a song bout may be disproportionately important. It is unclear whether song components at *transition hubs* (points at which song may diverge into, or converge from, different paths) differ in some way from those only found in stereotyped (linear) sequences.

The overarching goal of this chapter was to apply network approaches to characterize the structural rules underlying the highly complex song of the European starling, and to determine whether nonmimetic and mimetic sounds were used in different structural ways. I wanted to test the hypothesis that mimicry has a unique structural role in song, which is proposed under the structural function hypothesis. The starling, like the nightingale, sings a song of many components (in this case, *motifs* – sets of one to ten notes repeated as a discrete unit). Previous findings suggest that male song characteristics influence female choice (Eens et al. 1991) and that starling motifs serve different functions. For example, Adret-Hausberger and Jenkins (1988) found that certain motifs were only used in an introductory or conclusory context. They also found that 60% of motifs were repeated, and each motif was repeated a predictable number of times (Adret-Hausberger and Jenkins 1988, Hausberger et al. 1995). These observations suggest that starling motifs have may have different functional effects and may be treated differently by listeners. Some studies have found that females choose males based on sequence stereotypy (Gentner and Hulse 2000a), although others emphasize the importance of repertoire size (Mountjoy 1994). For both male and female listeners, motifs in the second half of song bouts are more important for individual recognition (Gentner and Hulse 2000b, Knudsen et al. 2010). Females also showed preference for long song bouts, although they never listened to a full bout (Gentner and Hulse 2000a), indicating that song structure differs between long and short bouts. These results suggest that song structure is important; however, it is unknown how different motifs function within a song bout, or whether there are specific motifs that serve as transition hubs.

The starling is a talented mimic that incorporates mimicked sounds into many of its motifs (e.g. Hindmarsh 1984). Across vocal mimic species, mimicry may increase song repertoire size (Dalziell et al. 2014), song diversity (Coleman et al. 2007) or serve another function. As starlings do not use mimicry to directly increase repertoire size (Chapter 2), I expected simply distinguishing between “mimetic” and “nonmimetic” motifs would uncover differences in the structural treatment of motifs. For example, males may use mimicry more at song transition hubs for emphasis or may repeat mimetic motifs more than nonmimetic ones. To explore what function mimicry may have in starling song structure, I first used network analysis to describe overall song features. Networks allow visualization of birdsong and the transitions between song units, and are a useful tool for quantitative comparisons. I focused on variation in the song structure of individual males. I then analyzed the differences between nonmimetic and mimetic motifs in two structural components: number of transitions leading to and from each motif, and repetitions of every motif. I hypothesized that mimicked sounds would be used preferentially at certain positions within a song bout (specifically at points of structural diversity) because mimicry is obvious and could add emphasis to important parts of song. I also hypothesized that if mimetic motifs served as emphasis within song bouts, they would be repeated less often than nonmimetic ones. Finally, I plotted structural measurements against repertoire size to determine whether there was a relationship between diversity in song structure and the size of a male's repertoire. I expected no association between structure and repertoire size.

## Methods

I focused only on the warbling song of male starlings. Warbling song has a clear organizational structure of three sections containing different types of motifs: several introductory whistle motifs followed by a series of rambling, repeated, variable motifs, and concluding with a series of high-frequency, loud terminal motifs (Chapter 2; e.g. Adret-Hausberger and Güttinger 1984, Eens et al. 1989, Gentner and Hulse 1998, Gentner and Hulse 2000a&b). All recording methods and spectrogram analyses were the same as for Chapter 2.

### *Network Analysis*

Transition networks have become a tool for disentangling the structural organization of complex songs (Marsh wren, Verner 1975; California thrasher, Sasahara et al. 2012, Cody et al. 2016; Common nightingale, Weiss et al. 2014). Transition networks are a type of network in which the *nodes* (circles) represent song motifs and the *edges* (lines) indicate transitions between motifs. This network therefore shows whether song units are arranged in a nonrandom manner. Motifs that are always sung in sequence will have stronger associations (thicker lines or edges between them) between them than motifs that appear randomly throughout a song bout. As such, a male's most commonly sung sequence will be displayed as the thickest line. Additionally, the number of transitions to (*in-degree*) and from (*out-degree*) each motif can yield information about song (Sasahara et al. 2012). For example, some motifs may be points of convergence or *bottlenecks* with high in-degree; preceded by a variety of motifs, but always followed by only one. Other motifs may be points of divergence or *branching points* leading to a variety of different motifs (high out-degree; Sasahara et al. 2012).

I created transition networks using the package *igraph* in R (v. 3.6.0, Csardi and Nepusz 2006; R Core Team 2019) for the songs of 19 males. Each network was a composite of all song sequences from a male. I excluded any sequences shorter than five motifs to avoid potential bias from motifs only sung as isolated song. I calculated edge weights for each transition by dividing the number of a given transition, such as from motif A → motif B, by the total number of transitions in a male’s song. I then calculated weighted effective degrees for each motif (McDonald and Hobson 2018; Figure 3.1). Weighted effective degree was the reciprocal of the sum of edge weight proportions for a given motif (McDonald and Hobson 2018). For each motif, I calculated effective degrees separately for transitions to (*effective in-degree*) and from (*effective out-degree*) that motif. Effective in- and out-degree show the level of stereotypy in the pattern of transitions leading to and from a motif. Motifs with high effective degree are connected by many equally-weighted edges; there are many paths leading to and/or from that motif. Motifs have low effective degree when there are few paths leading to/from them, or when a minority of edges are disproportionately favored, such that they are only ever sung in specific sequences. The lowest possible effective in- or out-degree is zero (if a motif only ever starts or ends a song bout), while the highest possible effective degree values are bounded by a male's repertoire size. This method allowed me to capture the differences in the stereotypy of motif transitions without devaluing diversity in transition strengths for each motif.

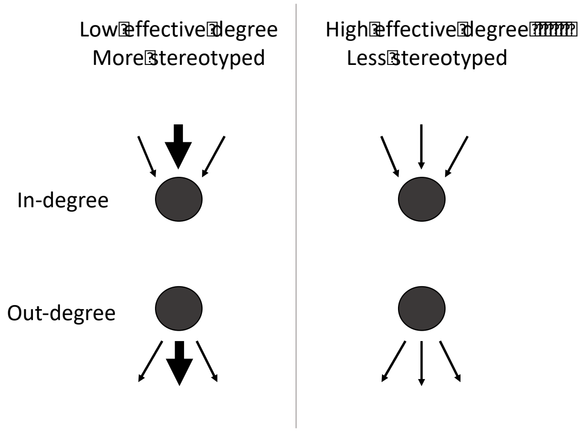

*Figure 3.1. Effective in- and out-degree of nodes. Low effective in- and/or out-degree indicates a high likelihood that the transitions follow one path (thicker arrow or edge), resulting in a more stereotyped song. High effective in/out-degree yields a less stereotyped song.*

### *Linearity Index Scores*

The linearity index is another way to describe the structure of song sequences. Developed by Gil and Slater (2000) to describe willow warbler song, the linearity index score for starlings is calculated by dividing the number of unique motifs in a bout by the number of unique transition types within that song bout. The lower the linearity, the more syntactically complex the song. I calculated the linearity scores for all 1,069 song bouts. For this calculation, I included repetitions (such as motif A → motif A) as unique transitions. Therefore, any score equal to or higher than one indicates a linear song (highly stereotyped). I determined 1) how much variation there was between males, and 2) whether the relationships between the linearity score and either mimetic or nonmimetic motifs differed.

### *Motif Repetition*

Since there are differences in the number of repetitions of different starling motifs, I wanted to investigate how this characteristic of song structure compared across males. I found the total count of each motif as well as the number of occurrences of each motif disregarding sequential repetitions (*"appearances"*). I also determined the mean number of repetitions per appearance for every motif. Only sequences longer than five motifs were included, and the values were used to determine whether different categories of motifs (such as from different song sections or mimetic versus nonmimetic) were used differently in song.

### *Statistical Analysis*

First, I wanted to determine whether effective in- and out-degree differed between whistle, variable, and terminal motifs, and across mimetic and nonmimetic categories, as well as to determine a typical song bout's structure. I ran a generalized linear mixed model in R using Satterthwaite's method, with male as random effect, followed by posthoc ANOVA Type III and Tukey tests. I used a Spearman's rank correlation to determine whether males were consistent in level of stereotypy across song sections.

Second, I looked at individual variation in the song structure by comparing degree distributions for each male using an Anderson-Darling k-Sample test with the *k-Samples* package in R (Scholz and Zhu 2019). This is a nonparametric test that allowed me to determine whether males had different effective in- and out-degree distributions of their motifs. I used posthoc Tukey tests to determine how many males differed in either effective in- or out-degree. To determine whether degree was related to repertoire size, I used linear regression to compare repertoire size and effective in- and out-degree for all males.

I then compared effective degree differences tabulated across males between nonmimetic and mimetic categories of the three motif sections (whistle, variable, terminal motifs) using a linear mixed model. I also used a t-test to determine whether total effective degree (pooled effective in- and out-degree) differed between mimetic and nonmimetic motifs.

I ran an ANOVA to determine whether males differed in song bout linearity scores. I used a linear regression to determine the relationship between linearity index scores and the number of both unique nonmimetic and mimetic motifs within song bouts. I wanted to know whether mimetic and nonmimetic motifs had different effects on linearity. I used a second linear regression to determine whether linearity increased or decreased as bout duration increased.

Finally, I analyzed variation in motif repetition – repetitions per appearance, appearances, and counts of each motif. I used a linear mixed model with male as random effect, followed by posthoc ANOVA Type III, to determine differences in repetition data between mimetic and nonmimetic motif categories for whistle, variable, and terminal song sections. Another ANOVA was used to determine whether males differed in repetitions per appearance, appearances, and total counts. Linear regression was used to look at the relationship between mean repetitions per appearance and total effective degree values of motifs.

## Results

### *Differences in Structure of Song Sections*

The three sections of European starling song have different structure (Figure 3.2). The whistle section is nonlinear, with no clear pattern in motif sequence. Whistle motifs had significantly higher effective out-degree on average than the other two sections (mean whistle = 2.84, mean variable = 1.7, mean terminal = 1.97; ANOVA results: F-stat = 78.63, $p < 0.001$), and the pattern was the same for effective in-degree (mean whistle = 2.53, mean variable = 1.89, mean terminal = 1.98; ANOVA results: F-stat = 22.72, $p < 0.001$). The whistle section has higher average effective in- and out-degree because there are many equally-probable transitions between motifs, giving the overall structure a hairball-like appearance (Figure 3.2a). Whistle motifs had significantly higher effective out-degree than effective in-degree (mean out = 2.835, mean in = 2.53, t-stat = 3.27, $p = 0.001$). The section therefore ends chaotically, with many whistle motifs feeding into the variable motifs section.

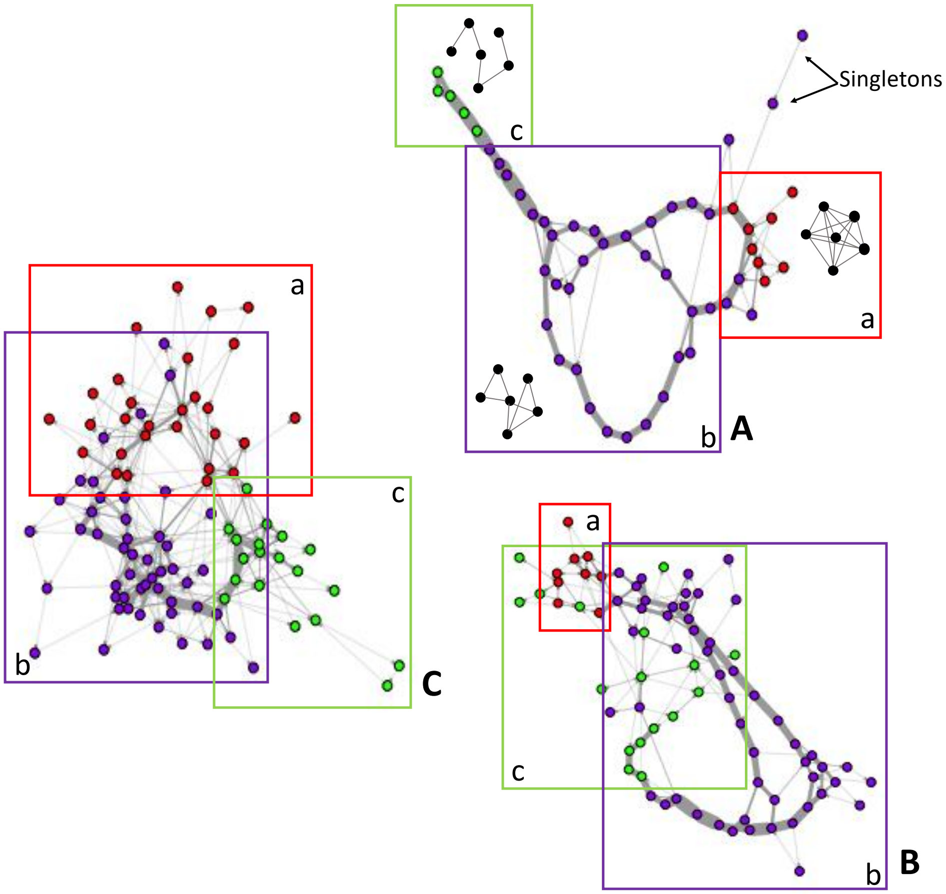

*Figure 3.2.* *Song transition networks of the songs of three male European starlings. Each network is a composite of all song bouts sung by a male. Song bouts begin with whistle motifs (red;* ***a****) with a convoluted hairball structure, then continue into variable motifs (violet;* ***b****), which are nonrandomly arranged, and end in highly stereotyped terminal motifs (green;* ***c****). Diagrams of section structure are shown alongside the network in part A. Individuals vary along a gradient of how well their songs adhere to this structure, with distinct sectional differences in some networks (****A****), to increasingly indistinct sections as a male's song repertoire increases (****C****). Singletons are motifs sung only once. The coordinates and distance between nodes are unimportant.*

The variable section is characterized by motifs connected by a few, high-probability transitions, although rare ("singleton") motifs may cause deviations from the pattern (Figure 3.2b). As a result, variable motifs have lower effective in- and out-degree than whistle motifs. The differences between variable and terminal motifs in effective out-degree (Tukey posthoc tests: z-value = -1.292, $p = 0.4$) and effective in-degree (Tukey posthoc tests: z-value = 0.49, $p = 0.87$) were not significant. However, variable motifs had significantly higher effective in-degree than out-degree (mean in = 1.89, mean out = 1.70, t-stat = -4.696, $p < 0.001$). Structurally, the variable motif network begins from many different transitions (from whistle motifs) and becomes more regimented as the songs transition into the terminal section. The variable motifs follow at least one pathway that appears more often than other transitional paths.

The level of stereotypy of the terminal section varied across males. It was the most regimented for some males, whose song had a single stereotyped terminal sequence across song bouts (Figure 3.2A), but not for other males (Figure 3.2C). There was no difference in effective out- and in-degree for terminal motifs (mean out-degree = 1.97, mean in-degree = 1.98).

Effective degree values from variable and terminal motif sections were correlated. Individuals singing a less stereotyped variable motif sequence (high effective out- and in-degree) also had significantly less stereotyped terminal motif sequences (effective out-degree: $r_s = 0.78$, $p < 0.0001$; effective in-degree: $r_s = 0.69$, $p = 0.001$). This association did not hold true when comparing whistle motifs to the other sections.

### *Variation in Male Song Structure*

Song structure was not consistent across all males (Figure 3.2): the effective in- and out-degree distributions of the 19 males were significantly different in some cases (effective in-degree: AD = 70.69, $p < 0.001$; effective out-degree: AD = 83.9, $p < 0.001$). Effective in-degree for whistle motifs was the most similar across males (no significant differences). Comparisons within all other categories (effective out-degree for the three song sections, effective in-degree for variable and terminal motifs) showed some significant differences between males ($p < 0.001$). Variable motifs had the most variation between males in mean effective in- and out-degree. Deviations in individual means from the mean combined effective degree was similar for whistle and variable motifs (coefficients of variation were 25.2 and 26.3, respectively), while variation for terminal motifs was slightly higher (coefficient of variation = 38.6).

There was no significant relationship between mean effective in- or out-degree and repertoire size across males (effective in-degree: $R_2 = 0.003$, $F = 0.04$, t-stat = 0.21, $p = 0.84$; effective out-degree: $R_2 < 0.001$, $F < 0.001$, t-stat = -0.01, $p = 0.99$) and the three song sections ($p > 0.2$ for all comparisons). The variation in stereotypy was independent of repertoire size.

### *Mimetic and Nonmimetic Motifs*

In general, nonmimetic motifs had higher effective out- and in-degree than mimetic motifs (effective out-degree: nonmim = 2.18, mim = 1.85; t-stat = -3.78, $p < 0.001$; effective in-degree: nonmim = 2.15, mim = 1.96; t-stat = -2.15, $p = 0.03$). These trends were driven by nonmimetic whistle motifs having significantly higher effective out-degree (nonmim = 3.02, mim = 2.45; t-stat = 2.6, $p = 0.01$). There were no significant differences in effective in-degree across sections. Together, these results mean that total effective degree was significantly higher for nonmimetic motifs than for mimetic motifs – nonmimetic motifs were found in less-stereotyped sections of song (nonmimetic mean: 4.33, mimetic mean: 3.81; t-stat = 3.49, $p < 0.001$; Figure 3.3).

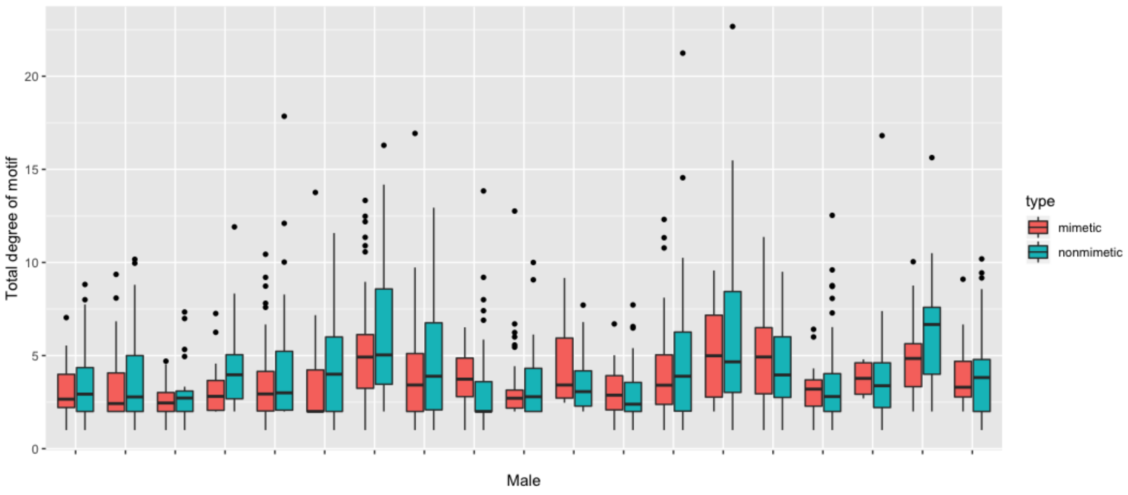

*Figure 3.3.* *Boxplots of total effective degree for mimetic and nonmimetic motifs of each male. On average, nonmimetic motifs had greater effective in- and out-degree (and therefore total degree) than mimetic motifs, indicating that nonmimetic motifs were more likely to be in less-stereotyped sequences than mimetic motifs.*

### *Linearity Index Scores*

Males varied in the linearity (stereotypy) of their song bouts (Figure 3.4A). Some males had a lot of variation in linearity scores between song bouts, while the scores of other males were more consistent. Some differences in mean linearity between males were significant (mean linearity = 0.66, min = 0.33, max = 1.2, F-value = 5.295, $p < 0.001$). Linearity was significantly negatively related to number of unique motifs in a bout, as would be expected, although the trend was weak ($R_2 = 0.11$, t-stat = -11.32, $p < 0.001$). The relationships between linearity and nonmimetic and mimetic motifs were both weak and effectively identical (nonmimetic: $R_2 = 0.07$, t-stat = -9.16, $p < 0.001$; mimetic: $R_2 = 0.07$, t-stat = -8.94, $p < 0.001$). As bout length increased, linearity decreased (R2 = 0.265, F-value = 385.6, t-stat = -19.64, $p < 0.001$; Figure 3.4B).

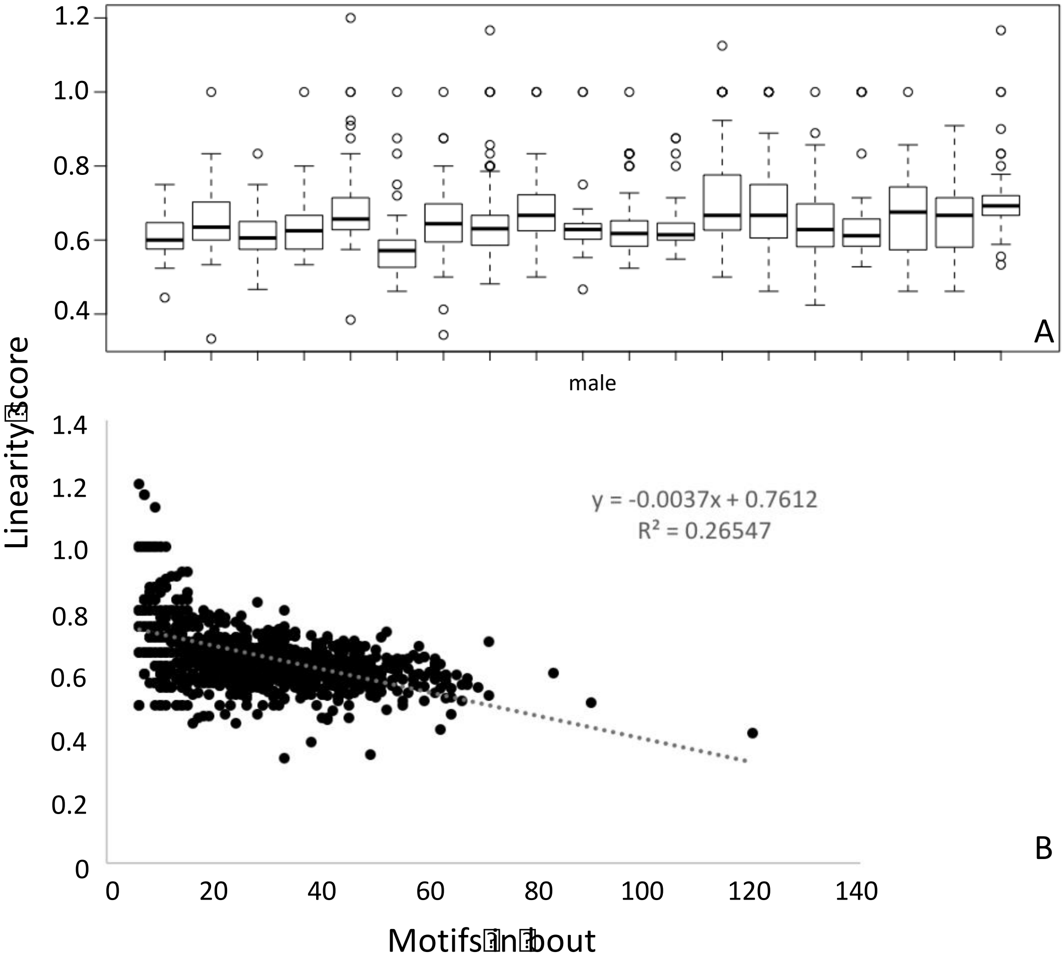

*Figure 3.4. Linearity index scores. Variation in linearity scores across males (A) and the significant, negative relationship between bout length (measured as total number of motifs in bout) and the linearity score of each song bout (B).*

*Repetitions*

Overall, variable motifs were repeated most often (mean = 1.94), followed by terminal motifs (mean = 1.611) and whistle motifs (mean = 1.275). These differences were significant ($F = 92.78$, $p < 0.001$; Figure 3.5a). Differences in number of appearances and total counts of motifs also were significant across song sections (variable > terminal > whistle; appearances: $F = 18.41$, $p < 0.001$; totals: $F = 42.8$, $p < 0.001$). The whistle section is composed of singleton motifs that are rarely repeated. In contrast, variable and terminal sections contain more repetition, and motifs from these sections also appear more across the song bouts of a male. Some males were significantly different in the repetition metrics (mean repetitions per appearance: F = 4.96, $p < 0.001$; number of appearances: F = 16.55, $p < 0.001$; total count of motifs: F = 10.64, $p < 0.001$; Figure 3.6). Combined effective degree was negatively correlated with repetitions by appearance (t value = -3.45, F = 11.93, $p < 0.001$). Males using more repetition sang song sequences that were more linear than those using less repetition.

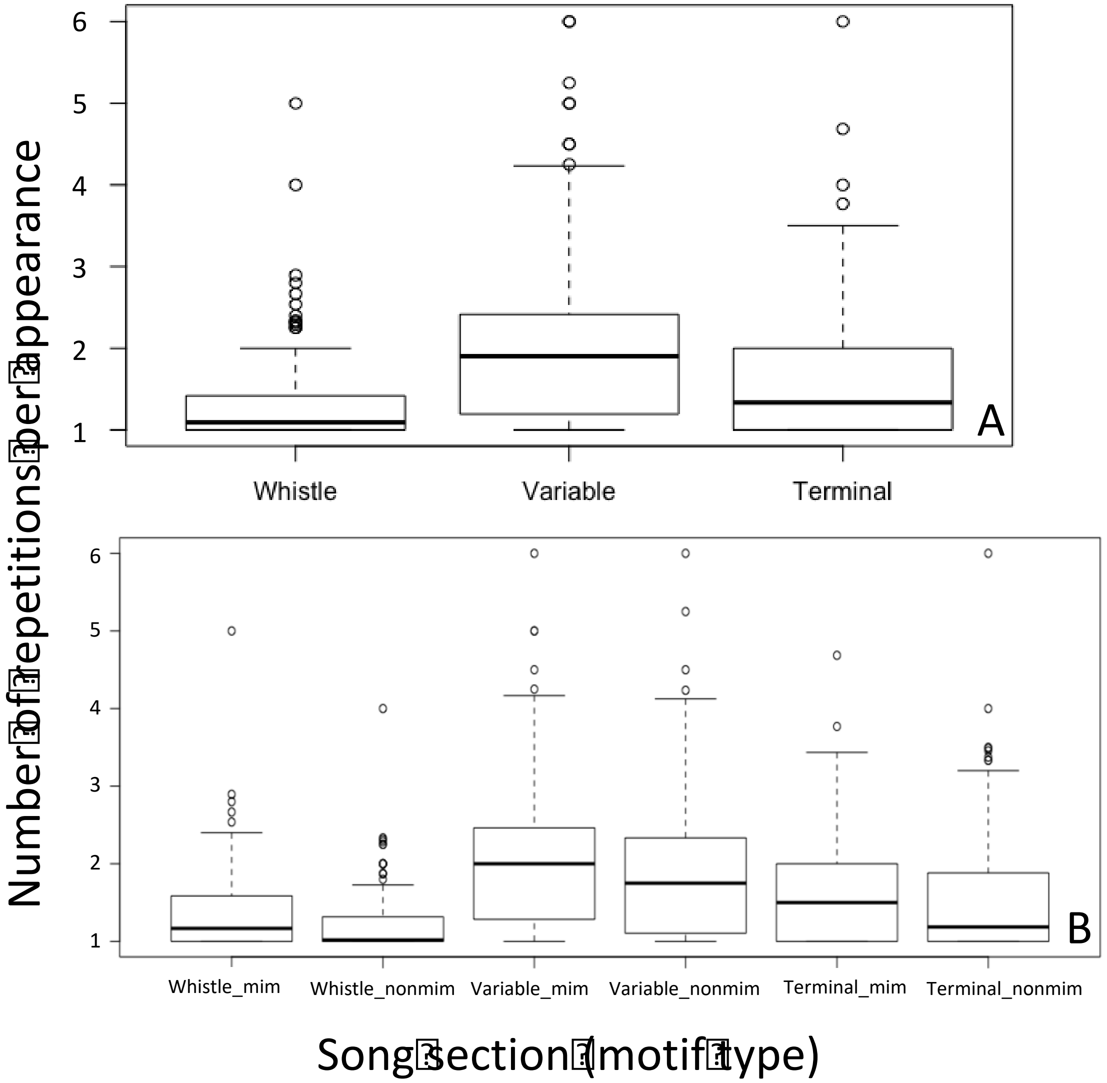

*Figure 3.5. Mean repetitions per appearance divided into the three sections of a song bout (**A**) and further divided into mimetic and nonmimetic motifs (**B**). Variable motifs*

*were repeated significantly more than terminal motifs, which were also repeated significantly more than whistle motifs.*

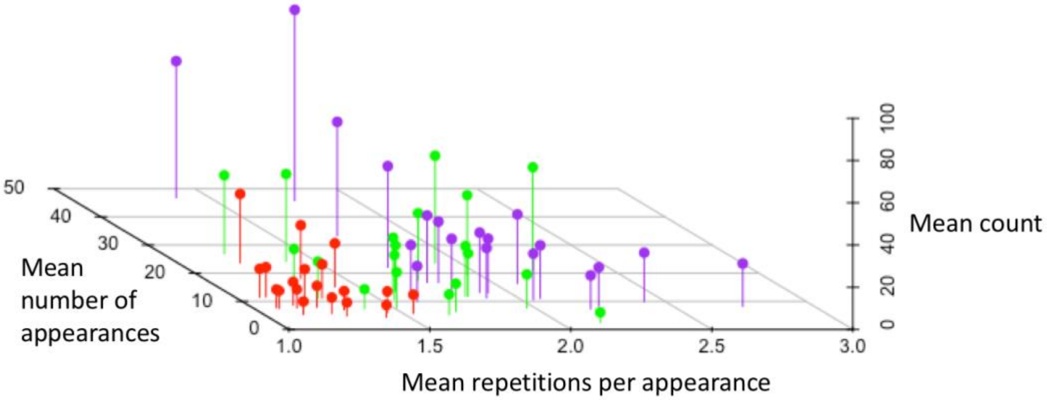

*Figure 3.6. Three-dimensional plot of the variation in repetition metrics across males. Mean repetitions per appearance, number of appearances, and count are shown for the whistle (red), variable (purple), and terminal (green) motifs of each male. Variable motifs had the greatest range, followed by terminal motifs, and then whistle motifs.*

Mimetic motifs were repeated significantly more often per appearance than nonmimetic motifs (nonmim = 1.61, mim = 1.84; F value = 25.7, $p < 0.001$). This pattern did not, however, hold true when comparing mimetic and nonmimetic motifs within whistle motifs (nonmim = 1.22, mim = 1.385, p = 0.27; Figure 3.5b), variable motifs (nonmim = 1.875, mim = 2.006, p = 0.34), or terminal motifs (nonmim = 1.55, mim = 1.74, p = 0.31). Number of appearances was more uniform across sections, and there was no significant difference between mimetic and nonmimetic motifs (p = 0.48). Total counts of motifs were more variable, emphasizing the difference between core repertoire and rare motifs, and mimetic motifs had higher count (nonmim: 21.08, mim: 24.38; F value = 8.73, p = 0.003). Again, no differences within song sections between mimetic and nonmimetic motifs were significant.

## Discussion

### *Variation in Song Structure*

Marler (1970, 1997) proposed that each species has some song features – such as syntax, structure, or content – that are innate and help guide the song learning process. While previous studies of European starling song described the three song sections and gave basic information about motifs (e.g., Hindmarsh 1984, Adret-Hausberger and Jenkins 1988, Eens et al. 1989, Mountjoy and Lemon 1995), few details were given about structural or sequential variation. I found that some song bouts were perfectly linear while others were not. Additionally, each song bout began with a low level of stereotypy (the whistle motifs) that increased throughout the bout. Some males had a highly stereotyped ending sequence of terminal motifs while others had songs that never became stereotyped. This pattern resembles the song structure of at least one other species, the willow warbler. Willow warbler song is also composed of three structurally distinct sections (intro, middle, and end), although in this species the final section of song is the least stereotyped (Gil and Slater 2000). This difference in stereotypy across sections is interesting. Gentner and Hulse (2000a) suggested predictability of transitions (stereotypy) was more important to females than repertoire size or song content. Furthermore, females prefer long song bouts (Eens et al. 1991, Gentner and Hulse 2000a), which I found to be less linear. Bout length was positively related to immune function (Duffy and Ball 2002) and linearity may therefore provide information to females about male quality. It will take further study to understand exactly what females are focusing upon, whether on an increase in stereotypy within a song bout, reduced linearity in longer bouts, some other structural feature present in long bouts but not in short bouts, or perhaps linearity (or lack thereof) within a given song section.

Male starlings differed in key structural features, such as effective in- and out-degree, motif repetitions, and use of individual motifs. This suggests that structure is somewhat plastic and that listeners may be able to differentiate individuals based on the overall structure of their songs. Song is perceived by listeners as a gestalt of characteristics. Because of this, individual singers potentially unable to perform all song features equally well may specialize in different song components and achieve acceptable or attractive songs in different ways. For example, the level of stereotypy within each song section (whistle, variable, or terminal motifs) varied from total stereotypy or linearity (all song bouts following a single sequence without deviation) to high diversity (no apparent transitional pattern). These differences may provide information of singer quality to listeners. Similarly, some males preferred repeating motifs while others used repetition less frequently. In both cases, listening for these differences would be easier and take less time than counting motifs to determine repertoire size. Interestingly, effective degree of motifs and repertoire size were unrelated, although motif appearances and total counts decreased with increasing repertoire size. Since repetitions were independent of repertoire size, this suggests that adding motifs leads to a proportionate decrease in both total count and number of appearances. As such, sequential stereotypy may be independent of repertoire size, supporting the idea that assessment of only one song parameter is too simplistic for studies of song variation.

It is unclear what components of song structure conspecifics focus on, though there is evidence that song structure and stereotypy are more important than repertoire size (Gentner and Hulse 2000a). Perhaps females focus on the stereotyped sequences in which males incorporate the most mimicry. Alternatively, females may favor males capable of singing appropriate species-specific motifs at points of convergence or divergence in a song sequence. In playback studies, male and female starlings selectively paid attention to specific cues throughout the song bout (Knudsen et al. 2010). In this study, nonlinear motifs with more than two transitions were more common than linear motifs, and it would be interesting to investigate whether listener attention differs between these categories. Given the structural diversity and complexity present in European starling song, I propose that song structure may be an important component of mate choice in this species. The variation present in the structural components highlighted here would be easier for conspecifics to assess than would comparing repertoire sizes of potential mates.

### *Mimicry and Song Structure*

Contrary to my predictions, nonmimetic motifs had higher effective in- and out-degree than did mimetic ones. In other words, mimetic motifs tended to emerge from or lead into *more* stereotyped (linear) sequences. Mimetic motifs were also repeated significantly more often in an appearance than were nonmimetic motifs. A similar pattern of low-degree song units being sung most frequently was found in house wrens (Deslandes et al. 2014). These findings contradict my hypothesis that mimicry was used to emphasize points of structural diversity within a song bout. There appears to be a tradeoff between high degree and repetition, but it is unclear what effect repetitions (and repetitions of mimicked sounds) have within a song bout. What is clear is that there are differences in how nonmimetic and mimetic motifs are used structurally in song, and these categories of motifs may therefore serve different functions.

The permissive learning hypothesis favored by some authors suggests that many mimicking species acquire imitations passively from the soundscape and treat them the same as species-specific sounds (Garamszegi et al. 2007). My findings contradict this hypothesis, as motifs including mimicry appear to have a different structural role than nonmimetic motifs. Why this is the case, and whether this is true of mimetic song components in other species, is unclear. Payne (1979) noted in passing that mimetic indigobird song units were longer and harder to distinguish than nonmimetic ones. However, very little is known about mimicry and song structure. My findings support the structural function hypothesis but there are many unanswered questions that will need to be addressed before we understand the importance of mimicry in starling song. Studying how differences in structural roles between mimetic and nonmimetic motifs affect starling reproductive success may help us understand how mimicry influences mate choice in other species.

### *Importance of Song Structure*

Studies of the song of other species support the idea that song structure serves an important function in conspecific communication. In house finches, song structure varied based upon the social function of a song bout, with bouts used in counter-singing encounters having the most variation and sequential branching (Ciaburri and Williams 2019). Palmero et al. (2012) found that although spectacled warbler song bouts vary in length, the balance of motif repetition and diversity was maintained. The existence of common structural patterns across species (e.g., repetition of each motif, nonrandom transitions, positioning of motifs) hints at the evolutionary origins of song structure in songbirds. In canaries, specific neurons hold information about previously sung phrases and transitions, allowing an individual to know which phrase to sing next (Cohen et al. 2019). Therefore, the ability of a male to sing a song with the correct structure may be correlated with normal brain development. In a different study, juvenile zebra finches with restricted diets did not learn song structure as well as properly nourished juveniles, although song complexity was not affected by treatment (Brumm et al. 2009). Finally, domesticated Bengalese finches sing nonlinear, clumped song sequences, while their wild ancestors sing linear, stereotyped songs (Okanoya 2004). Okanoya (2004) hypothesized that mutations selected against in the wild are expressed in captivity, allowing more complex song structure to develop. When combined, the findings from these three studies suggest that song structure conveys information to a listener about the singer's history and may serve an important function in mate choice.

Furthermore, studies of European starlings across continents also suggest the importance of song structure. American individuals had larger repertoires than European males (Hausberger 1997), and both American and European individuals mimic more than Australian males (Adret-Hausberger 1989). However, general structural rules of song appear to be conserved across continents. Although the song structure of European and Australian individuals needs to be studied in more detail, it appears that repertoire size may not be the most important measure of song diversity. Syntax and repertoire size may be regulated by different mechanisms and may give conspecifics different pieces of information. Although structure has only recently become a major focus in birdsong research, studies of structural variation have already enhanced our understanding of birdsong diversity.

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# CHAPTER IV: VOCAL MIMICRY, ACOUSTIC TRAITS, AND CONTRAST WITHIN SONG SEQUENCES

## Abstract

Various song characteristics are used by avian listeners to assess singer quality. One honest indicator of quality could be vocal mimicry. The acoustic function hypothesis suggests that mimetic sounds could be functioning acoustically in the songs of some mimicking species. I wanted to determine whether mimicry added acoustic diversity to song and whether positioning of mimicked sounds increased acoustic contrast in the songs of European starlings (*Sturnus vulgaris*). I quantified eight song metrics using the songs of 19 males and compared mimetic to nonmimetic motifs. Mimicry expanded the acoustic range of song in both frequency and amplitude. However, acoustic contrast between motifs within song sequences was lower for mimetic sections than for nonmimetic sections. Additionally, transition versatility within sequences was highest in sections without mimicry. These findings support the hypothesis that mimicry has acoustic function/s within starling song. Listeners could potentially use mimicry within song to assess singer quality. Additional study is required to determine whether mimicry has a similar function in the songs of other mimicking species. The acoustic structure of songs and the role of mimicry therein is a ripe avenue for understanding the relationship between song learning and mate choice.

## Introduction

In songbirds, song is thought to function in mate attraction, mate choice, and territorial defense (e.g. Kroodsma and Byers 1991). As such, variation in song and singing ability can allow females to compare males and demonstrate preferences. There is evidence suggesting that different song characteristics are important to the mating preferences of different species. For example, females of some species prefer greater song output and song rate (Nowicki and Searcy 2004). In this case, increasing song output and song rate is difficult and can therefore function as an honest indicator of singer quality (Nowicki and Searcy 2004). Male quality has also been found to be correlated with other characteristics, such as song duration, timing of singing, aesthetic quality of song, and extent of mimicry, in different species (Kroodsma and Byers 1991).

Mimicry – the imitation of heterospecific and environmental sounds – could signal quality in a variety of ways. For example, male satin bowerbird (*Ptilonorhynchus violaceus*) quality appears to be reflected in mimetic accuracy (Coleman et al. 2007), as it seems to be in song sparrows (*Melospiza melodia*, Beecher and Brenowitz 2005). This relationship corresponds with the learning and performance hypothesis, which suggests that an individual’s ability to learn or produce mimicked sounds is important in mate choice (Coleman et al. 2007, Dalziell et al. 2014). This hypothesis has received some support but is often overlooked in species-specific studies of mimicry, as mimetic accuracy is relatively difficult to quantify. Alternatively, mimicry could be used in a different way, such as to (1) introduce novel sounds to a repertoire, (2) expand the acoustic range of an individual’s song, or (3) create contrast in song. These potential functions fall under the acoustic function hypothesis, which has not often been considered in studies of mimicry in birdsong.

The incorporation of sounds that are unique or novel may give singers an advantage. “Sexy” or “special” syllables are unique sounds that are relatively difficult to produce and may therefore be favored by females (Vallet et al. 1998) and/or serve important social functions in song (Gil and Gahr 2002). For example, female canaries (*Serinus canaria*) prefer a song syllable with a lot of frequency modulation, which may demonstrate the function of a male's respiratory and motor control systems (Vallet et al. 1998, Vallet and Kreutzer 1995). The quality of the Snarr note of water pipits (*Anthus spinoletta*) indicates the dominance rank of males (Rehsteiner et al. 1998). Listeners could use the difficulty of producing song or specific song components to assess singer quality (Leitao et al. 2006). Female swamp sparrows (*Melospiza georgiana*) prefer songs as close to the population maximum performance thresholds of frequency range and trill rate as possible (Ballentine et al. 2004). In mimicking species, mimicry could either introduce potential "sexy" syllables or allow individuals to sing more impressive songs.

Similarly, mimicry may allow singers to expand the acoustic range of their songs. For example, mimicked sounds in Northern mockingbird (*Mimus polyglottos*) song extend song maximum frequency and therefore frequency bandwidth (Gammon and Lyon 2017). Extending acoustic features in this way may yield a more attractive song. Hermit thrushes (*Catharus guttatus*) use songs of high or low frequency at different times of day (Roach et al. 2012), suggesting that song frequency parameters transmit information about singer quality. However, little is known about this potential function, and further study is needed.

Finally, the presence of sufficient contrast in song may be important to listeners. Hartshorne (1956) postulated that singers must avoid reaching a monotony threshold in song to retain listener interest, and therefore should limit repetition and lack of versatility. While this anti-monotony hypothesis initially described song rate and diversity of song types, it may be expanded to an expectation that females prefer songs that are more heterogeneous and less repetitive, as is true for zebra finches (*Taenopygia guttata*, Neubauer 1999) and chaffinches (*Fringilla coelebs*, Leitao et al. 2006). That is, females should prefer songs that are more “interesting”. In species that sing songs composed of strings of song units, heterogeneity may vary based on what these song units are, and how they are strung together. In mimicking species, incorporating mimetic sounds may allow individuals to increase diversity or contrast within their songs. For example, by alternating between nonmimetic and mimetic sounds, an individual could draw a listener’s attention and/or demonstrate singing prowess.

As the metabolic cost of singing is not insignificant (Oberweger and Goller 2001), songs that are more demanding in any of these three ways – through the addition of novel sounds, increased acoustic range, or increased acoustic contrast – could potentially indicate male quality. As such, mimicry could possibly influence mate choice in songbird species. I wanted to determine whether mimicry plays an acoustic role in the songs of male European starlings. Several lines of evidence support this idea. Mimicked notes are not used to increase repertoire size (Chapter 2). Motifs incorporating mimicry were repeated more often than species-specific sounds, and mimicry was significantly associated with more stereotyped transitions, suggesting that mimicry serves a structural role in song (Chapter 3). Based on these findings, it appears that mimicry is used differently from species-specific sounds, and is not passively incorporated into song.

To determine whether mimicry serves an acoustic function in starling song, I asked two questions. First, are there quantitative differences between mimetic and nonmimetic motifs? I expected that mimetic motifs would extend the amplitude and frequency range of starling song. Second, if there are quantitative differences, do these differences create greater contrast in sequences? I hypothesized that transitions between mimetic and nonmimetic motifs would have greater contrast in acoustic features than transitions between either two mimetic or two nonmimetic motifs. In both cases, mimicry should increase the heterogeneity of a male's song.

## Methods

European starling warbling song is composed of *motifs*. Each motif can be thought of as analogous to words in human speech and is composed of a set of one to ten notes repeated as a discrete unit. Each male has a repertoire of species-specific and mimetic motifs that is distinct from that of other males. Song has a clear organizational structure of three sections containing different types of motifs: several introductory *whistle motifs* followed by a series of rambling, repeated, *variable motifs*, and concluding with a series of high-frequency, loud *terminal motifs* (e.g. Adret-Hausberger and Güttinger 1984, Eens et al. 1989, Gentner and Hulse 1998, Gentner and Hulse 2000). Starlings regularly incorporate mimicry in songs, and motifs with mimicked components comprise an average of 46% of the repertoire of unique motifs of an individual male (Chapter 2). Mimicked sounds can appear in any of the three motif sections; however, mimicry is overrepresented within the variable motif section of song (Chapter 2).

I used the same recordings and motif libraries as I did for Chapters 2 and 3 for each of the 19 males.

### *Motif quantitative trait differences*

I quantified eight acoustic traits for one exemplar of each motif, including minimum, maximum, and mean frequency, frequency range, mean and maximum amplitude, motif duration, and number of notes or components in each motif. The number of components in each motif were counted manually. Motif duration was found with manual selection of the motif in the analysis window of the program Praat (v. 6.0.23; Boersma and Weenink 2019). I filtered out as much background noise as possible for all motifs before measuring other acoustic features. Due to the complexity of starling motifs, the noise filter could not be stringently employed. I then used the 'show pitch' and 'show intensity' analysis tools in Praat to measure frequency and amplitude features of all motifs. To avoid measuring remaining background noise as much as possible, I often measured a motif using multiple steps. I did this by drawing analysis boxes around specific motif components, saving all the measurements within each box, and then pooled measurements across boxes to calculate means, minima, and maxima. Frequency range was calculated as the difference between maximum and minimum frequency of a motif.

To determine the uniformity of my quantitative measurements, I measured 10 replicates of a subset of 18 motifs. I then used the R package *rptR* (Stoffel et al. 2017; R Core Team 2019) to calculate repeatability, or intraclass correlation, of the eight song metrics for each motif (Table 4.1). Standard error was found using 1000 bootstrap iterations and zero permutations.

*Table 4.1. Repeatability of measurements of motif metrics across 10 replicates of 18 motifs +/- standard error. All repeatability scores had a p-value less than 0.0001.*

| | |
|---|---|
| mean frequency | 0.591 +/- 0.095 |
| min frequency | 0.374 +/- 0.095 |

| | |
|---|---|
| max frequency | 0.671 +/- 0.093 |
| frequency range | 0.635 +/- 0.096 |
| mean amplitude | 0.48 +/- 0.1 |
| max amplitude | 0.492 +/- 0.1 |
| duration | 0.741 +/- 0.074 |
| components | 0.659 +/- 0.087 |

Once all traits were measured, I ran a linear mixed model with male as random effect with the package *nlme* (Pinheiro et al. 2019) in R, followed by ANOVA, to compare nonmimetic and mimetic motifs in all three song sections. This allowed me to determine whether mimetic motifs differed quantitatively from nonmimetic motifs. Final sample sizes were 224 nonmimetic whistles, 118 mimetic whistles, 365 nonmimetic and 370 mimetic variable motifs, and 175 nonmimetic, and 82 mimetic, terminal motifs.

### *Contrast within variable motif sequences*

I only used the longest, middle section of song (the variable motifs) for contrast analysis. Both the whistle and terminal motif sections are characterized by high frequency whistles, and mimicry is mostly added to the end of these motifs, instead of embedded within them (Chapter 2). As such, I focused on the variable motif section.

Contrast within song sequences was measured in two ways. First, I calculated differences in all eight traits between adjacent motifs, such that I had four transition types: nonmimetic to nonmimetic, nonmimetic to mimetic, mimetic to nonmimetic, and mimetic to mimetic. In my analysis, I used the absolute value of all differences in statistical tests to focus on the size of contrast, while using the true values for comparisons of the distributions. For contrast in max and mean frequency, max and mean amplitude, duration, and number of components, my sample sizes were: 2816 nonmimetic – nonmimetic, 1704 nonmimetic – mimetic, 1909 mimetic – nonmimetic, and 2661 mimetic – mimetic. For contrast in minimum frequency and frequency range, the sample sizes were 2810, 1699, 1907 and 2662, respectively.

Second, I calculated a *transition versatility* score (adapted from Gil and Slater 2000) for each song bout. Transition versatility was the number of unique transitions divided by the total number of transitions, per bout. I excluded transitions between the same motif, such as motif A → motif A, from the numerator to keep scores between 0 and 1.0. I then compared transition versatility to the number of unique nonmimetic and mimetic motifs in each bout. In total, I had transition versatility scores from 1,069 song bouts.

I determined the difference in contrast for all eight traits using a linear mixed model in R with male as random effect, followed by ANOVA and Tukey-HSD posthoc tests. I also compared distributions of contrast between the four transition types using Anderson-Darling tests in the R package *kSamples* (Scholz and Zhu 2019).

Finally, I determined the relationships between transition versatility score and either nonmimetic or mimetic motifs by using two linear mixed-effects models with male as random effect. I used the two models to determine the effects of number of unique, and total number of, nonmimetic and mimetic motifs in bouts.

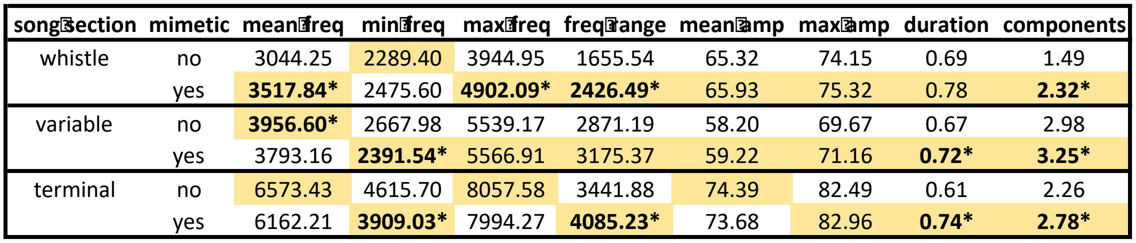
## Results

### *Motif quantitative trait differences*

There were significant differences in motif traits of mimetic and nonmimetic motifs in all song sections, although the specific patterns differed across song sections (Table 4.2). In the whistle section, mimetic motifs had significantly higher mean and maximum frequency, as well as frequency range (Figure 4.1). In contrast, in the variable motif section, mimetic motifs had significantly lower mean frequency and significantly lower minimum frequency. Mimicry in this section decreased the song frequency and increased motif duration. Mimetic terminal motifs, like variable motifs, had lower minimum frequency and longer duration. In this section, mimicry also increased the frequency range of motifs.

Mimetic motifs in all three sections were composed of significantly more components (notes).

*Table 4.2. Quantitative trait means for mimetic and nonmimetic motif categories in the three song sections. Bolded means are significantly different from the respective other mean in that category.*



| song section | mimetic | mean freq | min freq | max freq | freq range | mean amp | max amp | duration | components |
|---|---|---|---|---|---|---|---|---|---|
| whistle | no | 3044.25 | 2289.40 | 3944.95 | 1655.54 | 65.32 | 74.15 | 0.69 | 1.49 |
| | yes | **3517.84*** | 2475.60 | **4902.09*** | **2426.49*** | 65.93 | 75.32 | 0.78 | **2.32*** |
| variable | no | **3956.60*** | 2667.98 | 5539.17 | 2871.19 | 58.20 | 69.67 | 0.67 | 2.98 |
| | yes | 3793.16 | **2391.54*** | 5566.91 | 3175.37 | 59.22 | 71.16 | **0.72*** | **3.25*** |
| terminal | no | 6573.43 | 4615.70 | 8057.58 | 3441.88 | 74.39 | 82.49 | 0.61 | 2.26 |
| | yes | 6162.21 | **3909.03*** | 7994.27 | **4085.23*** | 73.68 | 82.96 | **0.74*** | **2.78*** |

*All significance at p < 0.01

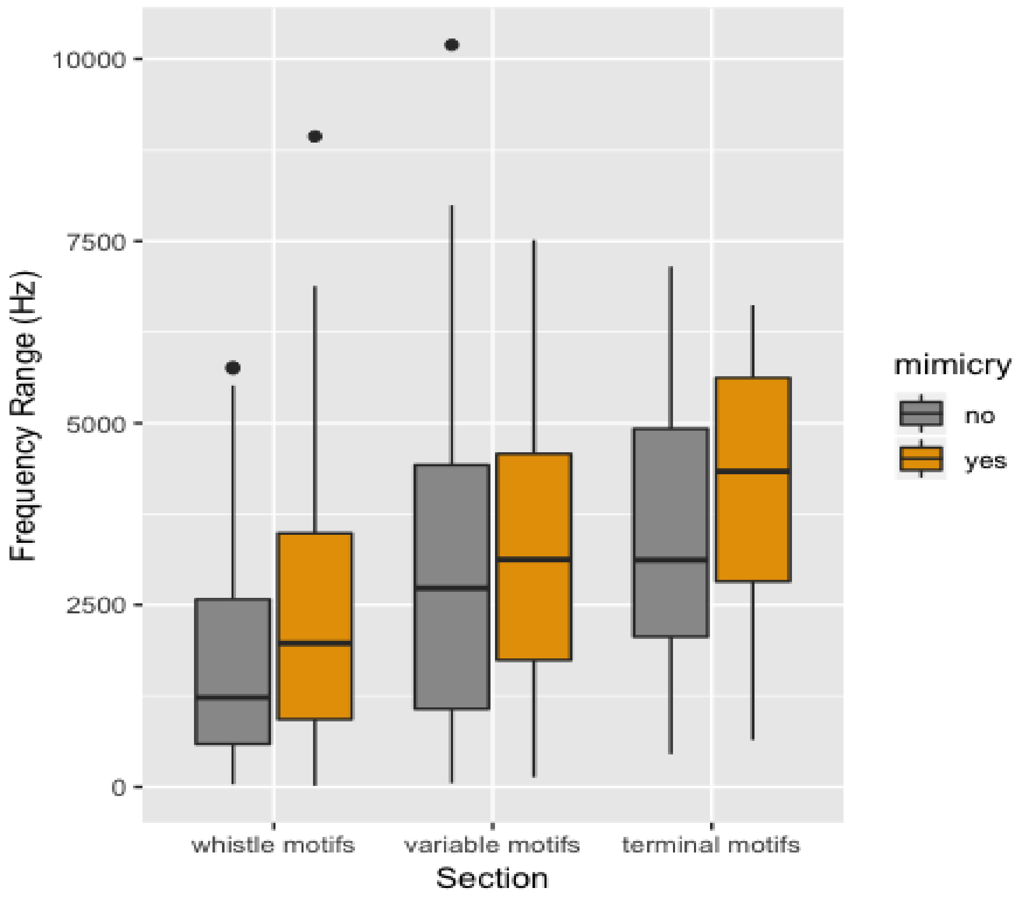
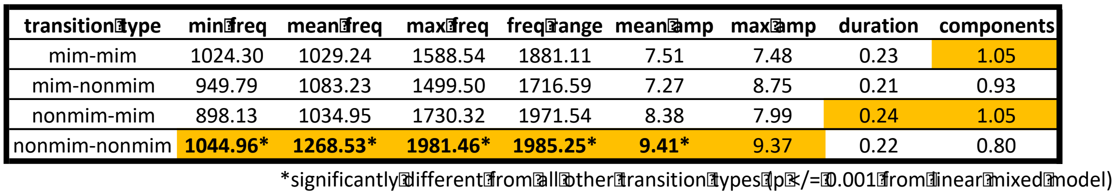


*Figure 4.1. Mean differences in frequency range of nonmimetic and mimetic motifs of the three song sections. Frequency range was significantly higher in mimetic motifs for whistle and terminal motifs.*

*Contrast within variable motif sequences*

The size of the difference in mean, minimum, and maximum frequency, frequency range, and mean amplitude was significantly highest in transitions between two nonmimetic motifs (Table 4.3, Figure 4.2).

*Table 4.3. Mean differences in the eight song metrics for the four transition types.*



| transition type | min freq | mean freq | max freq | freq range | mean amp | max amp | duration | components |
|---|---|---|---|---|---|---|---|---|
| mim-mim | 1024.30 | 1029.24 | 1588.54 | 1881.11 | 7.51 | 7.48 | 0.23 | 1.05 |
| mim-nonmim | 949.79 | 1083.23 | 1499.50 | 1716.59 | 7.27 | 8.75 | 0.21 | 0.93 |
| nonmim-mim | 898.13 | 1034.95 | 1730.32 | 1971.54 | 8.38 | 7.99 | 0.24 | 1.05 |
| nonmim-nonmim | **1044.96*** | **1268.53*** | **1981.46*** | **1985.25*** | **9.41*** | 9.37 | 0.22 | 0.80 |

*significantly different from all other transition types (p </= 0.001 from linear mixed model)

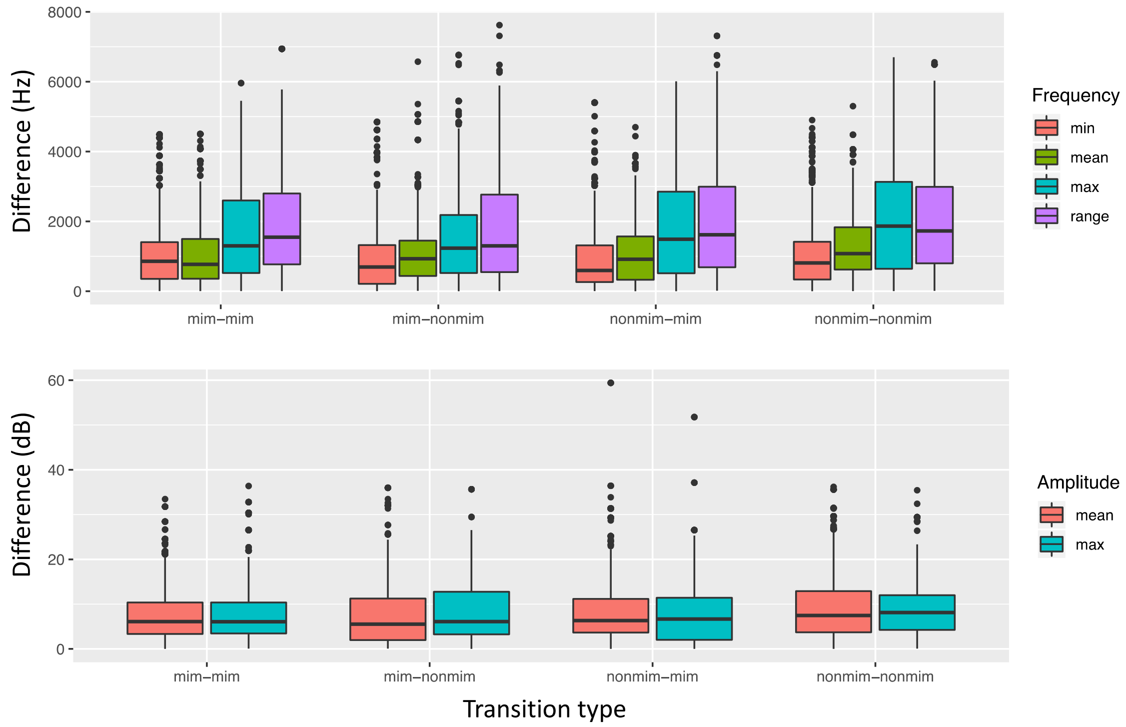


*Figure 4.2. Boxplots of the difference in frequency (A) or amplitude (B) metrics for the four transition types: nonmimetic to nonmimetic, nonmimetic to mimetic, mimetic to nonmimetic, and mimetic to mimetic.*

Transitions between two nonmimetic motifs and two mimetic motifs had significantly different levels of contrast in all quantitative traits except for duration. The two types of heterogeneous transitions (between nonmimetic and mimetic motifs) differed in contrast of maximum frequency, frequency range, mean amplitude, duration, and number of components. Mimetic to nonmimetic motif transitions had the lowest contrast scores for four of the eight motif traits.

The contrast distributions of the four transition types were significantly different for all eight traits (e.g. duration, with the largest p-value: F-value = 4.87, p = 0.002, through max frequency: F-value = 74.5, p < 0.0001; Figure 4.3). Transition types did not, therefore, only differ in the size of the difference in traits (absolute value) between adjacent motifs, but also in the direction of the difference (raw value). Transitions between mimetic motifs had less contrast than sequences of nonmimetic, species-specific motifs. The nonmimetic-nonmimetic difference distribution for maximum frequency (Figure 4.3A) had a trimodal shape.

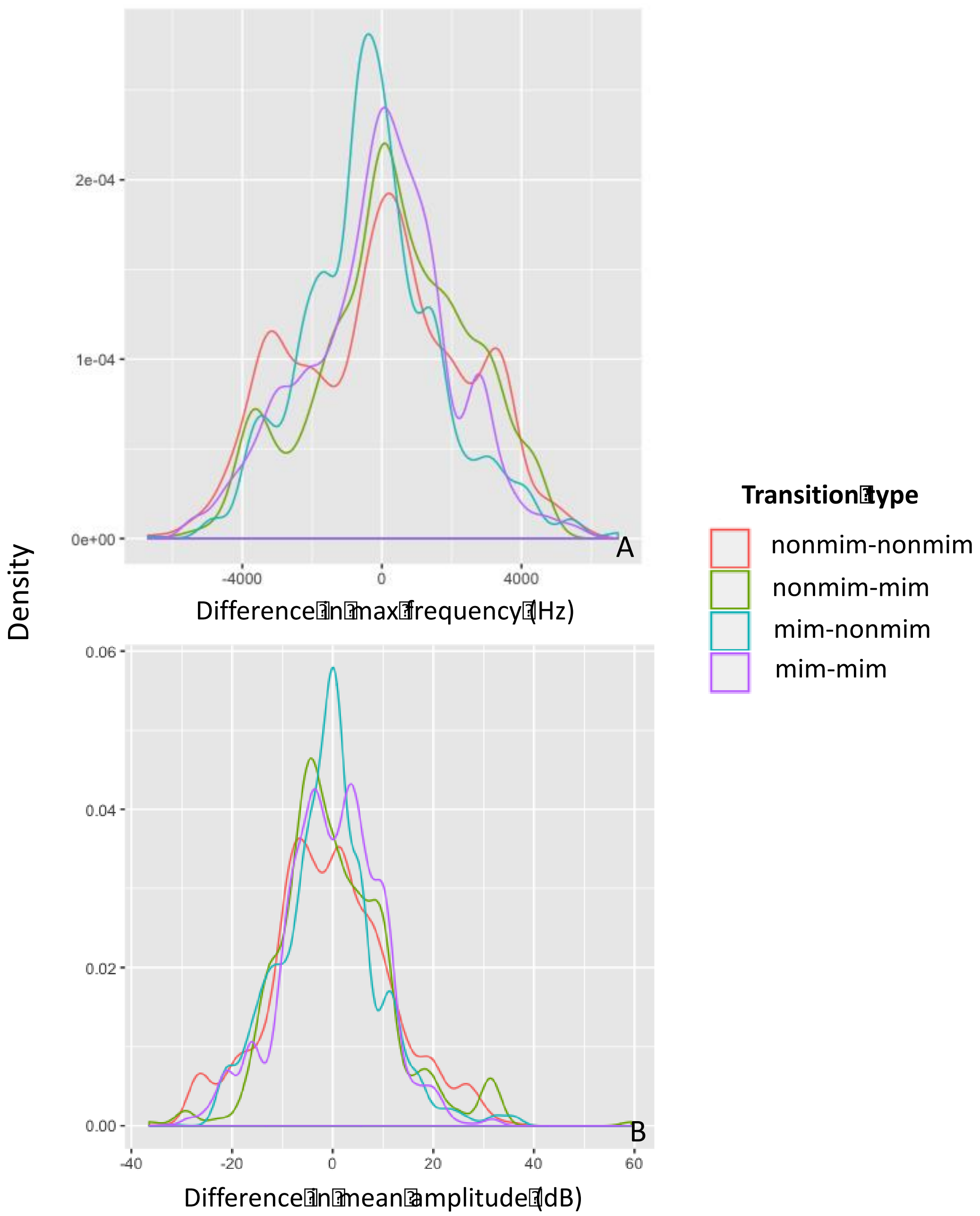


*Figure 4.3. Density distribution of the difference in max frequency (A) and mean amplitude (B) for the four transition types. Mimetic sequences have less contrast than nonmimetic ones.*

Contrary to our predictions, the transition versatility of song bouts was negatively related to the number of unique mimetic motifs in a bout (*lme*: t-value = -4.06, $p < 0.01$) but not to the number of unique nonmimetic motifs (*lme*: t-value = 1.06, $p = 0.29$). Thus, as the number of unique mimetic motifs increased, the transition versatility decreased for a song bout (Figure 4.4). There was also less variation in transition versatility at high numbers of unique mimetic motifs (Figure 4.4B) than for nonmimetic motifs (Figure 4.4A). Total number of nonmimetic or mimetic motifs (including repetitions of the same motif) had a significant negative effect on transition versatility (*lme*: nonmimetic – t-value = -6.16, p = 0; mimetic – t-value = -3.81, p <0.01).

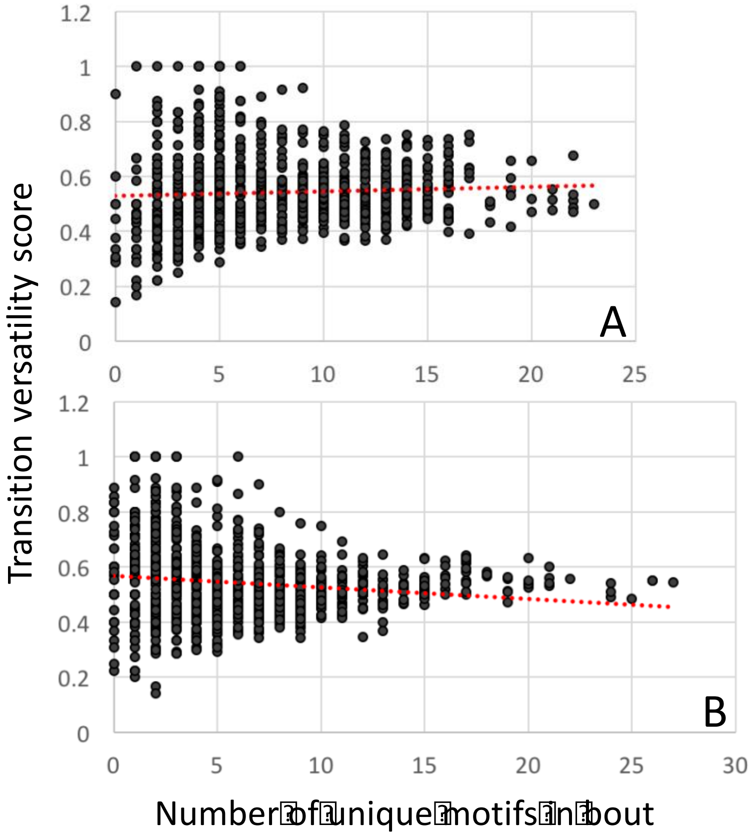


*Figure 4.4.* *Transition versatility scores for nonmimetic (A) and mimetic (B) motifs. There is less variation in transition versatility at high numbers of unique mimetic motifs than there is with many nonmimetic motifs. The trend in (B) is small but significant.*

## Discussion

The acoustic function hypothesis emphasizes ways in which singers could use mimicry to develop attractive song. Three proposed ways in which mimicry could function are by (1) introducing novel sounds to the song repertoire, (2) expanding acoustic range, and/or (3) adding contrast. Although no inferences can be made about novel sounds, mimicry did allow males to increase their acoustic range. Mimetic and nonmimetic motifs in European starling song are acoustically different. Some of the pattern is clear. Four traits (maximum amplitude, frequency range, duration, and number of components) are all extended by mimicry, in all three song sections. As mimicry often takes the form of imitated notes attached to the end of motifs (Chapter 2), it makes sense that duration and number of components increase with mimicry.

Variation in the other acoustic traits is less clear. Male starlings appear to also increase the loudness (amplitude) and vocal range (frequency range) of songs by incorporating mimicry. Mimicry in the variable and terminal motif sections lowered the minimum frequency and increased the maximum frequency of motifs. In the whistle section, mimicry instead led to greater mean frequency of song. Different acoustic features seem to be more important in different song sections, and mimicry may emphasize these differences. Furthermore, the fact that mimicry extends the acoustic range of song may yield additional advantages.

Females of many species focus on specific aspects of a male's singing behavior. In several studies, females have shown preferences for higher frequency (zebra finch, Ritschard et al. 2010; rock sparrow, *Petronia petronia*, Nemeth et al. 2012), amplitude (dusky warbler, *Phylloscopus fuscatus*, Forstmeier et al. 2002), and complexity (chaffinch, Leitao et al. 2006). Often, specific song characteristics may serve as honest signals of male quality. For example, stress early in life negatively affects song learning, as well as adult body size and immune function (Nowicki and Searcy 2004), which may be reflected in a less-developed song. It will take further study to determine whether mimetically-extended frequency bandwidth of song, such as was found in this study, and in Northern mockingbirds (Gammon and Lyon 2017), makes the singer more attractive to female listeners.

Our results present a puzzling pattern with respect to the role of mimicry in increasing acoustic contrast in songs. Mimetic motifs expanded the overall acoustic range of the songs; however, at the level of transitions between two consecutive motifs, sequences that contained mimetic motifs showed reduced acoustic contrast. Furthermore, as the number of unique mimetic motifs increased, song versatility decreased in a song bout. Mimetic motifs “fit into” a song (created less contrast) than did nonmimetic, species-specific motifs. Thus, while mimetic motifs can expand the overall spectral range of notes, starlings do not structure their song to use mimicry to emphasize contrast. Indeed, it appears that starlings are using mimicry to decrease contrast within song bouts, which indicates that contrast may be something males attempt to minimize. These findings correspond with previous results showing that mimetic motifs are not necessarily used at key points within the song structure of starlings – e.g., at points of convergence or divergence within song sequences – although they are repeated more often than nonmimetic motifs (Chapter 3). Female starlings prefer long song bouts (Gentner and Hulse 2000), which are more linear or stereotyped than shorter bouts (Chapter 3). As such, they may also prefer reduced contrast between neighboring motifs within bouts. Therefore, mimetic motifs affect the overall properties of a starling’s motif repertoire, but not the specific properties of a song sequence. This result suggests that the song learning template of starlings may be relatively rigid when it comes to structure.

Our study suggests that species-specific syntactical rules of complex songs may constrain how mimetic sounds can be used. While our interpretation of the anti-monotony hypothesis (Hartshorne 1956) suggests that songs that are more heterogeneous and "interesting" are preferable, song must still follow a set of species-specific guidelines. While preference shown by female Bengalese finches led to an increase in syntactical complexity of song, complexity was always bounded by what listeners perceived as song (Sasahara and Ikegami 2003). In swamp sparrows, females preferred regular syntax over innovative songs (Nowicki et al. 2001), and in many songbird clades, song diversity has decreased over time (Byers and Kroodsma 2009). Oropendola song versatility has remained relatively constant across evolutionary time, while peak frequency and frequency shift within songs have diverged across species (Price and Lanyon 2002). As there are constraints on song complexity, species-specific sounds may need to drive contrast within song bouts in European starlings, so that the song never becomes incomprehensible to listeners. Mimicry may then function within those bounds to increase the attractiveness of a singer.

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# CONCLUSION

Marshall (1950) declared that vocal mimicry must have a purpose. The research presented in this doctoral thesis investigates the function of vocal mimicry from a variety of perspectives and lends support to this statement. In Chapter I, I showed that vocal mimicry is found across the oscine songbird phylogeny and independently evolved numerous times. In Chapter II, I found that mimicry does not directly increase repertoire size in European starlings. Furthermore, Chapters III and IV demonstrated that mimicked motifs function differently from nonmimetic sounds, both structurally and acoustically, in song. My findings also lend credence to the conclusion by Catchpole and Slater (2008) that the permissive learning hypothesis is too simplistic and allows the premature dismissal of potential alternative hypotheses for the functions of mimicry.

A hindrance to understanding the evolution of vocal mimicry has been a narrow focus on its function for every species. My work details many possible dimensions of function of vocal mimicry (repertoire, syntax, acoustic properties, etc...) within one song type of one species. Instead of determining the specific function of mimicry by every mimetic species, we can use model systems such as starlings to pursue more detailed questions about mimicry and learning. For example, we could determine female starling responses to songs with different mimetic composition and measure reproductive fitness of the respective singers. We could also use starling mimicry to address important questions about learning in general. All birds hear many sounds and we have yet to understand (1) what sounds they end up incorporating into song, (2) how they do this, and (3) what or who they learn from. In other words, how do social interactions lead to the learning and retention of certain sounds over others? (Beecher and Burt 2004). West et al. (2003) accurately described starlings as “vocal mirrors” that reflect sounds heard around them. Social interaction is necessary for individuals to develop appropriate songs, as song use is a skill that changes based on listener feedback (West et al. 2003). For this reason, starlings are one system in which mimicry could be used to begin to untangle the interplay between sociality and learning.

Song learning has been central to the success and diversification of songbirds. Learning can allow greater precision and accuracy of the transmission of knowledge, lead to heightened complexity and variety, and allow easier transmission of information (Slater 1989). Learning is also closely tied to cognition (Whiten and van Schaik 2007) and song learning ability may potentially reflect other behaviors such as the foraging ability of an individual (Huber et al. 2001, Slagsvold and Wiebe 2011, Riebel et al. 2012). As such, studying song learning can yield important information about songbird diversity and evolution, as well as cognition and individuality.

This thesis emphasizes variation in the song of individuals. As in most aspects of biology, plasticity and variation shape the nature of song learning and mimicry (Mesoudi et al. 2016). Soha (2017) noted that there are multiple complementary ways in which song must be revised and shaped throughout the learning process. Additionally, multiple layers of learning are required (West et al. 2003). Individuals also vary in their tendency and ability to learn, as well as in their use of learning strategies (Mesoudi et al. 2016). As individuals’ past experiences, their condition, age, sex, and cultural background all shape learning (Mesoudi et al. 2016), studying individual differences will be key to discovering details about the song learning process.

West et al. (2003) asserted that (song) cultural evolution is a process that works on the individual rather than on isolated behaviors. A culture is a behavioral pattern shared by a group, which is reliant upon socially learned and transmitted information (Whiten and van Schaik 2007, Laland and Hoppitt 2003) as well as the persistence of that information (Boyd and Richerson 1996). Focusing on individual variation and experience instead of a single behavior is crucial to understanding how learning leads to the emergence of song culture (Whiten and van Schaik 2007). This is important because song learning is one of the few examples of cultural evolution in nonhuman animals (Boyd and Richerson 1996) and song culture can affect other aspects of biology integral to a bird's success (Aplin 2018). For example, vocal traditions influence mating preferences (Freeberg et al. 2001), group-level organization (Cantor et al. 2015), and may mirror genetic or social adaptation to local conditions (Slater 1989, Laland and Hoppitt 2003). While song changes over time, it is still unclear how this occurs (Slater 1989), and limitations of the flexibility of song learning are also not yet understood (Ellers and Slabbekoorn 2003). Studying mimicry could be one way to trace the transformation of song and to further our understanding of learning and its integral role in songbird evolution.

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# APPENDIX I. Glossary of important terms

| Term | Definition |
|---|---|
| Acoustic function hypothesis | Suggests that mimetic sounds could function acoustically in song. For example, mimicry could increase acoustic range or acoustic contrast in a song. |
| Core repertoire | The part of an individual's song repertoire that is sung most frequently. |
| Effective degree (weighted) | Measure of the stereotypy of the song sequences leading to and from a motif. Calculated as 1 / sum of edge weight proportions for a motif. High effective degree indicates low stereotypy (many paths leading to or from a motif), while low effective degree indicates one path is strongly favored. |
| Learning and performance hypothesis | An individual’s ability to learn or produce mimicked sounds is important to listeners. |
| Linearity | How well a song sequence follows one path. |
| Linearity index | The number of unique motifs in a bout divided by the number of unique transitions within that bout. The lower the linearity, the more syntactically complex (less stereotyped) the song. |
| Motif | Discrete unit of song composed of one to ten notes. Analogous to words in human speech. Generally repeated a specific number of times before song continues. |
| Note | A continuous sound that may or may not be combined with others to create motifs. |
| Permissive learning hypothesis | Increased song complexity requires a relaxed (permissive) song template that limits song structure and not content, allowing passive acquisition and inclusion of mimicked sounds. |
| Point of convergence | Position in a song sequence where multiple song paths come together; a bottleneck. |
| Point of divergence | Position in a song sequence where a linear song path diverges into multiple; a branching point. |
| Repertoire size | In starlings, the number of unique motifs in a male's vocabulary. This number changes for individuals from year to year. |

| | |
|---|---|
| Repertoire size hypothesis | Increased song complexity requires a relaxed (permissive) song template, which may allow passive acquisition of mimicked sounds. |
| Sexy syllable | A unique sound that is relatively difficult to produce, and is preferred by females and/or has a specific social function. |
| Song bout | One iteration of a male's song containing a subset of the motifs in his repertoire, and lasting about 30 - 60 seconds. |
| Song content | The makeup or composition of motifs - what types of notes compose a motif and what/how sounds are included. |
| Song structure | Arrangement of motifs and connections between them. Also referred to as syntax. |
| Stereotypy | The level of predictability of a song sequence; high stereotypy indicates high linearity - song almost always conforms to a specific path. |
| Structural function hypothesis | Suggests that mimetic sounds have a structural function in song different from that of species-specific sounds, such as by diversifying song structure or emphasizing specific components. |
| Transition hub | Point of convergence or divergence within a song sequence. |
| Transition versatility index | Number of unique transitions in a bout divided by the total number of transitions in that bout; as transition versatility increases, the song becomes more complex. |