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MACROECOLOGY AND MACROEVOLUTION OF BIRDSONG

Makroekologie a makroevoluce ptačího zpěvu

Dissertation thesis

Supervisor: prof. Tomáš Albrecht, Ph.D.

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A male village weaver *Ploceus cucullatus* represents oscine passerines. Members of this clade produce remarkably variable songs. Their songs are learnt and often used as sexual signals. Limbe, Cameroon, 2017. © Peter Mikula



Gray kingbird *Tyrannus dominicensis* is a representant of Suboscines, passerine clade with innate songs. Cabo Rojo, Puerto Rico, 2018. © Peter Mikula



Female of Southern fiscal *Lanius collaris*. Females of many (particularly) tropical passerine species, including fiscals, produce songs similarly as males do. Naivasha, Kenya, 2015. © Peter Mikula

PROHLÁŠENÍ

Prohlašuji, že jsem závěrečnou práci zpracoval samostatně a že jsem uvedl všechny použité informační zdroje a literaturu. Tato práce ani její významná část nebyla předložena k získání jiného nebo stejného akademického titulu.

DECLARATION

I declare that this thesis has not been submitted for the purpose of obtaining the same or any other academic degree earlier or at another institution. My involvement in the research presented in this thesis is expressed through the authorship order of included publications and manuscripts. All literature sources I used when writing this thesis have been properly cited.

Peter Mikula

Praha, Czech Republic, 30th June 2020

STATEMENT OF CONTRIBUTION

This thesis is the cumulative work consisting of the four contributions (two published papers, one submitted manuscript being under the review at the time of submission of this thesis and one unsubmitted manuscript). I am the first author in all contributions. Details on my contribution to the each of the chapters included in thesis are specified in detail below.

CHAPTER 1

Mikula, P., Valcu, P., Brumm, H., Blažková, B., Bulla, B., Dale, J., Forstmeier, W., Petrusková, T., Kempenaers, B. & Albrecht, T. Global variation in birdsong complexity is best explained by environmental variability. (*unsubmitted manuscript*)

Contribution of Peter Mikula: Conception, data collection, contribution to statistical analysis, interpretation of results and writing of manuscript.

prof. Tomáš Albrecht, Ph.D.

CHAPTER 2

Mikula, P., Petrusková, T. & Albrecht, T. 2018. Song complexity – no correlation between standard deviation of frequency and traditionally used song complexity metrics in passerines: A comment on Pearse et al. (2018). *Evolution* **72**: 2832–2835.

Contribution of Peter Mikula: Conception, data collection, statistical analysis, interpretation of results and writing of manuscript.

prof. Tomáš Albrecht, Ph.D.

CHAPTER 3

Mikula, P., Valcu, M., Brumm, H., Bulla, M., Forstmeier, W., Petrusková, T., Kempenaers, B. & Albrecht, T. A global analysis of song frequency in passerines provides no support for the acoustic adaptation hypothesis but suggests a role for sexual selection. (*under review*)

Contribution of Peter Mikula: Conception, data collection, interpretation of results and writing of manuscript.

prof. Tomáš Albrecht, Ph.D.

CHAPTER 4

Mikula, P., Tószögyová, A., Hořák, D., Petrusková, T., Storch, D. & Albrecht, T. 2020. Female solo song and duetting are associated with different levels of territoriality in songbirds. *Behavioural Ecology* **31**: 322–329.

Contribution of Peter Mikula: Conception, data collection, interpretation of results and writing of manuscript.

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ABSTRACT

Birdsong is one of the most astounding natural sounds which profoundly shaped our evolutionary thinking since the 19th century. Despite a strong interest in birdsong for over 100 years, our understanding of birdsong ecology and evolution over large spatial and phylogenetic scales is still very fragmentary. Answering many basic questions requires a global synthesis covering vast diversity of extant bird species and adoption of multidisciplinary approaches. In presented dissertation thesis, my co-workers and I have explored important patterns in macroecology and macroevolution of song in passerines (Order: Passeriformes), the most diverse and widespread bird order. We have focused on three key song phenomena: (1) song complexity, (2) song frequency and (3) the presence of song in female birds. We have exploited birdsong “big data” available on public citizen science databases and other open sources in order to fill several important gaps in the current knowledge. These data were analysed by a combination of phylogenetically-informed cross-species analyses and spatial macroecological approaches.

Since the publication of Darwin's seminal work, elaborated songs are generally agreed to be the result of sexual selection. We developed a simple but reliable song complexity metric to explore a global diversity in song complexity across 4,939 passerine species. Our analyses revealed that song complexity in Oscines, a clade with learned songs, and Suboscines with innate songs, is associated with several life-history, social and environmental indices of sexual selection in assemblage-based analyses. However, these effects largely disappeared when we accounted for spatially non-random distribution of passerine clades across assemblages or in a phylogenetic cross-species analyses. Song complexity in Oscines, but not Suboscines, positively correlated only with habitat generalism in cross-species models. We conclude that, at least in Oscines, song complexity might indeed be shaped by sexual selection, possibly via environmentally-driven processes, but large proportion of its variation remains unexplained (**Chapter 1**). We then explored associations between widely accepted and biologically relevant song complexity metrics, such as syllable repertoire size and the number of syllable types per song, and several novel metrics derived by machine learning techniques. Those novel metrics, if reliably capturing song complexity, could significantly increase the efficiency of comparative data collection on song complexity; unfortunately, we found no inter-correlation between these two types of metrics (**Chapter 2**).

Passerines use their songs mainly for long-distance communication with conspecifics. In the next step, we therefore explored global diversity in peak song frequency, a signal parameter that greatly affects song propagation, with the use of 5,085 passerine species. Body size is expected to constrain song frequency and frequency may also be sexually selected. Moreover, habitat density, through the habitat-specific patterns of signal degradation, have been proposed to explain the variation in song frequency. We found that song frequency was negatively associated with body mass and sexual size dichromatism, while habitat density had weakly positive or no effect on peak song frequency (**Chapter 3**).

Finally, we tested an effect of several social and environmental traits on the distribution of female song across 269 songbird species of South Africa and Lesotho. We found that, in species in which females produce solo songs, seasonal territoriality was predominant, whereas duetting species defended their territories mainly year-round. This indicates that female solo song and duetting could be distinct song categories associated with different levels of territoriality (**Chapter 4**).

ABSTRAKT

Ptačí zpěv je jedním z nejužasnějších zvuků v přírodě, který významným způsobem ovlivnil naše chápání procesu evoluce od jeho formulace v devatenáctém století. Přes intenzivní vědecký zájem za posledních více než 100 let je naše chápání ekologie a evoluce ptačího zpěvu na velkých prostorových a fylogenetických škálách značně neúplné. Odpověď na mnohé základné otázky by mohla přinést globální syntéza zahrnující velkou část světové diverzity ptáků a kombinující mezioborový přístup. V předložené disertační práci jsem proto spolu se svými spolupracovníky prozkoumal vzory v makroekologii a makroevoluci zpěvu pěvců (Řád: Passeriformes), které představují nejdiverzifikovanější a nejvíc rozšířený ptačí řád současnosti. Zvláštní pozornost jsme věnovali trojici klíčových zpěvných fenoménů: (1) komplexitě zpěvu, (2) výšce (frekvenci) zpěvu a (3) přítomnosti samičího zpěvu. Abychom vyplnili některé důležité mezery v našem současném poznání, využívali jsme v rámci řešení tohoto projektu "velká data" z volně dostupných databází založených na bázi občanské vědy a ostatních otevřených zdrojů. Tato data byla následně analyzována pomocí kombinace fylogenetických komparativních a prostorových makroekologických analýz.

Od publikace Darwinova průkopnického díla jsou komplexní zpěvy obecně považovány za výsledek sexuální selekce. Vytvořili jsme jednoduchou ale spolehlivou metriku zpěvné komplexity a použili ji k exploraci globální diverzity v komplexitě zpěvu napříč 4 939 druhy pěvců. Zjistili jsme, že komplexita zpěvu u skupiny zpěvných (Oscines), kteří se učí zpěvu, a křikavých (Suboscines) s vrozeným zpěvem byla asociovaná s několika life-history, sociálními a environmentálními indikátory pohlavního výběru v prostorových analýzách. Tyto efekty se ale většinou vytratily, když jsme vzali do úvahy prostorově nenáhodnou distribuci pěvčích linií a ve fylogenetických komparativních modelech, kde komplexita zpěvu u zpěvných ale ne u křikavých pozitivně korelovala jenom s mírou jejich habitatového generalizmu. To indikuje, že přinejmenším u zpěvných pěvců mohla být komplexita zpěvu skutečně formována pohlavním výběrem, možná prostřednictvím environmentálně poháněných procesů. Velká část její variability ale zůstává nevysvětlena (**Kapitola 1**). Následně jsme prozkoumali vztah mezi široce akceptovanými a biologicky relevantními metrikami zpěvné komplexity, jako velikostí slabikového repertoáru a počtem typů slabik na zpěv, a několika novými metrikami, které byly odvozeny pomocí technik strojového učení. Tyto nové metriky by mohly, pokud by spolehlivě zachycovaly zpěvnou komplexitu, významně zvýšit efektivitu sběru komparativních zpěvných dat. Zjistili jsme ovšem, že tradiční a nové metriky spolu vůbec nekorelují (**Kapitola 2**).

Pěvci používají zpěv hlavně k dálkové komunikaci s jedinci stejného druhu. V dalším kroku jsme proto prozkoumali globální diverzitu ve výšce zpěvu, faktoru významně ovlivňujícím kvalitu přenosu zpěvu, napříč 5 085 druhy pěvců. Velikost těla zřejmě představuje silné omezení ve vztahu k produkované výšce zpěvu a výška zpěvu by mohla také být pod sexuální selekcí. Navíc hustota habitatu byla dřívějšími studiemi navržena jako možné vysvětlení variace ve výšce zpěvu. Zjistili jsme, že výška zpěvu byla negativně asociovaná s velikostí těla a sexuálním dimorfizmem v tělesné velikosti, zatímco hustota habitatu měla slabě pozitivní anebo žádný efekt na výšku zpěvu (**Kapitola 3**).

Nakonec jsme otestovali vliv několika klíčových sociálních a environmentálních faktorů na distribuci samičího zpěvu napříč 269 druhy pěvců Jižní Afriky a Lesotha. Zjistili jsme, že druhy, kde samice zpívají samostatně, obhajují svoje teritoria jenom sezónně, zatímco duetující druhy obhajují teritoria celoročně. To indikuje, že samičí sólo zpěv a duety mohou být dvě odlišné zpěvné kategorie asociované s odlišnými druhy teritoriality (**Kapitola 4**).

Introduction

BIRDSONG, ITS COMPLEXITY AND SEXUAL SELECTION

“... some animals emit sound while others are mute, and some are endowed with voice: of these latter some have articulate speech, while others are inarticulate; some are given to continual chirping and twittering some are prone to silence; some are musical, and some unmusical; but all animals without exception exercise their power of singing or chattering chiefly in connexion with the intercourse of the sexes” Aristotle (4th Century BCE), translated by Thompson (1910).

The songs of birds are one of the most remarkable and beautiful sounds in the nature, fascinating human across cultures and continents (Tidemann & Gosler 2012). Birdsong has inspired generations of naturalists and artists including famous painters, writers, poets and music composers. Birdsong has become an important model trait for intraspecific and comparative studies of the animal behaviour, vocal learning and cognition in vertebrates (Darwin 1859, 1871, Price 1998, Baker 2001, Slabbekoorn & Smith 2002a, Beecher & Brenowitz 2005, Catchpole & Slater 2008, Mason *et al.* 2017). Songs of particularly one avian clade, passerines (Order: Passeriformes), have received a vast amount of attention from researchers because their songs are extraordinarily diverse in shape, form and function (Catchpole & Slater 2008).

Since Darwin's formulation of the mechanism of sexual selection, passerine song became one of the most fundamental traits in the research of animal sexual signalization (Darwin 1871, West-Eberhard 1983, Price 1998, Catchpole & Slater 2008). Song is an important trait involved in the establishment and maintenance of pre-mating reproductive barriers in birds (Price 1998). Song facilitates species recognition, and evolutionary divergences in song may lead to reproductive isolation in bird populations and subsequently to speciation (Price 1998, Irwin *et al.* 2001, Seddon 2005, Mason *et al.* 2017). Birdsong is involved in several aspects of bird behaviour but it has two key functions: *mate attraction* and *territory defence* mainly against same-sex intruders (Kroodsma & Byers 1991, Nowicki & Searcy 2004, Catchpole & Slater 2008).

The substantial body of research focused on the song complexity of passerines which has diversified astonishingly over the course of evolution, ranging from very simple call-like

songs in many Suboscines (Tyranni) to extremely large repertoires of thousands of different syllables in some Oscines (Passeri, songbirds) (Beecher & Brenowitz 2005, Snyder & Creanza 2019). In general, complex songs are thought to be costly to develop and maintain and, hence, could serve as honest indicators of male quality; indeed, males of several species with exaggerated repertoires are more successful at mate attraction and territorial defence than males with simpler songs (Searcy & Andersson 1986, Catchpole 1987, Gil & Gahr 2002, Nowicki & Searcy 2004). Hence, sexual selection, through female choice and male–male competition, is widely accepted to be a major evolutionary driver of elaborated acoustic ornaments in male passerines (Searcy & Andersson 1986, Catchpole 1987, Gil & Gahr 2002, Nowicki & Searcy 2004).

Comparative research largely seeks to find drivers that lead to the remarkable diversity in song complexity of passerines throughout the world. Comparison across species is an important issue if we want to understand processes driving above species-level variation in song complexity. Most of the comparative studies on the association between song complexity and sexual selection to date have used various indices indirectly related to the strength of sexual selection, such as sexual size dimorphism (Mahler & Gil 2009, Medina & Francis 2012), mating systems (Shutler & Weatherhead 1990, Read & Weary 1992, Snyder & Creanza 2019) and plumage dichromatism (Shutler & Weatherhead 1990, Cooney *et al.* 2018). Other studies used factors associated with environmental variability, such latitude, environmental seasonality and predictability (Botero *et al.* 2009, Medina & Francis 2012, Cooney *et al.* 2018), ecological generalism (Tobias & Seddon 2009, Gomes *et al.* 2017), or migration (Botero *et al.* 2009, Mahler & Gil 2009, Medina & Francis 2012, Byers 2015).

However, the studies conducted so far have yielded mixed results, and our understanding of the role of sexual selection in the evolution of song complexity over broader taxonomic and spatial scales remains incomplete. The heterogeneity of results is probably attributed to the approach widely adopted in avian bioacoustics, focusing mostly on single genus or family or small subsets of global avifauna, testing the effect of only single or few particular factors on song complexity, as well as the absence of a unified definition of “song complexity”. In an attempt to resolve these issues, in **Chapter 1**, we have quantified song complexity in 4,939 passerine species using a single metric and related it to the collated information on key life-history and environmental factors.

WHAT IS A SONG COMPLEXITY? ARE DIFFERENT METRICS CONCORDANT?

“Why certain bright colours and certain sounds should excite pleasure, when in harmony, cannot, I presume, be explained any more than why certain flavours and scents are agreeable; but assuredly the same colours and the same sounds are admired by us and by many of the lower animals” (Darwin 1871).

What is generally meant by the term “complexity” of the song? Marked variation in songs across passerines makes a single definition challenging because the complexity of songs can be described in multiple ways (Nowicki & Searcy 2004, Benedict & Najar 2019, Najar & Benedict 2019). The complexity of birdsong has been characterized by a myriad of metrics including between- and within-song diversity in unique elements and syllables, their duration, the tempo of production, frequency parameters, as well as other structural components of song (reviewed in Najar & Benedict 2019). The lack of unified definition is linked to the history of research in this field. Different researchers have focused on different species and groups of birds, which often exhibit considerable variation in song structure and complexity; as such, various metrics have been described in an *ad hoc* manner for specific groups. Importantly, not all metrics are well-suited for large-scale comparisons across species because their application across phylogenetically distant species is problematic.

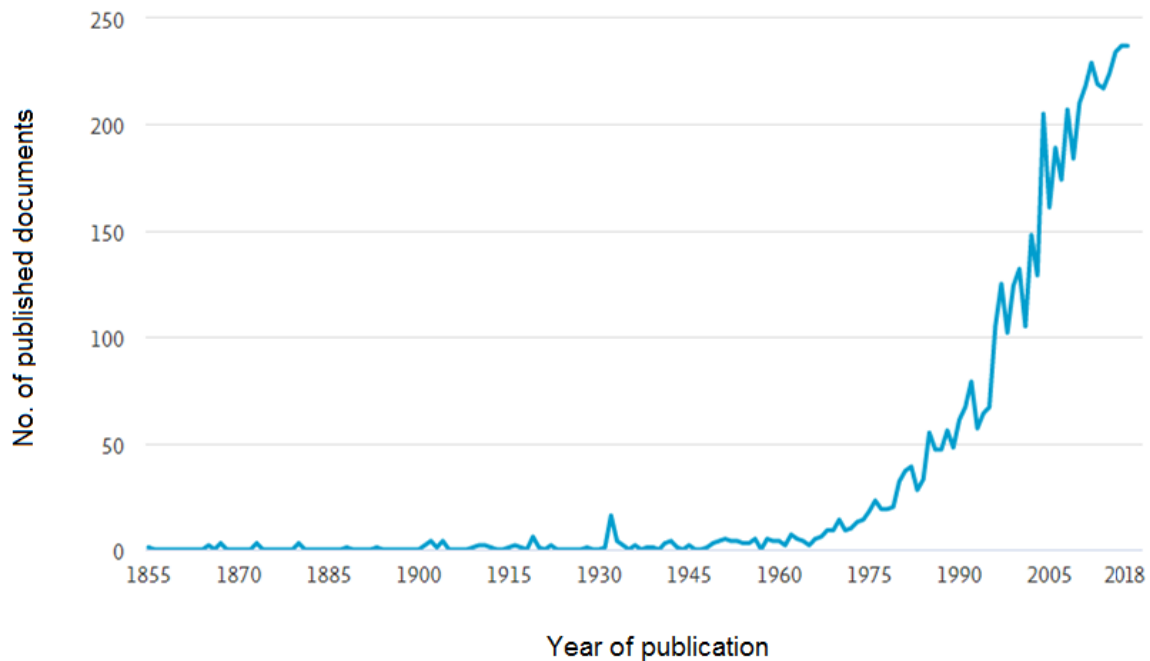
Despite large inconsistencies in song complexity definitions, it is generally agreed that between- and within-song variability in unique elements and syllables capture robustly vocal complexity of emitter. These metrics seem to have good biological relevance and link to sexual selection because, for instance, females of many songbird species have been reported to choose mates based on them (Nowicki & Searcy 2004, Mennill *et al.* 2006, Hill *et al.* 2017). Hence, these complexity measurements and their derivations represent a benchmark and fundamental metrics for comparative research (Nowicki & Searcy 2004, Botero *et al.* 2009, Soma & Garamszegi 2011, Weir & Wheatcroft 2011, Medina & Francis 2012, Najar & Benedict 2019, Snyder & Creanza 2019).

When comparing results of previous studies, we implicitly assume that various measures commonly referred to as “complexity” of song are mutually comparable and

concordant, i.e. have similar functions, evolved under similar modes of evolution, are mutually interchangeable or are at least correlated. Although the validity of this assumption is crucial for comparative research, it was almost never explicitly and empirically tested. To date, only a few, mainly intraspecific, studies have addressed this issue; their results often conclude that the tendency to equate multiple signal components together as complexity is inappropriate and misleading (Botero & Vehrencamp 2007, Cardoso & Mota 2007, Najar & Benedict 2019). For instance, Benedict & Najar (2019) estimated seven regularly used song complexity metrics in a song of the rock wren *Salpinctes obsoletus* and found that almost all of them were mutually not inter-correlated. Likewise, comparative studies, which defined a song complexity by metrics derived from a number of unique syllables found that song complexity is high in temperate zones and decreases toward the equator (Botero *et al.* 2009, Medina & Francis 2012) whereas the reverse pattern was found when frequency-derived metrics were used (Pearse *et al.* 2018). Altogether, the lack of basic knowledge on the mutual relationship between various song complexity metrics used in existing studies impedes their direct comparison and produces contradictory and controversial outcomes; these discrepancies can be overcome only by a thorough comparison of song complexity across multiple dimensions.

Nowadays, animal vocalization attracts large attention in ecological and evolutionary research. Interest in birdsong has undergone an explosion in popularity during the past five decades and papers, books and conference contributions on avian song are generated at unprecedentedly exponential rates (*Fig. 1*). Rapid growth in the amount of knowledge on this topic was precipitated mostly by the development of technological innovations (e.g. upgrade and increased availability of recording devices), and analytical (e.g. sound processing software capable to transform recorded vocalizations into the visible spectrogram-derived tracks) and statistical methods enabling effective analysis of song parameters. The field of avian bioacoustics has also been revolutionized by public access to the internet, which enables virtually instantaneous online sharing of sound recordings of birds and other animals. This has created a solid foundation for large-scale citizen science projects, including web-based biological collections, such as xeno-canto (<https://www.xeno-canto.org/>) and Macaulay Library (<https://www.macaulaylibrary.org/>), where members of the scientific community, as well as enthusiasts from general public, can deposit their acoustic recordings.

Figure 1. The number of scientific documents related to birdsong in Scopus database (<https://www.scopus.com>). Altogether, 5,267 published documents have been published on this topic between 1855 to 2018. The terms (“birds” OR “bird”) AND “song”) were used in the searching formula, the search was restricted to title, abstract and keywords. Date of search: 23 June 2019.



A steep rise in published research has significantly widened our knowledge and opened new horizons for future research, but also brought new challenges. Studies on macroecology and macroevolution of any biological trait largely rely on quantification of its structure and comparison across different contexts. Therefore, progress in large-scale comparative research is tightly linked to the development of tools that enable us to effectively and meaningfully capture variation in the target trait. A large-scale analysis of passerine song relies on metrics that can be easily and effectively quantified and compared across distant lineages that markedly differ in the structure and complexity of their vocal displays. Therefore, the importance of exploring new possibilities of cost-effective data collection is growing particularly now, during the “big data” era, where scientists are overwhelmed by the volume of available data. This prompted a rapid development of systems using artificial intelligence (artificial neural networks and machine learning techniques) which have undoubtedly a great potential to significantly improve the range, accuracy and effectiveness of data collection, and hence are prospective for a massive involvement in the study of animal bioacoustics or behaviour in general (Cheng *et al.* 2012, Lasseck 2014, Tachibana *et al.*

2014). Unfortunately, yet, only a few works have already attempted to use automatically derived metrics to characterize song complexity over large scales (e.g. Pearse *et al.* 2018).

The use of automated approaches in biological research is at the beginning, being prone to mistakes and practical pitfalls (Kampichler *et al.* 2010, Valletta *et al.* 2017). An effective grouping of song elements and syllables based on their similarity by automated detection algorithms is currently still difficult, hence, researchers utilizing automated approaches tend to use more simplistic metrics, such as complexity derived from frequency oscillations in song of species (Pearse *et al.* 2018). These novel automatically derived metrics, if reliably capturing song complexity across species, would significantly facilitate interspecific quantification of birdsong elaboration. However, it is essential to place them into the context of the rich history of previous research on song complexity. In **Chapter 2**, we therefore assessed whether correlations exist between traditionally-used song complexity metrics based on between- and within-song diversity of unique syllables and several novel frequency-derived metrics.

FACTORS AFFECTING THE EVOLUTION OF SONG FREQUENCY

“[The song frequency of] ...the Horned Owl is about the center of the baritone range, and the Catbird's mew falls just above the contralto's high and about the middle of the soprano's range. The call of the Veery, and the bell-like songs of the Thrushes are all above the human register; in fact they are pitched about the high of the violin” (Brand 1935).

Animals use acoustic signalization primarily for a long-distance communication between conspecifics (Bradbury & Vehrencamp 1998). Therefore, it is crucial for a producer to transmit information accurately to the receiver over long distances. Song is an important acoustic signal for communication over long distances in passerines (Catchpole & Slater 2008). A song faces many distortions during its propagation through the natural environments, including absorption, reverberation, scattering and boundary interference; the effectiveness of its propagation is affected mainly by the structure of the signal and acoustic properties of the environment (Morton 1975, Wiley & Richards 1982, Brown & Handford 1996, Slabbekoorn & Smith 2002b, Padgham 2004).

The frequency is a fundamental characteristic of a song, which, despite its extraordinary diversity, has historically received much less attention than song complexity. For instance, at the end of 19th century, Charles A. Witchell, in one of the first books ever to focus exclusively on the interspecific variation and evolution of birdsong, stated that, *“In making my records I have paid no attention to actual pitch I believe that this has no scientific value”* (Witchell 1896). It is only since the second half of 1970s that ecologists and evolutionary biologists more intensively started to explore mechanisms generating the diversity of song frequency across different taxa, including birds. The study of acoustic frequency was popularized by Eugene S. Morton who identified the association between acoustic properties of habitat and the physical structure of avian vocalizations, a concept later known as *Acoustic Adaptation Hypothesis* (AAH) (Morton 1975). This hypothesis proposes that direct habitat-dependent selection on birds, in order to enhance transmission of acoustic signals and minimize their degradation, has shaped the evolution of song characteristics. In general, songs of low-frequency transmit further than high-frequency ones and high frequencies are attenuated more strongly in densely vegetated habitats (e.g. forest) than in open habitats (e.g. steppes) (Morton 1975, Marten & Marler 1977, Wiley & Richards 1978).

Based on these rules, it has been predicted that birds producing songs with low-frequency, narrow-frequency ranges, and low-frequency modulations should prevail in habitats with dense vegetation, whereas birds with high-frequency songs, broad-frequency range, and high-frequency modulations should be found in open areas (Morton 1975). Although the effect of properties of the environment on song propagation has been supported by experimental evidence, the validity and generality of predictions by the AAH remain unclear for wild-living animals in their natural environment (Morton 1975, Badyaev & Leaf 1997, Buskirk 1997, Bertelli & Tubaro 2002, Blumstein & Turner 2005, Boncoraglio & Saino 2007, Snell-Rood & Badyaev 2008, Ey & Fischer 2009). For instance, a meta-analysis by Boncoraglio & Saino (2007) found that although song frequencies were significantly lower in closed compared with open habitats, the size of the effect of habitat was generally small. Likewise, Ey & Fischer (2009) reviewed available evidence for the AAH for birds, anurans, and mammals, and revealed that empirical support for environment-related adjustments in the structure of vocalizations is not as widespread as previously thought.

In addition to habitat type, the effect of body size seems to be of particular importance. Larger birds generally produce lower-frequency songs than smaller sized species, indicating that body size may act as an important morphological and physiological constraint influencing song frequency phenotype (Ryan & Brenowitz 1985, Wiley 1991, Tubaro & Mahler 1998, Bertelli & Tubaro 2002, Snell-Rood & Badyaev 2008, Gillooly & Ophir 2010, Gonzalez-Voyer *et al.* 2013, Tietze *et al.* 2015). The allometry between song frequency and body size is probably mediated through an association between body size and other anatomical factors, including the size of vocal apparatus and its compartments (such as syrinx), which constraint production of low-frequency signals in small birds (Gillooly & Ophir 2010, Riede & Goller 2014). Body size is one of the most important organismal traits, interacting with a plethora of morphological, physiological, and ecological traits (Calder 1984, Jennings & Mackinson 2003, Woodward *et al.* 2005, Ricklefs 2010). Hence, cross-habitat variation in song frequency may be strongly confounded by variation in body size.

Relatively little is known about the role of song frequency in the context of sexual selection over large-scales. Male song of passerines is commonly used as a sexual signal (Searcy & Andersson 1986, Catchpole 1996, Gil & Gahr 2002, Nowicki & Searcy 2004) in which honesty is presumably maintained by various constraints that ensures the information advertising an individual's quality cannot be faked (Gil & Gahr 2002). Therefore, if a body mass acts as a strong constraint on the production of low-frequency songs, then low song

frequency may act as an indicator of individual quality and be the subject of sexual selection (Hall *et al.* 2013, Geberzahn & Aubin 2014). On interspecific scale, this may lead to the correlated evolution between song frequency and indices of sexual selection such as sexual dimorphism in body size. However, this topic remains largely unexplored.

Previous studies addressing these questions were restricted to very small subsets of extant passerine diversity, leaving most of the global diversity in song frequency unexplained. Therefore, in **Chapter 3**, we aimed to identify the ecological and evolutionary underpinnings of the observed patterns in song frequency across 5,085 passerine species.

FEMALES SING IT TOO!

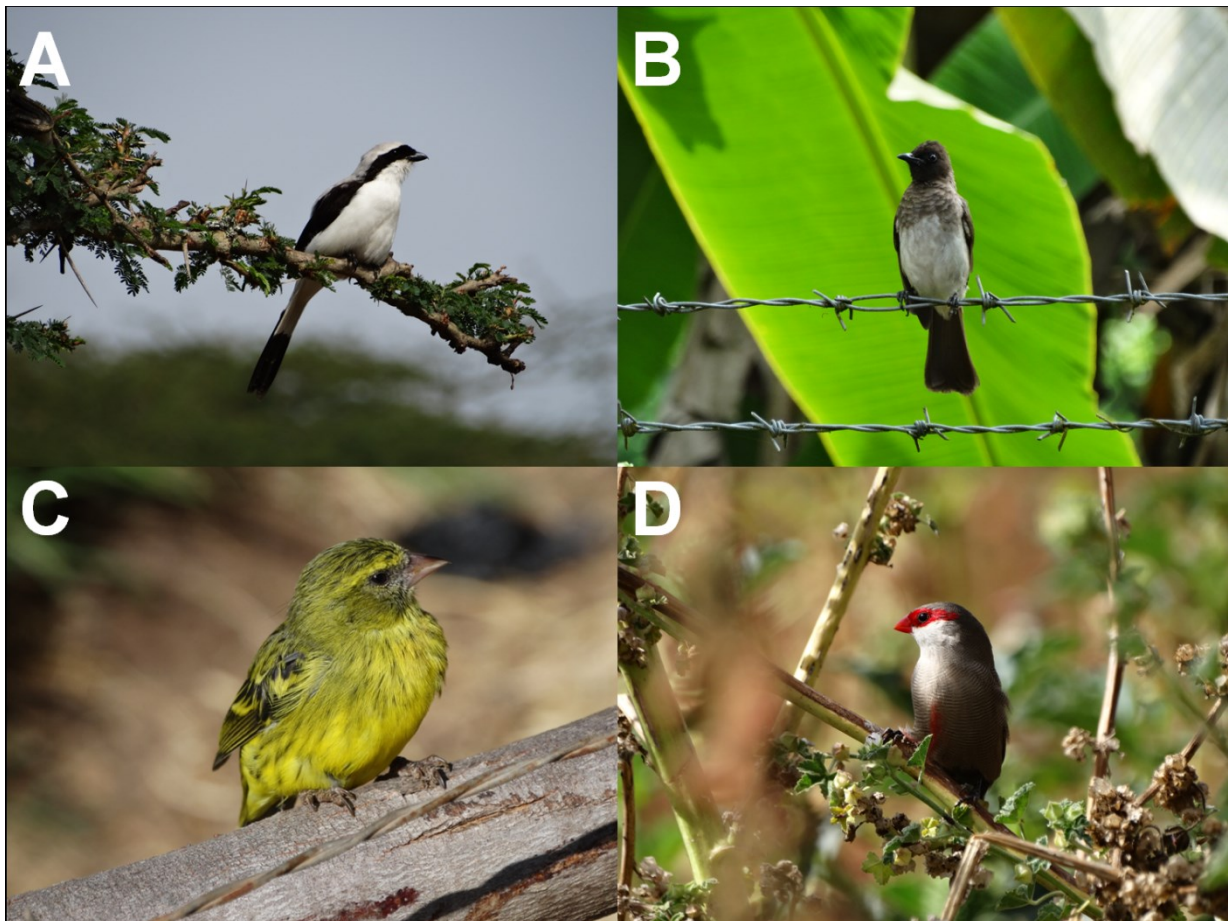
“There are... exceptional cases in which the males, instead of having been selected, have been the selectors. We recognise such cases by the females having been rendered more highly ornamented than the males...” (Darwin 1871).

Extravagant ornaments, including complex songs in passerines, have long been attributed almost exclusively to males (Darwin 1871, Searcy & Andersson 1986, Catchpole 1987). Darwin himself felt that the contribution of females to sexual selection was restricted mostly to the judgement of male qualities by stating *“I can see no good reason to doubt that female birds, by selecting, during thousands of generations, the most melodious or beautiful males, according to their standard of beauty, might produce a marked effect”* (Darwin 1859). The traditional view of female song as evolutionary obscurity stems from a strong geographic bias toward northern temperate regions where female song is rarer than in tropical regions (Garamszegi *et al.* 2007, Price 2009, Tobias *et al.* 2016). However, recent studies have documented that female song is phylogenetically widespread and likely was present in the ancestors of modern songbirds (Odom *et al.* 2014, Tobias *et al.* 2016, Webb *et al.* 2016). Moreover, there is increasing empirical evidence that sexual dimorphism in song ornaments is often a result of repeated secondary losses in females rather than gains in males (Price 2015, 2019). Although interest in female ornaments has long been marginalised, new evidence indicates that we need to re-evaluate our long-standing assumptions on female song evolution and to look at it through the lens of sexual selection.

Despite the fact that female song is more widespread than previously thought, its distribution is geographically and taxonomically clustered. This indicates that there could be some selection pressures favouring the evolution of song in female birds. Females sing more often in tropical than temperate regions and, thus, female song may be associated with tropical environmental conditions as well as life-history, social and environmental traits (Garamszegi *et al.* 2007, Price 2009, Odom *et al.* 2015, Tobias *et al.* 2016). Tropical regions are generally more productive and less seasonal than temperate regions (Ji *et al.* 2017), promoting the evolution of slow pace-of-life syndromes in tropical birds (Wiersma *et al.* 2007, Londoño *et al.* 2015). Indeed, female song has been found to be associated with traits, such as year-round territoriality, long-term social bonds, social monogamy, cooperative

breeding, and absence of migration (Odom *et al.* 2015, Tobias *et al.* 2016). Tropical birds have to deal with increased competition for mates and resources, which may represent strong selection forces for the evolution of signals enhancing the defence of territories and partners in both sexes (Tobias *et al.* 2016). However, females of many tropical birds are silent (Fig. 2), and a closer look at the distribution of female song within tropical regions could bring new insights into what drives sexual dimorphism in song presence across birds.

Figure 2. Examples of tropical passerine species where females produce songs (A, B) and species with non-singing females (C, D). (A) Gray-backed fiscal *Lanius excubitoroides*, (B) common bulbul *Pycnonotus barbatus*, (C) African citril *Crithagra citrinelloides*, (D) common waxbill *Estrilda astrild*. Credits: Peter Mikula.



Deriving from available evidence, females presumably use song in similar contexts as males, acting either as an ornament, i.e. as an attractant to the opposite sex, or armament, i.e. weapon against intrasexual competitors (Langmore 1998, Amundsen 2000, Hall 2004).

Female birds produce song either in solo (i.e. independent of male) or in duets with a mating partner, and these performances differ in multiple aspects (Odom *et al.* 2015, Tobias *et al.* 2016). Therefore, female solo song and duetting might evolve under different selection pressures. However, comparative tests for the importance of various life-history, social and environmental of the two vocal performances, with respect to each other, are still missing. In **Chapter 4**, we addressed this knowledge gap by exploring interspecific variability in female solo song and duetting in association to social and environmental predictors across 269 species of songbirds occurring in subtropical to tropical region of South Africa and Lesotho.

OUTLINE OF THE THESIS

In this dissertation thesis, my collaborators and I have aimed to explore macroecological and macroevolutionary patterns of avian song and its association with key life-history, behavioural, and environmental variables. We focused on passerine birds (Order: Passeriformes), which with ~6,000 extant species (60% of extant avian diversity) and global distribution, are the most diverse and widespread extant bird order (Jetz *et al.* 2012). Passerines represent a compelling study system because the evolution of their songs, and other traits, have diverged to an extraordinary diversity (del Hoyo *et al.* 2003, Catchpole & Slater 2008). We have primarily focused on the song of males, which is the sex that usually sings (**Chapters 1–3**), but last chapter of the thesis is focused on female song (**Chapter 4**).

In **Chapter 1**, we have developed a simple but reliable song complexity metric that was applied to a sample of 4,939 passerine species. We tested whether elaborated male songs could be the result of sexual selection. We found that complex songs both in Oscines, a clade with learned songs, and Suboscines with innate songs, were associated with several of several widely used life-history, social and environmental indices of the strength of sexual selection in assemblage analyses. However, these effects disappeared when accounting for spatially non-random distribution of passerine lineages across assemblages. In a phylogenetically informed cross-species analyses, we found that song complexity in Oscines, but not Suboscines, was positively correlated only with habitat generalism. We conclude that sexual selection, at least in Oscines, may be involved in song complexity evolution, but a large proportion of its variation remains unexplained.

In **Chapter 2**, we investigated associations between two traditionally used song complexity metrics, namely, syllable repertoire size and the number of syllable types per song, and several novel frequency-based metrics derived by machine learning. We found that traditional and these novel metrics are not correlated. This calls for a more integrative approach when studying song complexity, and the development of simple, but robust, metrics capturing reliably variation in birdsong across highly variable lineages of passerines.

In **Chapter 3**, we explored global diversity in peak song frequency, using a sample of 5,085 passerine species. We found that peak song frequency exhibited extraordinarily high variation, ranging from 215 to 10,659 Hz. We used cross-species approach to test the three most profiling hypotheses (morphological constraints, sexual selection and acoustic

adaptation hypothesis) and showed that taxonomic heterogeneity in peak song frequency was best explained by body mass of species. We also found that a part of the variation in peak song frequency was associated with sexual size dimorphism, hence, sexual selection could underlie peak song frequency evolution. In contrast to predictions of acoustic adaptation hypothesis, we revealed weakly positive or no effect of habitat density on peak song frequency. Altogether, our results indicate that morphological constraints and sexual selection, rather than habitat density, explain diversity in peak song frequency across passerines.

In **Chapter 4**, using a sample of 269 songbird species of South Africa and Lesotho, we tried to disentangle the direction and magnitude of effects of social traits (territoriality, social bonds, cooperative breeding) and environmental productivity on the occurrence of female solo song and duetting in local passerines. We found that species where females produce solo songs defend their territories for shorter periods (exhibited mainly seasonal territoriality) than females in duetting species (exhibited mainly year-round territoriality). Our results suggest that the two song performances could represent distinct female song categories associated with specific levels of territoriality.

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