

Transfer of Status Report

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1

Introduction

General introduction

Animal culture and social learning

Culture was once considered the sole domain of humans. Over the past few decades this view has been steadily challenged, and today it is common to find allusions to non-human animal cultures in scientific journals and the popular press alike (Whiten 2019a). To be sure, some energetically oppose the notion, and there is no shortage of disagreement over the definition of the term ‘culture’ (Laland & Hoppitt 2003; Heyes 2020). Intricate and distinctive as human culture might be, an increasing number of students of behaviour and evolution suspect that the difference must be one of degree and not kind (Whiten et al. 2017).

What constitutes culture, then? For our purposes, we can define it as any behavioural trait that is maintained in a population by virtue of being learnt from others; not genetically inherited, nor independently acquired. (See definitions in Whiten et al. 2017; Laland & Hoppitt 2003.) Human ritual funerary practices are cultural, so is the game of croquet. And, under this definition, so are tool use in capuchin monkeys, homing efficiency in pigeons, the songs

of many birds, some feeding behaviours in humpback whales, and even mate preferences in fruit flies (Slater 2003; Allen et al. 2013; Falótico et al. 2019; Sasaki & Biro 2017; Danchin et al. 2018).

Social learning is ubiquitous among animals, and a prerequisite for culture. Although it may not always be beneficial (Henrich & Boyd 1998; Giraldeau et al. 2002; Whitehead & Richerson 2009), there is ample evidence that many of the things that animals must learn to survive and reproduce can only be acquired by observing or interacting with others (Galef & Laland 2005). Learning will happen more often from animals that are closer in space or within the same social group. This simple fact creates opportunities for behaviours to change differently in different populations, which may happen if, for example, individuals vary in their learning abilities, the environment is heterogeneous, or there are random forces at play (Araya-Salas et al. 2019; Mesoudi et al. 2016; Aplin 2016). When these differences—beneficial or not—accumulate and persist over time, a cultural tradition is born (Tchernichovski et al. 2017; Nunn et al. 2009).

Whether found in humans or other animals, cultures can be transient or long-lasting, disorderly diverse or monolithically uniform. To give two primate examples, chimpanzees (*Pan troglodytes*) may have used stone tools in a similar way for thousands of years (Mercader et al. 2007; Carvalho et al. 2008), and white-faced capuchin monkeys (*Cebus capucinus*) frequently invent and abandon quirky social conventions such as eyeball-poking, hand-sniffing and tail-sucking (Perry et al. 2003).

Culture in birds

That other animals have a cultural dimension was recognised very early in birds, perhaps before any other group. In 1773, Barrington, who conducted some of the earliest experiments in song learning, wrote that “[t]hese differences in the song of birds of the same species cannot perhaps be compared to any thing more apposite, than the varieties of provincial dialects” (1773). In 1920’s South East England, some birds in the tit family started perforating the wax-board or metal foil that sealed milk bottles to guzzle the cream accumu-

lated at the top. This behaviour increased in frequency and geographic spread in the following decades (Fisher & Hinde 1949), in what became a famous case of possible cultural transmission. Many years later, Aplin et al. (2015b) carried out experiments in a wild population of great tits (*Parus major*) which demonstrated that new foraging behaviours can indeed spread socially and persist over more than one generation.

Another aspect of the lives of some birds that could have an important cultural component is their migration. There is mounting evidence that the information acquired by individuals and groups when flying along a route can accumulate in populations and, over time and even generations, lead to distinct migratory cultures (Jesmer et al. 2018; Sasaki & Biro 2017; Berdahl et al. 2018). There are many other examples of social learning and cultural phenomena in birds, see Aplin (2019) for a recent review.

But it is their song, especially that of passerines, that has provided some of the clearest examples of bird cultures. Songs can carry information about the identity and social position of a bird; they are shaped by natural and sexual selection, stochastic processes and directional cultural change, are partly learnt and partly innate, and can crucially be recorded and analysed in minute detail. So it is perhaps not surprising that they should have attracted the attention of researchers from a wide range of fields, from linguistics to evolutionary ecology. The resulting body of literature is vast and cannot be reviewed here: what follows is a short introduction to bird song.

Bird song: a short introduction

Historical

Every culture that has ever existed has probably conferred special status to bird song, due to its music-like qualities and the ability of some species to imitate myriad sounds. In his *Historia Animalium* (350 B.C.E), Aristotle wrote that birds were capable of learning their songs, especially ‘broad-tongued’ ones, and that sometimes their voice changed with the ‘diversity of locality’ (Book 4, Chapter 9) like those of humans. Aristotle’s is perhaps the earliest recorded

attempt at a systematic study of communication, and the first in a long tradition of analogies drawn between bird song and human language (Zirin 1980; Kleczkowska 2015).

Many centuries later, in 1650, the German Jesuit Athanasius Kircher used musical notation to transcribe bird songs in an early musicology treatise, *Musurgia Universalis*. The first known recording of a singing bird was made in 1889 by Ludwig Koch—the pioneering sound recordist and broadcaster—when he was only eight years old. Then, in the 1940s, the invention of the sound spectrograph at the Bell Telephone Laboratories paved the way for a new generation of studies that were, for the first time, able to measure songs in all manner of detail (Koenig et al. 1946; Baker 2001). The best example of these is an exhaustive study of the development of the song in the chaffinch *Fringilla coelebs* by Thorpe (1958), which was followed by an explosion of interest in the matter—both in the field (Marler & Tamura 1962, 1964) and the laboratory (see, for example, Nottebohm et al. 1976 on the neurobiology of song production)—that continues unabated to this day.

Why do some birds learn their songs?

Most birds vocalise, but vocal learning only occurs in three orders (Psittaciformes, Apodiformes, and Passeriformes; (Kroodsma 2004; Päckert 2018)). Within the passerines, commonly referred to as the perching birds, oscines learn their songs, while suboscines do not. Song learning requires a considerable investment of time and a dedicated brain system, so why might it have evolved and be maintained?

There are many hypotheses that try to explain the possible benefits of vocal learning. These include a better ability to match the acoustic requirements of different habitats(Hansen 1979; Ríos-Chelén et al. 2012), possible benefits gained from sharing songs with neighbours (Payne 1982), and the ability of learned songs to serve as an ‘honest signal’ of developmental stability (Nowicki et al. 2002; Ritchie et al. 2008). Most of the available evidence points to two broad functions: attracting and keeping mates and keeping rivals away (Collins 2004). However, there is ample variation between species, and the

current fitness consequences of song learning, on which these ideas are based, do not necessarily bear on its evolutionary origins.

Not all birds that learn their songs do so at the same point in their lives or for the same period of time. Some can only learn during the first months after they are born: zebra finch (*Taeniopygia guttata*) juveniles, for example, can only learn and develop their song when they are between ~ 20 and 80 days old (Liu et al. 2004). Other birds can continue to learn and perhaps invent new sounds throughout their lives, like the European starling (*Sturnus vulgaris*). And many birds that disperse early in their lives have a ‘sensitive period’ for learning that extends to the time when they establish their first territory (Liu et al. 2004; Beecher & Brenowitz 2005). Although this range of variation is often summarised into two categories—open and closed-ended learners—it may be better understood as a spectrum (Brenowitz & Beecher 2005). Lastly, there is extraordinary variability in repertoire size and complexity among vocal learners. Some birds learn and sing a single song, which they repeat endlessly. Other species, like the brown thrasher (*Toxostoma rufum*), never seem to stop incorporating new sounds to their songs (Boughen & Thompson 1981).

(Some of) The forces that shape bird song

In this section I will discuss physiological constraints on song production and phylogenetic inertia, ecological factors, and sexual selection. These are crucial in driving large-scale patterns of song evolution, but not the focus of my research. I will then introduce some ideas about cultural transmission dynamics, innate learning biases, and spatial, social and demographic factors. They affect the change in frequency of socially learnt songs and their properties, that is, their cultural evolution (Whiten 2019b). It is these that I will explore throughout my thesis. All of these processes and their often complex interactions influence bird song and its evolution, but their relative weight is debated.

Physiological constraints and phylogenetic inertia

Birds produce their songs using an organ called the syrinx, which is located at the base of the trachea in an air sac close to the lungs (Larsen & Goller 2002). Its structure and precise location vary between species; those with more complex songs tend to have more syringeal muscles, which allows for precise control of sound (Suthers 2004). The sounds produced by the syrinx are then filtered and modulated by the trachea and the beak, which together constitute the vocal tract (Podos et al. 2004). The body mass of a species is correlated with the size of its syrinx, which in turn influences the fundamental or lowest resonant frequency of the sounds that it can produce (Ryan & Brenowitz 1985; Martin et al. 2011).

This means that vocal evolution will be constrained by any selective pressures impinging on body size, as well as the particular evolutionary trajectory of the species. The same is true in the case of the beak: there is ample evidence that different beak morphologies influence the pace at which a bird can produce notes and the range of their frequencies (Podos 2001; Seddon 2005; Derryberry et al. 2012, 2018). These and other constraints, not least those derived from neural development and energy expenditure, will determine the degrees of freedom afforded to any other factors driving song evolution.

Ecological factors

Sound propagates differently in different habitats. For example, vegetation attenuates sound amplitude, filters some frequencies more than others, and causes reverberation. Different physical environments have different levels of background noise, with varied acoustic characteristics; there may be sounds of abiotic origin, such as wind, streams and rain, and a cacophony of other species striving to be heard. For songs to be effective they need to be detectable, and this process of acoustic adaptation is thought to be important in driving the evolution of song and other social signals (Grant & Grant 2010; Tobias et al. 2010; Endler 1992; but see Mikula et al. 2020).

There are other ecological factors that can lead to song divergence. Body size and beak morphology often change when a population of birds adapts to a

different foraging niche, which, as mentioned earlier, can influence some of the acoustic and temporal features of songs as a by-product. (Dobzhansky 1937; Podos 2001; Mayr 1963). Songs can also change if coexistence between species (sympatry) favours those that can distinguish them more easily, which can help avoid the fitness costs of hybridization or aggressive interactions; this is a mechanism known as character displacement (Seddon 2005). Interestingly, the opposite—convergent character displacement in sympatry—might also happen if better recognition of competitors is advantageous (Tobias & Seddon 2009; Tobias et al. 2014; Grant 1972).

Sexual selection

Bird song has traditionally been considered a male ornament that evolved through female preference. It is true that in the northern temperate region—where most research has historically taken place—females do not often sing. But recent phylogenetic analyses suggest that, at least in the oscine passerines, dimorphism in the trait is a consequence of multiple losses of elaborate female song rather than gains in males (Odom et al. 2014).

Most of the work done in the field of behavioural ecology over the past decades has focused on how females respond to songs and how males use them in territorial interactions. As a result, there is a vast literature detailing how songs can encode multiple messages and serve different, sexually selected functions, with great variation between species and sometimes inconsistent results (see Catchpole & Slater 2008 for reviews). To name just a few themes: song frequency can be a reliable indicator of body size (Ryan & Brenowitz 1985), temporal and spectral consistency can evidence the nutritional stress suffered in early life (MacDonald et al. 2006), and sharing songs with other males can influence territory acquisition and the outcome of agonistic encounters (Krebs et al. 1978; Demko et al. 2016). Bird song is a highly complex communication signal, so it should be no surprise that it does not have a single, universal function.

Learning biases and cultural dynamics

The process of learning introduces a host of new variables that can influence which songs a bird sings, their structure, and how they change over time. First, songs have to be learnt from someone. A bird may learn them from any other bird or, instead, some ‘tutors’ may be preferred: perhaps birds that are older, louder, or sing more often(Greig et al. 2012). This is variously referred to as a tutor, model or demonstrator bias in the cultural evolution literature [ref]. If the cultural transmission of a song happens from parents to offspring it is said to be vertical; horizontal if it happens from other birds in the same generation, and oblique from unrelated individuals in the previous generation [ref]. Sometimes, tutor choice can have extreme consequences: if a female pairs up with a male of a different species because he sings the same song as her father, and her father learnt the ‘wrong’ song, this can lead to the production of hybrid offspring [Grant & Grant (1997); Grant1997a].

Some songs might be preferred independently of who sings them—a ‘content bias’ (Richerson & Boyd 2005). For example, some song types might be intrinsically harder to sing than others, and male birds could favour learning either easy-to-sing songs or the opposite if singing difficult songs is rewarded. More broadly, there is a very well documented tendency for birds to learn the songs sung by members of their own species (Slabbekoorn & Smith 2002), or even subspecies (Nelson 2000). Preferences can arise through the interaction of innate biases for some regions of the syntactic or phonetic ‘trait space’, exposure to sounds during early life and the learning process itself (Verzijden et al. 2012; Fehér et al. 2009, 2017). Importantly, this interaction can be highly complex and show great variation between individuals (see Cate & Rowe 2007; Mets & Brainard 2019, 2017; James et al. 2020).

Birds can also learn a song based on how frequently they have heard it, or how many other birds sing a particular variant (Aplin et al. 2015a; Leeuwen et al. 2015). The relationship between the frequency of a trait in a population and the probability that it is learnt can be linear: if this is the case, transmission is unbiased. However, if more popular traits are more likely to be learnt than it would expected given their frequency, learning is said to be conformist, or positively frequency-dependent. And if the opposite is true the pattern is one

of anti-conformism, or negative frequency-dependence. Conformist learning seems to be a common strategy in nature, perhaps because it can help individuals to leverage collective information to make decisions about locally adaptive behaviour (Whiten 2019b; Pike & Laland 2010; Danchin et al. 2018). All else being equal, cultural traits will have a slower rate of change if their learning is conformist. Conversely, anti-conformist biases will cause faster turnover (Acerbi & Alexander Bentley 2014), and might arise if individuals have a preference for novelty (but see Smaldino & Epstein 2015).

Another determinant of the pace of change of a population’s songs is how accurately birds learn them. Some authors have tried to calculate ‘cultural mutation rates’ for different species to reflect how much songs change from one generation to the next: chaffinches, for example, appear to learn their songs very accurately (Slater 1986; Lachlan & Slater 2003), which slows change down. But determining this quantity is complicated by the fact that many other factors also influence the tempo of cultural change. One is the learning strategy used by individuals, already mentioned. Another is the fact that songs can be modified during the learning process in non-random directions, in a process sometimes called convergent transformation or cultural attraction (Claudière et al. 2018; Heyes 1993; Gray et al. 2007; Morin 2016). This can be illustrated by an elegant experiment carried out by Fehér et al. (2009): song tutoring lineages were started with birds that were raised in isolation, and each new bird learned from the previous—mimicking natural generations of tutors and pupils. Many of the song features that are typical in the species arose over the course of just a few generations, presumably as a consequence of directional modifications introduced by the learners.

The available evidence suggests that the changes brought about by cultural dynamics are often neutral or even negative [ref], akin to random genetic drift (Grant & Grant 2010). However, in some cases, cultural change might help birds adapt to novel acoustic landscapes (Slater & Lachlan 2003; Ríos-Chelén et al. 2012), or fine-tune the song’s characteristics to better match the shifting perceptual preferences of the receivers (Renoult & Mendelson 2019). At larger timescales, the accumulation of either neutral or directional cultural changes in songs might promote reproductive isolation between populations. Nevertheless, and although this possibility has attracted much interest, the evidence

for it is lacking (Lachlan & Servedio 2004; Verzijden et al. 2012; Yeh & Servedio 2015). Finally, it is important to note that songs are not necessarily fixed sets of notes or phrases, and different elements might change at different rates and be affected by different cultural, sexual or ecological pressures (see, for example, Williams et al. 2013).

Spatial, social and demographic factors

The most fundamental determinant of the interactions that lead to vocal learning in a population is the habitat that it occupies. Its physical features, vegetation structure and distribution of resources—which are all tightly linked—bound the use of space made by individuals. This in turn influences their social interactions and emergent social organisation (see He et al. 2019 for a review) and, ultimately, who learns from whom.

Spatial proximity will typically be correlated with vocal similarity if the birds in a population learn their songs with some accuracy and their dispersal is limited. The precise nature of this pattern will depend on whether birds disperse before or after they learn, how many songs they learn, and from how many birds (Williams & Slater 1990; Ellers & Slabbekoorn 2003), as well as the many sources of learning bias discussed above. When birds remain close to the location where they learned, or if they settle in places where they hear familiar songs, dialects or local song ‘neighbourhoods’ may emerge (Podos & Warren 2007). It then follows that increased dispersal between any two areas within a population will increase vocal sharing, and that the influx of immigrants from other populations will introduce new variation—a phenomenon that has been attested in wild populations (Fayet et al. 2014).

The size of a group and its rate of turnover are also important. First, smaller groups are expected to be more influenced by stochastic factors, paralleling the effects of genetic drift on small populations (Kimura & Crow 1964). As a consequence, smaller group sizes can increase the probability of extinction of any given song variant (Nunn et al. 2009), and lead to idiosyncratic changes in song structure (Lachlan et al. 2013). Second, higher background mortality and emigration will also lead to faster rates of change, independently of

the learning strategy employed by individuals or the fidelity of their learning (Slater 1986; Nunn et al. 2009).

A few theoretical and experimental results suggest that the number, distribution and connectedness of individuals in a population could influence the complexity of cultural traits in addition to its frequency distribution (see, for example, Derex et al. 2018; Creanza et al. 2017; Kempe & Mesoudi 2014; Derex & Boyd 2016). Bird song is strongly constrained by ecological and cognitive factors, as well as sexual selection, so there is little reason to think that this phenomenon—which might be of great importance in human culture—could alone lead to appreciable gains in its complexity. There is, however, some evidence from laboratory experiments that suggests that the availability of tutors and the quality of their instruction can reduce the influence of genetically inherited biases (Mets & Brainard 2019, 2017). This mechanism could help to explain the losses of song cultural diversity observed in some fragmented populations (Hart et al. 2018; Paxton et al. 2019): lower densities and fewer individuals might reduce opportunities for learning, which would increase the influence of strong genetic contributions to the song phenotype.

* * *

As we have seen, learning biases and strategies, space use, sociality and demography are all thought to contribute to shaping temporal and spatial patterns of bird song diversity. But their relative importance is not well known, and neither is how they interact in wild populations. A long and fruitful history of field studies has provided us with many examples of some of these processes; however, these works have typically been limited by a) small sample sizes, b) a lack of data for individual birds, c) the use of handpicked acoustic features to characterise songs, and d) the aprioristic assumption that population-wide ‘song types’ exist. Learning biases and the process of cultural transmission of bird song have been studied in the laboratory with great precision, but it is difficult to judge how well they represent natural conditions.

This thesis will provide a comprehensive exploration of these factors—as well as their interaction—in a wild great tit (*Parus major*) population that has been the subject of a long-term study (see [study system](#)). Great tits have become a model species for evolutionary, ecological and cognitive studies in natural

populations (Spurgin et al. 2019; Boyce & Perrins 1987; Charmantier et al. 2008; Cole et al. 2012; Aplin et al. 2017; Firth et al. 2018a, 2018b). Their life-history and behaviour are very well known, which, together with the characteristics of their song, makes them an ideal species to study. Male great tits sing a repertoire of one to eight simple song variants (Krebs et al. 1978; Rivera-Gutierrez et al. 2010), each consisting of a small number of notes that are repeated in a stereotypical manner. They learn these songs primarily from conspecifics and during their first year of life, until they have established a territory (McGregor & Krebs 1982, 1989), and as a consequence are more likely to share them with neighbouring males than with other birds (McGregor & Krebs 1982). In addition, there is some evidence that the similarity of their songs and the relative novelty and size of neighbourhood repertoires are influenced by spatial and demographic factors (Rivera-Gutierrez et al. 2010; Fayet et al. 2014).

Aims of the report

This report aims to do the following:

- Provide a broad overview of the framework and the kinds of questions that my thesis will try to answer — [Introduction](#).
- Detail some of the methods that I am using to study large amounts of song data in an unsupervised way — [Methods](#).
- Summarise the data recorded during the spring of 2020 — [Results](#).
- Present an updated plan for next year's field season — [2021 plan](#).
- Introduce a possible outline for the thesis — [Thesis plan](#).

2

Methods

Study system

The study was carried out in Wytham Woods, Oxfordshire, UK ($51^{\circ}46'N$, $1^{\circ}20'W$). Wytham Woods is a semi-natural deciduous woodland, around 415 hectares in extension, which is surrounded by farmland. Here, a population of great tits is monitored as part of a long-term survey that began in 1947. The majority of great tits nests in nestboxes with known locations. Every year, fieldworkers record the identities of breeding males and females, the dates of clutch initiation and egg hatching, clutch size, and fledgling success under standardised protocols. A large proportion of birds in the population are fitted with a unique British Trust for Ornithology (BTO) metal leg ring either as nestlings or as adults. During the breeding season, from March to June, great tit pairs are socially monogamous and defend territories around their nestboxes (Hinde 1952).

Song recording

Every nestbox in the study site is checked by fieldworkers at least once a week before and during egg-laying, which can last from one to 14 days (Perrins

1965). When a nestbox was marked as having great tit activity, which usually coincided with the laying of the first eggs, I placed an autonomous sound recorder in the vicinity of the nestbox—either in the same tree or in a suitable neighbouring tree. I recorded birds in this manner from early April until mid-May, leaving each recorder in the same location for three consecutive days before moving it to a different nestbox. I relocated ten recorders every day throughout the duration of the recording period.

I used 30 AudioMoth recorders (Hill et al. 2019), which were housed in waterproof, custom-built enclosures (See Fig X). Recording began approximately one hour before sunrise (\sim 05:36 – 04:00 UTC) and consisted of seven 59-minute-long (one hour minus one-minute pauses) recordings with a sample rate of 48 kHz.



Figure 2.1: Two different song types sung by a male. Each colour represents a different note; a combination of two constitutes a phrase, and each line is a complete song.

Definitions

There is not a consistent set of terms used to refer to the different levels at which the acoustic output of a bird can be described. For clarity, these are the definitions that I use throughout this work:

Term	Definition
Note	A single uninterrupted vocalisation; the smallest unit of analysis

Term	Definition
Phrase	The smallest set of different notes that are repeated stereotypically
Song	One or more repeated phrases preceded and followed by silences of a duration exceeding that of the longest silence between each note in a phrase
Song bout	A set of one or more songs that are preceded and followed by silences longer than 10 seconds. I will change this to a probabilistic definition based on the distribution of silence durations; typically a more or less arbitrary threshold is used but I'd rather have a better-grounded definition

Audio analysis

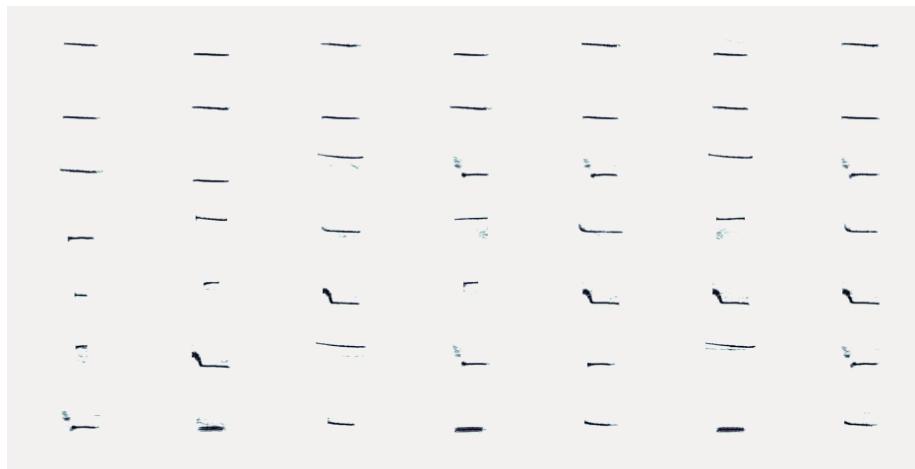


Figure 2.2: A small sample of notes from a male after preprocessing and segmentation.

Pre-processing and segmentation

Song segmentation

I inspected spectrograms for each raw recording aided by AviaNZ, an open-source Python program written by Marsland and colleagues (Marsland et al. 2019). I selected songs based on a simple criterion: that its notes were clearly distinct from background noise and other bird vocalisations. I chose entire songs where it was possible; where it was not, I selected the longest contiguous segment available.

I included songs produced from approximately one hour before sunrise to four hours after sunrise for each bird and day. If a 59-min recording solely contained rain or wind sounds I also included the following 59-min recording to maximise the chances of recording a bird.

Assigning song bouts to individuals

As a consequence of the automated nature of the recording process, there is a small chance that some of the songs recorded in the immediate vicinity of a given nest box do not belong to the focal bird. To minimise the chance of false positives, I discarded recordings with more than one vocalising bird if one was not distinctly louder than the rest. I also discarded all songs with a maximum amplitude below -16 dB, calculated as $20 \log_{10}(\frac{A}{A_0})$, with $A = 5000$ and $A_0 = 32767$ (the maximum value for 16-bit digital audio). This threshold derives from the observation that, in those cases where there are simultaneous recordings of several immediate neighbours, an amplitude cutoff greater than 4000 always separates a focal bird from its nearest neighbours. Note that these are not calibrated values and are, therefore, relative to the recording equipment and settings I used—as well as other factors like sound directionality and vegetation cover.

Note segmentation

I segmented the resulting song selections into their constituent notes using a dynamic threshold algorithm implemented by Sainburg et al. (2019). Briefly, the algorithm finds minima in the spectral envelope of a spectrogram, which are considered silences; if the length of the signal between these minima exceeds a maximum note duration, a new local minimum is defined that divides the signal in two shorter segments. This is repeated until multiple notes are defined or there are no local minima below a maximum amplitude threshold. Then, segments below a minimum note duration threshold are discarded. The minimum and maximum note length thresholds were determined by segmenting a small subset of songs ($n = 30$) with Chipper, an open-source, Python-based software developed by Searfoss et al. (2020). Figure 2.3 shows an example of this segmentation in a simple case.

Note: I am currently working on implementing a segmentation algorithm that deals better with reverberation. Sometimes the previous note overlaps with the next and the current algorithm fails to separate them.

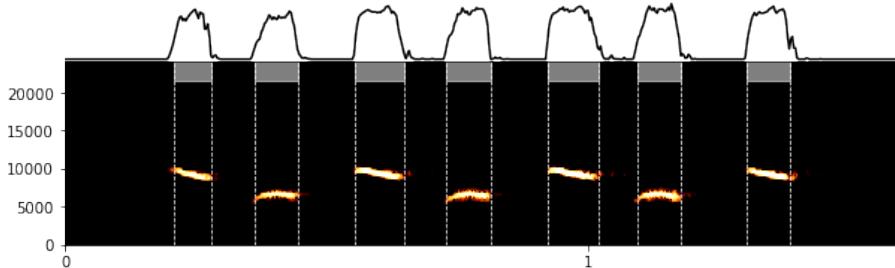


Figure 2.3: An illustration of the note segmentation process.

Spectrograms

I created spectrograms for each individual note in the dataset from its normalised and band-passed waveform. I then log-scaled each spectrogram and clipped all values within the fifth lowest percentile, to remove background noise of low amplitude. I then zero-padded each spectrogram with length be-

low the longest note and built a dataset containing the metadata for each note and its spectrogram.

Dimensionality reduction and clustering

At the population level

I prepared a $N \times d$ -dimensional array, with $N =$ total number of notes in the dataset and $d = 64 \times 132$, or the length of a flattened two-dimensional spectrogram array. I then projected the first array onto a low-dimensional embedding found using UMAP (Uniform Manifold Approximation and Projection, (McInnes et al. 2018)) and PHATE (Potential of Heat-diffusion for Affinity-based Trajectory Embedding, (Moon et al. 2019)), two non-linear manifold learning and dimensionality reduction algorithms. Full details of the implementation and parameters can be found in the corresponding [code module](#); see [Figure 2.4](#) for an example of a projection into two dimensions.

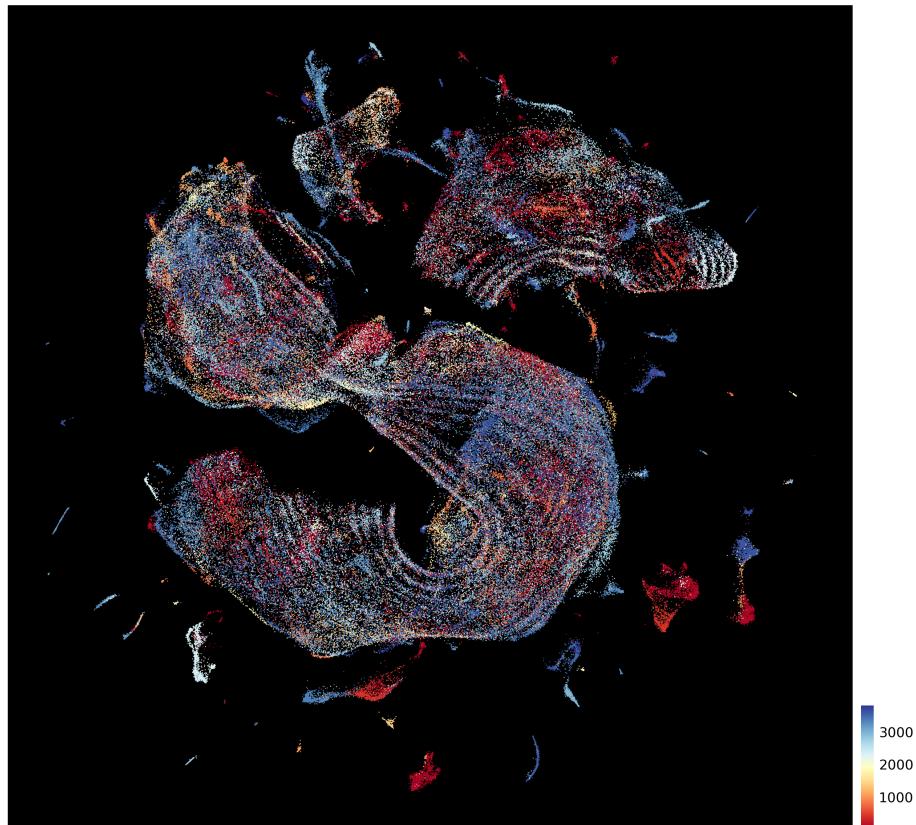


Figure 2.4: Embedding of the complete dataset using UMAP (Uniform Manifold Approximation and Projection, $n = 182.616$ notes). Colours represent distance in metres from a randomly selected point in the population.

For individual birds

In a similar way, I used UMAP to project every note sung by each bird onto a lower-dimensional space. Specifically, I created a two-dimensional projection for visualisation and a ten-dimensional projection for clustering. I then used the latter to infer the note types sung by each bird, by finding areas occupied more densely within the acoustic space using HDBSCAN (McInnes et al. 2017, see [Figure 2.5](#)).

Note: I am currently defining ‘hard’ clusters, where notes are labelled as either clusters or noise. This makes some clusters a little bit noisy. I might try to implement ‘fuzzy’ clustering, where cluster membership is defined by probability vectors, and deal more strictly with outliers. Density-based clustering from the UMAP embedding works well, but I will also define clusters using a linear embedding.

Inferring note transitions

I defined a directed weighted graph $G = (V, E, w)$ describing the repertoire of each bird, where the vertices V are the set of note clusters with > 10 members and the directed edges E and weight w correspond to first-order Markov transition probabilities between them. When a set of n notes consistently appeared in the same order I considered them a song type (see [Figure 2.5](#)).

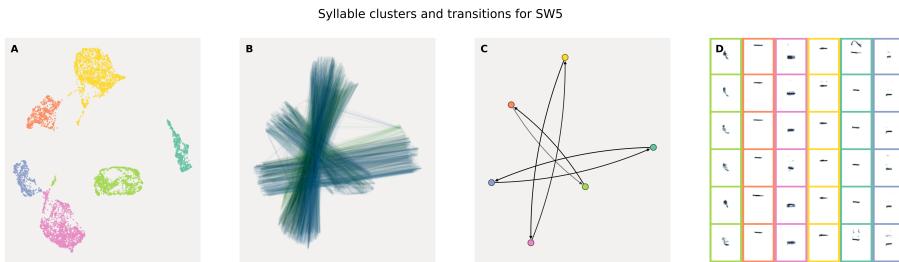


Figure 2.5: An illustration of the process used to classify notes and transitions for a random male in the dataset. **A:** Note clusters are defined using HDBSCAN, a density-based algorithm, on a 10-dimensional UMAP projection. **B:** a representation of the transitions between notes, where each line joins two notes sung consecutively. **C:** a directed graph with weights = first-order Markov transition probabilities between notes. **D:** Examples extracted at random from each cluster defined in A.

Models of sampling success

I modelled the number of recorded songs in a zero-inflated negative binomial generalized additive model, with the lag from the onset of egg-laying to the date of recording, the april lay date, and their interaction as population-level effects. Models fit with the brms package (Bürkner 2017) and compared using leave-one-out cross validation (Vehtari et al. 2017).

Measuring acoustic distance

I am currently extending a method devised by Mets & Brainard (2018) to measure learning accuracy in the lab to work with unknown tutors and in a larger acoustic space. Once this is ready I will build distance matrices at the note, phrase and song transition levels, and these will be the basis of all subsequent analyses.

Code availability:

The code necessary to reproduce all the analyses and figures in this report, along with more details about each method employed here, is available as an installable Python package from github.com/nilomr/0.0_great-tit-song. Note: this repository is not yet public; contact the author for access.

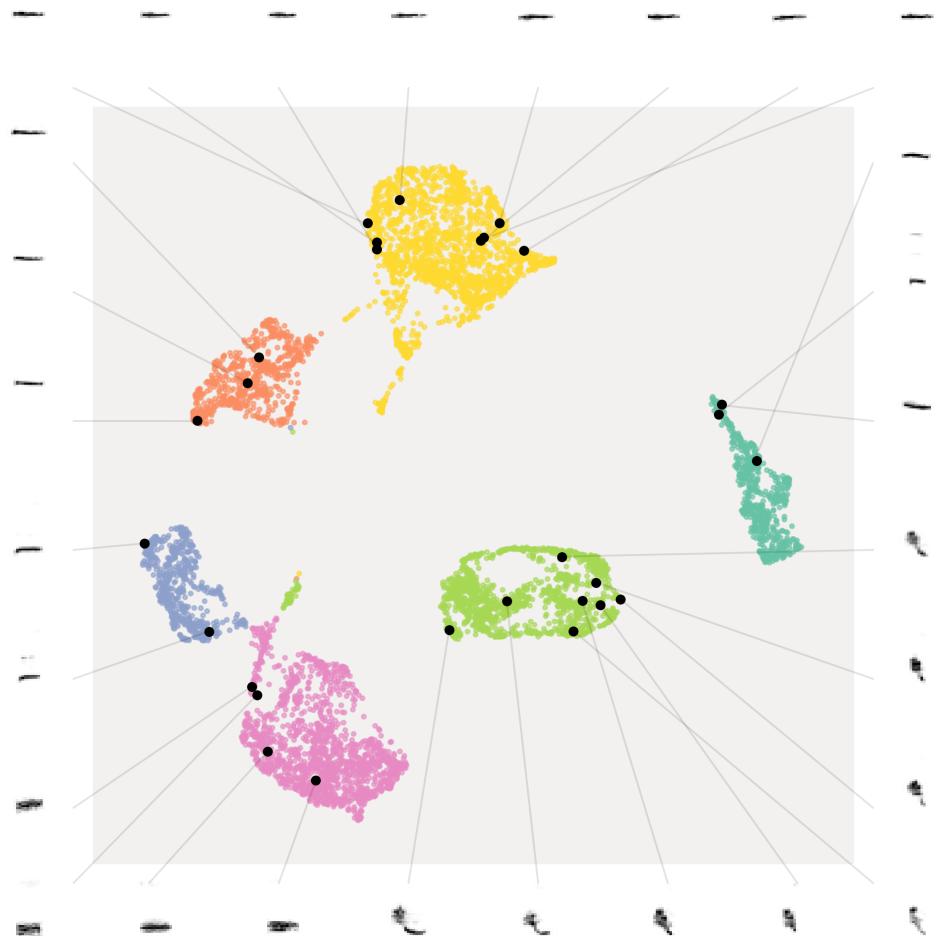


Figure 2.6: The entire repertoire of a great tit male, with examples of each note type.

3

Results and discussion

Quantifying the 2020 dataset

Sampling



Figure 3.1: Map of sampling locations and number of songs recorded in 2020.

I recorded a total of 6811 hours of sound over the course of 37 days, from

April 9 to May 15, in 240 nestboxes that were occupied by great tits. I detected at least one song in 201 of them (range 1-1972) which, after segmenting and filtering, resulted in a complete dataset of 18.847 songs, with a total of 182.616 individual notes. Of these 201 birds, 161 had enough notes to allow more detailed analyses. Finally, of the latter, 90 have known identities. In total, I recorded at 91.6% of the nestboxes that were marked as having a great tit nest during the entire breeding season (240 out of 262), and sampling was not spatially biased. You can find an interactive map of the spatial coverage, density and distribution of number of songs [here](#); see also [Figure 3.1](#).

Songs and notes

The distribution of note counts follows a power law: birds for which there is a large number of notes are much rarer than birds with only a few notes (see [Figure 3.2.B:B](#)). The mean number of note types per bird is 7, and they range from 2 to 16. If we take into account that most song types consist of two different notes this closely matches estimates by McGregor et al. (1981), who found that the population mean was close to 3 song types, and individuals sung from 1 to 8 song types (compare [Figure 3.2.A](#) and Fig. 6 in McGregor & Krebs 1982).

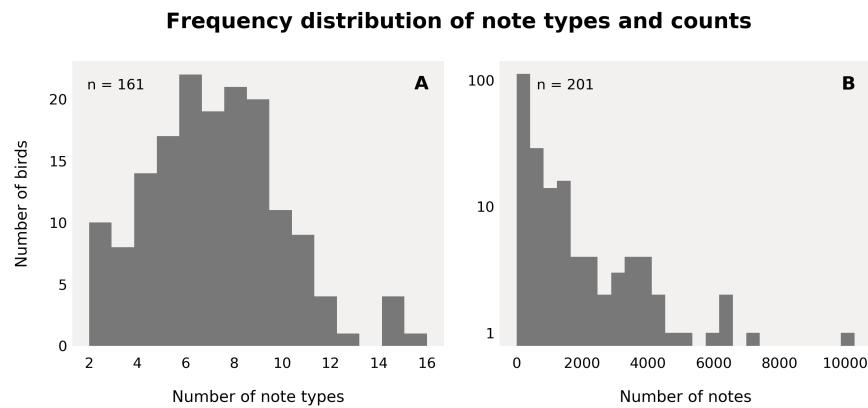


Figure 3.2: Frequency distribution of number of note type counts (A) and number of notes (B) in the 2020 dataset.

[Figure 3.3](#) shows how singing activity changed throughout the morning, with most songs recorded between 4 and 5 UTC, and [Figure 3.4](#) shows the distribution of note duration for all males in the dataset. Finally, [Figure 3.5](#) plots the cumulative number of song types against the number of songs recorded. Although it is likely that the dataset underrepresents the number of song types sung by some males, most curves reach an asymptote.

Sampling success

Longer lags between the date in which the first egg was laid in a given nest and the date in which I recorded the corresponding male were strongly associated with a decrease in the number of songs recorded (mean incidence rate ratio, IRR = 0.91, 95% CI [0.87- 0.95]). This lag did not interact with the april lay date (IRR = 1.0, 95% CI [0.99-1.01]), which was independently but more weakly associated with a decrease in the number of songs (IRR = 0.93, 95% CI [0.87-1.0]). [Figure 3.6.A](#) shows the full posterior distribution of the exponentiated parameter estimates reported here, which are from a simpler linear model to make interpretation easier. [Figure 3.6.B-C](#) shows the marginal effects of the same variables in a GAM model. Note the sharp decrease after the onset of egg laying and towards the end of the breeding season.

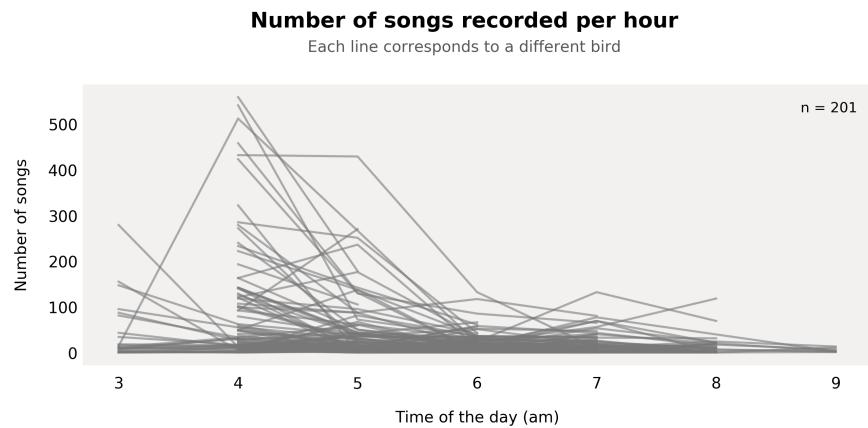


Figure 3.3: Singing activity throughout the morning with one-hour resolution. Each line represent a different bird in the dataset; times are UTC.

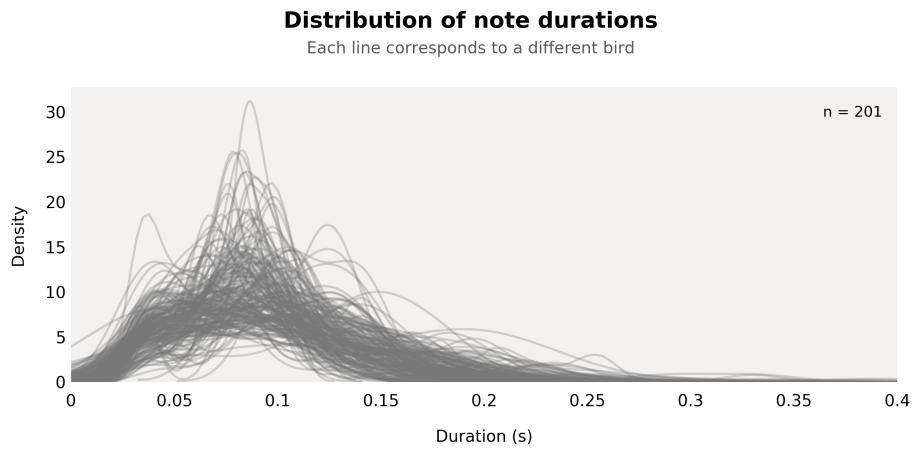


Figure 3.4: Kernel density estimation of the distribution of note durations for every male in the 2020 dataset.

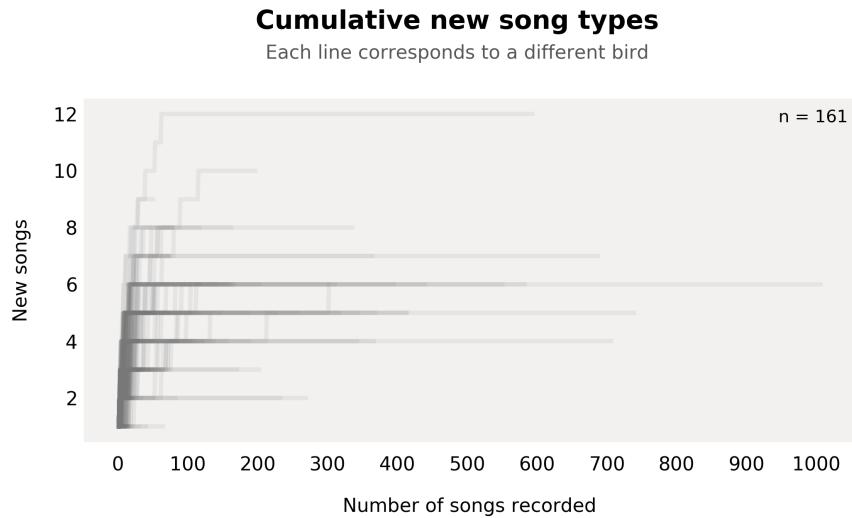


Figure 3.5: Cumulative number of songs including a note type not previously recorded (y) vs number of songs recorded (x) for every bird in the 2020 dataset with enough notes to allow classification ($n = 161$).

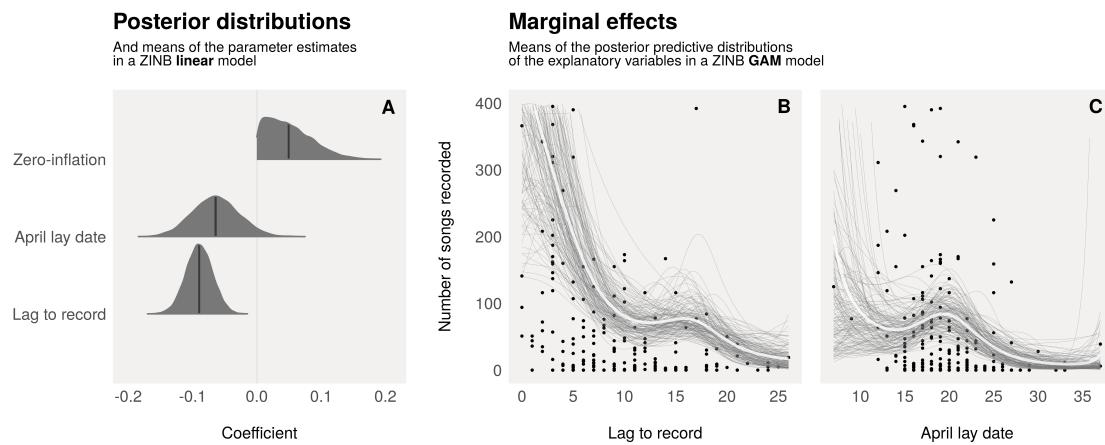


Figure 3.6: **A:** the main parameters in a zero-inflated negative binomial linear regression (ZINB) model with the number of songs recorded for each male as the outcome variable. **B, C:** plots for each covariate in a ZINB generalised additive model, showing draws from their marginal posterior predictive distributions (blue) and their means (white). The y-axes are trimmed to a maximum value of 400 to aid visualisation.

4

Fieldwork plan for 2021

Although this year's data collection effort has been reasonably successful, an analysis of the factors that influenced sampling success reveals that it can be optimised in the following years.

There is a sharp decrease in singing activity after the end of egg-laying, matching results from Mace (1987). Birds in nests with later lay dates also sing fewer songs, but the main correlate of sampling success is the time passed since the onset of egg-laying. This year (2020) I was not able to collect and reposition more than 10 recorders per day. For a brief period (~4 days), I would have needed to deploy ~30 new recorders per day in order to track the increase in the number of birds that started laying eggs. This delay accumulated and was not dissipated until the end of the recording period.

I will make an effort to reduce this lag in 2021 and 2022. This requires: a) earlier detection of nests with great tit activity, and b) better ability to cope with the influx of new nests. I am discussing different possibilities with my supervisors, including using RFID loggers mounted on nestboxes to monitor early use by great tits, acquiring a larger amount of remote recorders, and recruiting the help of a field assistant during the peak of the fieldwork season.

5

Thesis plan

You can find a project schedule in [Figure 5.1](#). It defines the data collection, data analysis and writing periods for each chapter.

Introduction

The introduction will provide a general background to the topic of song learning in birds. I will try to integrate ideas from three bodies of research that are sometimes disconnected: laboratory studies of song ontogeny, behavioural ecology and cultural evolutionary theory. The structure will be an iteration of the [introduction](#) above.

1. What do great tits sing?

The first chapter will provide an in-depth description of the variability present in great tit songs, from a bio-acoustic and information-theoretic perspective. This will include a very detailed case study from the Wytham population and

comparison with data from across the distribution range of the species, exploring the following questions:

Are ‘song types’ meaningful categories at larger spatial scales? Many birds, including great tits, are thought to learn and produce categorical vocal signals. These are characterised by narrow, clustered feature distributions. As a consequence, discretising individual repertoires is useful to understand the learning and interactions taking place between close neighbours. However, studies typically also classify songs into population-wide discrete categories, often hundreds of them, without clear statistical or theoretical justification. I will **characterise repertoires at different levels of description—from individual notes to transition probabilities between songs**—and use continuous measures of similarity, propagating uncertainty to analyses of the distribution of songs at the population level. Combining continuous measures with categorical song type definitions will then allow me to test the relationship between spatial scale and the robustness of song type categories.

Which song traits are more constrained, and which more free to vary? Some regions of the sound space are occupied more densely than others. I will identify these ‘attractors’, describe variability at the different levels of description already mentioned, and determine which song traits have better potential to encode individuality and geographic origin. This will help answer a related question: **Do great tits sing different classes of songs** that are subjected to different cultural evolutionary dynamics?

2. Song learning and learning biases

The second chapter will constitute the first step in understanding how the diversity described in [Chapter 1](#) emerges and evolves. The themes outlined in **song learning biases** will make up its backbone.

Are all songs equally likely to be learnt? Song learning might depend on the frequency with which they are heard, or on how many other males sing them. I will test whether there is evidence for frequency dependence in great tit song learning, or if, on the contrary, learning is unbiased. To do this, I will

compare every bird's songs with those of neighbouring males and measure the relationship between a) the number of males that sing a song around a focal bird, b) the number of times that the song was recorded, and the probability that the focal male sings it.

Where are songs more likely to be learnt—and from whom? I will compare the similarity of a bird's repertoire to the acoustic landscape of a) its natal grounds and b) its first territory and quantify the relative contribution of each. I will then test whether older males are more likely to serve as tutors than birds in the same generation.

Are some learning biases heritable? There is no evidence that repertoire composition, size or complexity are inheritable in great tits. Work done in the lab with other species suggests that birds might be better at learning songs that are similar in tempo to those of their fathers, and that mean frequency is partially heritable. I will explore if this is the case in known father-song pairs in a wild population after controlling for spatial effects.

Can learning fidelity explain song similarity at larger spatial scales? Many studies of bird song have concluded that learning is often extremely accurate, with some even estimating that syllable types can persist for longer than 500 years (e.g., Lachlan et al. 2018). Although accurate learning does occur, as laboratory studies show, the fact that innate biases alone can give rise to many species-typical song characteristics, even in isolate, deafened, and self-tutored birds (James & Sakata 2017; James et al. 2020; Fehér et al. 2009, 2017), suggests that strong convergent transformation during song ontogeny might difficult the estimation of mutation rates. I will explore this by fitting individual-based simulation models of song change to empirical data gathered in the Wytham population over the course of the DPhil, and from other European populations.

3. Space and demography

The third chapter will integrate the findings on individual learning biases in Chapter 2 with a detailed analysis of the influence of habitat structure, immi-

gration and dispersal ([introduction: space and demography](#)). Specifically, it will test whether their interaction can account for the pattern of song sharing and variation described in [Chapter 1](#), and ask the following questions:

How well does community structure predict acoustic structure at different scales? I will use occurrence data from PIT-tagged birds, collected from automated feeding stations equipped with RFID antennae, to construct social and movement networks (see ([Farine & Sheldon 2019](#))). I will then test whether the community structure inferred from them can partially explain the spatial distribution of song similarity.

Do any song traits change with population density? I will test whether birds living in higher-density areas, which might provide more opportunities for learning, sing more acoustically typical songs—after controlling for dispersal and number of immigrants, which are known to reduce and increase the diversity within an area, respectively ([Rivera-Gutierrez et al. 2010](#); [Fayet et al. 2014](#)). Relatedly, I will ask **whether being neighbours with more immigrant birds is correlated with (a) increased acoustic diversity or (b) having larger repertoires** at the individual level.

How is the rate of acoustic change affected by population turnover rates? The pace of cultural evolution of songs is likely to be influenced by generation times and the rate of turnover. I will test if areas with higher turnover show higher rates of acoustic change over the duration of the project.

4. The function of songs

This project will mainly study songs from a cultural evolutionary perspective, in contrast with a majority of studies firmly situated in the field of behavioural ecology. However, as discussed [in the introduction](#), bird song and song learn-

ing are shaped by selective forces and serve biological functions¹, and these need to be considered. Having a large, multi-generational dataset of songs matched to known individuals will allow us to test questions relating to the current fitness consequences of song-sharing and song performance, and these will constitute the last chapter of the thesis.

Is song-sharing beneficial? For whom? Song-sharing might be beneficial for young birds in some species (Beecher 2017), and perhaps even for both tutor and tutees (Beecher et al. 2020). I will ask whether this is the case in great tits.

Is singing common songs beneficial for males? Singing songs that are common in an area might be beneficial for males if they are important in territorial defence or if females prefer them.

Are a) consistency in song performance, b) repertoire size, or c) degree of song-sharing with neighbours positively correlated with reproductive success? If so, is this mediated by territory quality?

Does song production senesce? Are any song traits reliable signals of age?

Is there a trade-off between repertoire size and repertoire complexity?

Synthesis

A summary integrating the results of every chapter and placing them in a broader theoretical context.

¹As an example of how the nature of what is acceptable as explanation for animal behaviour has changed in the last fifty decades or so, here is a quote from an early paper on song learning by Thorpe: “[t]hat bird song is often an expression of irrepressible joy can be supported with some plausible arguments and is certainly not without some scientific justification” (1958, p. 536).

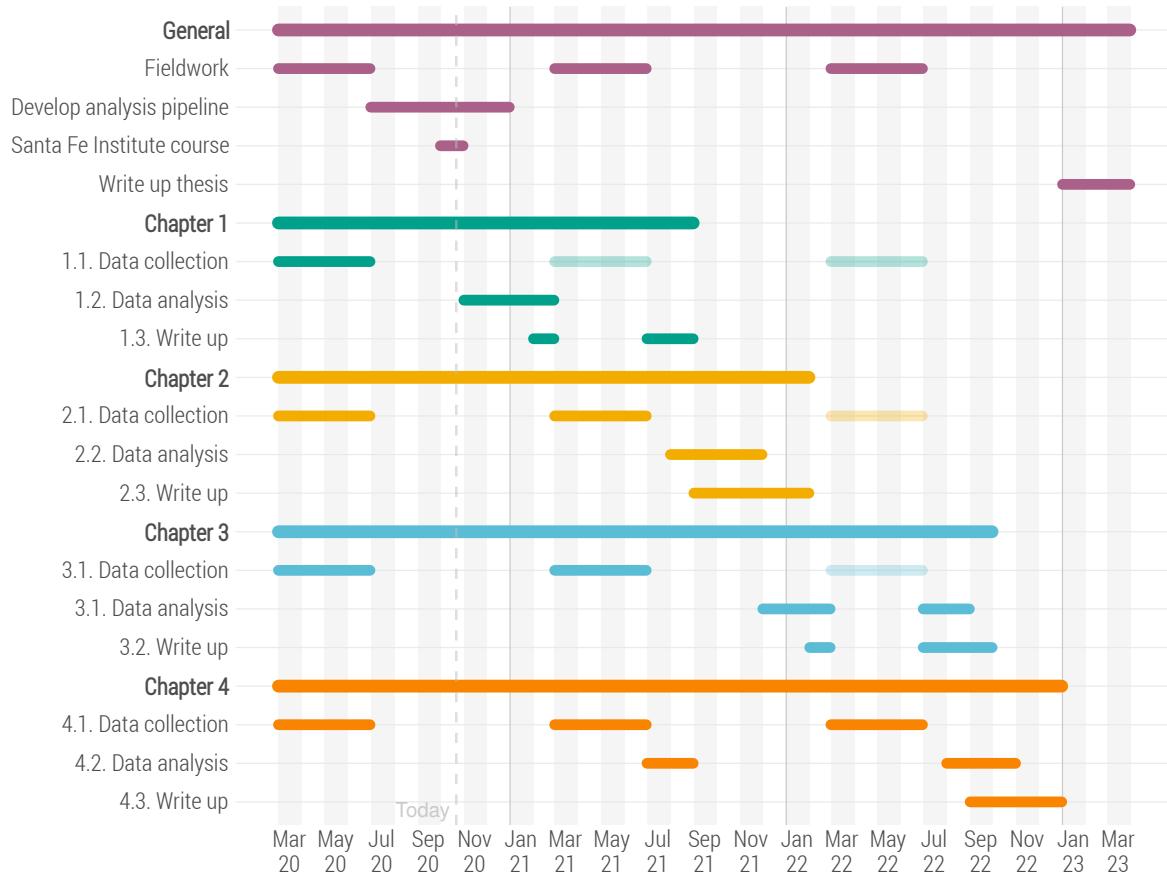


Figure 5.1: Gantt chart illustrating the DPhil schedule. Semi-transparent segments indicate data that is not indispensable to that chapter but would be beneficial.

6

Literature cited

- Acerbi, A. & Alexander Bentley, R.** 2014. Biases in cultural transmission shape the turnover of popular traits. *Evolution and Human Behavior*, **35**, 228–236.
- Allen, J., Weinrich, M., Hoppitt, W. & Rendell, L.** 2013. Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. *Science*, **340**, 485–488.
- Aplin, L.** 2016. Understanding the multiple factors governing social learning and the diffusion of innovations. *Current Opinion in Behavioral Sciences*, **12**, 59–65.
- Aplin, L. M.** 2019. Culture and cultural evolution in birds: a review of the evidence. *Animal Behaviour*, **147**, 179–187.
- Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A. & Sheldon, B. C.** 2015a. Counting conformity: Evaluating the units of information in frequency-dependent social learning. *Animal Behaviour*, **110**, e5–e8.
- Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A. & Sheldon, B. C.** 2015b. Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, **518**, 538–541.

- Aplin, L. M., Sheldon, B. C. & McElreath, R.** 2017. Conformity does not perpetuate suboptimal traditions in a wild population of songbirds. *Proceedings of the National Academy of Sciences of the United States of America*, **114**, 7830–7837.
- Araya-Salas, M., Smith-Vidaurre, G., Mennill, D. J., González-Gómez, P. L., Cahill, J. & Wright, T. F.** 2019. Social group signatures in hummingbird displays provide evidence of co-occurrence of vocal and visual learning. *Proceedings of the Royal Society B: Biological Sciences*, **286**,
- Baker, M.** 2001. Bird song research: the past 100 years. *Bird Behavior*, **14**, 3–50.
- Barrington, D.** 1773. XXXI. Experiments and observations on the singing of birds, by the Hon. Daines Barrington, Vice Pres. R. S. In a letter to Mathew Maty, M. D. Sec. R. S. *Philosophical Transactions of the Royal Society of London*, **63**, 249–291.
- Beecher, M. D.** 2017. Birdsong learning as a social process. *Animal Behaviour*, **124**, 233–246.
- Beecher, M. D. & Brenowitz, E. A.** 2005. Functional aspects of song learning in songbirds. *Trends in Ecology and Evolution*, **20**, 143–149.
- Beecher, M. D., Akçay, Ç. & Campbell, S. E.** 2020. Birdsong learning is mutually beneficial for tutee and tutor in song sparrows. *Animal Behaviour*, **166**, 281–288.
- Berdahl, A. M., Kao, A. B., Flack, A., Westley, P. A. H., Codling, E. A., Couzin, I. D., Dell, A. I. & Biro, D.** 2018. Collective animal navigation and migratory culture: From theoretical models to empirical evidence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **373**, 20170009.
- Boughey, M. J. & Thompson, N. S.** 1981. Song Variety in the Brown Thrasher (*Toxostoma rufum*). *Zeitschrift für Tierpsychologie*, **56**, 47–58.
- Boyce, M. S. & Perrins, C. M.** 1987. Optimizing great tit clutch size in a fluctuating environment. *Ecology*, **68**, 142–153.

- Brenowitz, E. A. & Beecher, M. D.** 2005. Song learning in birds: Diversity and plasticity, opportunities and challenges. *Trends in Neurosciences*, **28**, 127–132.
- Bürkner, P.-C.** 2017. brms : An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software*, **80**,
- Carvalho, S., Cunha, E., Sousa, C. & Matsuzawa, T.** 2008. Chaînes opératoires and resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. *Journal of Human Evolution*, **55**, 148–163.
- Catchpole, C. K. & Slater, P. J. B.** 2008. *Bird Song*. Cambridge: Cambridge University Press.
- Cate, C. ten & Rowe, C.** 2007. Biases in signal evolution: learning makes a difference. *Trends in Ecology and Evolution*, **22**, 380–387.
- Charmantier, A., McCleery, R. H., Cole, L. R., Perrins, C., Kruuk, L. E. B. & Sheldon, B. C.** 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science*, **320**, 800–803.
- Claidière, N., Amedon, G. K. kuma, André, J. B., Kirby, S., Smith, K., Sperber, D. & Fagot, J.** 2018. Convergent transformation and selection in cultural evolution. *Evolution and Human Behavior*, **39**, 179–190.
- Cole, E. F., Morand-Ferron, J., Hinks, A. E. & Quinn, J. L.** 2012. Cognitive ability influences reproductive life history variation in the wild. *Current Biology*, **22**, 1808–1812.
- Collins, S.** 2004. Vocal fighting and flirting: The functions of birdsong. In: *Nature's music: The science of birdsong*, (Ed. by P. Marler & H. Slabbekoorn), pp. 39–79. New York: Elsevier.
- Creanza, N., Kolodny, O. & Feldman, M. W.** 2017. Greater than the sum of its parts? Modelling population contact and interaction of cultural repertoires. *Journal of the Royal Society Interface*, **14**,
- Danchin, E., Nöbel, S., Pocheville, A., Dagaeff, A.-C., Demay, L., Alphand, M., Ranty-Roby, S., Renssen, L. van, Monier, M., Gazagne, E., Allain,**

- M. & Isabel, G.** 2018. Cultural flies: Conformist social learning in fruitflies predicts long-lasting mate-choice traditions. *Science*, **362**, 1025–1030.
- Demko, A. D., Reitsma, L. R. & Staicer, C. A.** 2016. Repertoire structure, song sharing, reproductive success, and territory tenure in a population of Canada Warblers (*Cardellina canadensis*) in central New Hampshire. *Canadian Journal of Zoology*, **94**, 283–290.
- Derex, M. & Boyd, R.** 2016. Partial connectivity increases cultural accumulation within groups. *Proceedings of the National Academy of Sciences*, **113**, 2982–2987.
- Derex, M., Perreault, C. & Boyd, R.** 2018. Divide and conquer: Intermediate levels of population fragmentation maximize cultural accumulation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **373**, 20170062.
- Derryberry, E. P., Seddon, N., Claramunt, S., Tobias, J. A., Baker, A., Aleixo, A. & Brumfield, R. T.** 2012. Correlated evolution of beak morphology and song in the neotropical woodcreeper radiation. *Evolution*, **66**, 2784–2797.
- Derryberry, E. P., Seddon, N., Derryberry, G. E., Claramunt, S., Seeholzer, G. F., Brumfield, R. T. & Tobias, J. A.** 2018. Ecological drivers of song evolution in birds: Disentangling the effects of habitat and morphology. *Ecology and Evolution*, **8**, 1890–1905.
- Dobzhansky, T.** 1937. *Genetics and the Origin of Species*. New York: Columbia University Press.
- Ellers, J. & Slabbekoorn, H.** 2003. Song divergence and male dispersal among bird populations: A spatially explicit model testing the role of vocal learning. *Animal Behaviour*, **65**, 671–681.
- Endler, J. A.** 1992. Signals, Signal Conditions, and the Direction of Evolution. *The American Naturalist*, **139**, S125–S153.
- Falótico, T., Proffitt, T., Ottoni, E. B., Staff, R. A. & Haslam, M.** 2019. Three thousand years of wild capuchin stone tool use. *Nature Ecology and Evolution*

tion,

- Farine, D. R. & Sheldon, B. C.** 2019. Stable multi-level social structure is maintained by habitat geometry in a wild bird population. *bioRxiv*,
- Fayet, A. L., Tobias, J. A., Hintzen, R. E. & Seddon, N.** 2014. Immigration and dispersal are key determinants of cultural diversity in a songbird population. *Behavioral Ecology*, **25**, 744–753.
- Fehér, O., Wang, H., Saar, S., Mitra, P. P. & Tchernichovski, O.** 2009. De novo establishment of wild-type song culture in the zebra finch. *Nature*, **459**, 564–568.
- Fehér, O., Ljubić, I., Suzuki, K., Okanoya, K. & Tchernichovski, O.** 2017. Statistical learning in songbirds: from self-tutoring to song culture. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **372**, 20160053.
- Firth, J. A., Cole, E. F., Ioannou, C. C., Quinn, J. L., Aplin, L. M., Culina, A., McMahon, K. & Sheldon, B. C.** 2018a. Personality shapes pair bonding in a wild bird social system. *Nature Ecology and Evolution*, **2**, 1696–1699.
- Firth, J. A., Cole, E. F., Ioannou, C. C., Quinn, J. L., Aplin, L. M., Culina, A., McMahon, K. & Sheldon, B. C.** 2018b. Personality shapes pair bonding in a wild bird social system. *Nature Ecology & Evolution*, **1**.
- Fisher, J. & Hinde, R. A.** 1949. The opening of milk bottles by birds. *British Birds*, **42**, 347–357.
- Fogarty, L. & Creanza, N.** 2017. The niche construction of cultural complexity: interactions between innovations, population size and the environment. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **372**, 20160428.
- Galef, B. G. & Laland, K. N.** 2005 June. Social learning in animals: Empirical studies and theoretical models. **55**, 489–499.
- Gil, D. & Gahr, M.** 2002 March. The honesty of bird song: Multiple constraints for multiple traits. **17**, 133–141.

- Giraldeau, L. A., Valone, T. J. & Templeton, J. J.** 2002 November. Potential disadvantages of using socially acquired information. **357**, 1559–1566.
- Grant, P. R.** 1972. Convergent and divergent character displacement. *Biological Journal of the Linnean Society*, **4**, 39–68.
- Grant, P. R. & Grant, B. R.** 1997. Genetics and the origin of bird species. *Proceedings of the National Academy of Sciences of the United States of America*, **94**, 7768–7775.
- Grant, B. R. & Grant, P. R.** 2010. Songs of Darwin's finches diverge when a new species enters the community. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 20156–20163.
- Gray, R. D., Greenhill, S. J. & Ross, R. M.** 2007. The Pleasures and Perils of Darwinizing Culture (with Phylogenies). *Biological Theory*, **2**, 360–375.
- Greig, E. I., Taft, B. N. & Pruett-Jones, S.** 2012. Sons learn songs from their social fathers in a cooperatively breeding bird. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 3154–3160.
- Hansen, P.** 1979. Vocal learning: its role in adapting sound structures to long-distance propagation, and a hypothesis on its evolution. *Animal Behaviour*, **27**, 1270–1271.
- Hart, P. J., Sebastián-González, E., Tanimoto, A., Thompson, A., Speetjens, T., Hopkins, M. & Atencio-Picado, M.** 2018. Birdsong characteristics are related to fragment size in a neotropical forest. *Animal Behaviour*, **137**, 45–52.
- He, P., Maldonado-Chaparro, A. A. & Farine, D. R.** 2019. The role of habitat configuration in shaping social structure: a gap in studies of animal social complexity. *Behavioral Ecology and Sociobiology*, **73**,
- Henrich, J. & Boyd, R.** 1998. The Evolution of Conformist Transmission and the Emergence of Between-Group Differences. *Evolution and Human Behavior*, **19**, 215–241.
- Heyes, C.** 2020. Culture. *Current Biology*, **30**, R1246–R1250.

- Heyes, C. M.** 1993. Imitation, culture and cognition. *Animal Behaviour*, **46**, 999–1010.
- Hill, A. P., Prince, P., Snaddon, J. L., Doncaster, C. P. & Rogers, A.** 2019. AudioMoth: A low-cost acoustic device for monitoring biodiversity and the environment. *HardwareX*, **6**, e00073.
- Hinde, R. A.** 1952. The Behaviour of the Great Tit (*Parus major*) and Some Other Related Species. *Behaviour. Supplement*, **2**, III–201.
- Irwin, D. E., Thimgan, M. P. & Irwin, J. H.** 2008. Call divergence is correlated with geographic and genetic distance in greenish warblers (*Phylloscopus trochiloides*): A strong role for stochasticity in signal evolution? *Journal of Evolutionary Biology*, **21**, 435–448.
- James, L. S. & Sakata, J. T.** 2017. Learning Biases Underlie “Universals” in Avian Vocal Sequencing. *Current Biology*, **27**, 3676–3682.
- James, L. S., Davies, R., Mori, C., Wada, K. & Sakata, J. T.** 2020. Manipulations of sensory experiences during development reveal mechanisms underlying vocal learning biases in zebra finches. *Developmental Neurobiology*, **80**, 132–146.
- Jesmer, B. R., Merkle, J. A., Goheen, J. R., Aikens, E. O., Beck, J. L., Courtemanch, A. B., Hurley, M. A., McWhirter, D. E., Miyasaki, H. M., Monteith, K. L. & Kauffman, M. J.** 2018. Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. *Science*, **361**, 1023–1025.
- Kempe, M. & Mesoudi, A.** 2014. An experimental demonstration of the effect of group size on cultural accumulation. *Evolution and Human Behavior*, **35**, 285–290.
- Kimura, M. & Crow, J. F.** 1964. The Number of Alleles That Can Be Maintained in a Finite Population. *Genetics*, **49**, 725–738.
- Kleczkowska, K.** 2015. Bird Communication in Ancient Greek and Roman Thought. *Maska*, **28**, 95–106.

- Koenig, W., Dunn, H. K. & Lacy, L. Y.** 1946. The Sound Spectrograph. *Journal of the Acoustical Society of America*, **18**, 19–49.
- Krebs, J., Ashcroft, R. & Webber, M.** 1978. Song repertoires and territory defence in the great tit. *Nature*, **271**, 539–542.
- Kroodsma, D. E.** 2004. The diversity and plasticity of birdsong. In: *Nature's music: The science of birdsong*, (Ed. by P. Marler & H. Slabbekoorn), pp. 108–131. San Diego: Elsevier.
- Lachlan, R. F. & Servedio, M. R.** 2004. Song learning accelerates allopatric speciation. *Evolution*, **58**, 2049.
- Lachlan, R. F. & Slater, P. J. B.** 2003. Song learning by chaffinches: How accurate, and from where? *Animal Behaviour*, **65**, 957–969.
- Lachlan, R. F., Verzijden, M. N., Bernard, C. S., Jonker, P. P., Koese, B., Jaarsma, S., Spoor, W., Slater, P. J. B. & Ten Cate, C.** 2013. The progressive loss of syntactical structure in bird song along an Island colonization chain. *Current Biology*, **23**, 1896–1901.
- Lachlan, R. F., Ratmann, O. & Nowicki, S.** 2018. Cultural conformity generates extremely stable traditions in bird song. *Nature Communications*, **9**, 2417.
- Laland, K. N. & Hoppitt, W.** 2003. Do Animals Have Culture? *Evolutionary Anthropology*, **12**, 150–159.
- Larsen, O. N. & Goller, F.** 2002. Direct observation of syringeal muscle function in songbirds and a parrot. *Journal of Experimental Biology*, **205**, 25 LP–35.
- Leeuwen, E. J. C. van, Kendal, R. L., Tennie, C. & Haun, D. B. M.** 2015. Conformity and its look-a-likes. *Animal Behaviour*, **110**, e1–e4.
- Liu, W. C., Gardner, T. J. & Nottebohm, F.** 2004. Juvenile zebra finches can use multiple strategies to learn the same song. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 18177–18182.
- MacDonald, I. F., Kempster, B., Zanette, L. & MacDougall-Shackleton, S. A.**

2006. Early nutritional stress impairs development of a song-control brain region in both male and female juvenile song sparrows (*Melospiza melodia*) at the onset of song learning. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 2559–2564.
- Mace, R.** 1987. The dawn chorus in the great tit *Parus major* is directly related to female fertility. *Nature*, **330**, 745–746.
- Marler, P. & Tamura, M.** 1962. Song "Dialects" in Three Populations of White-Crowned Sparrows. *The Condor*, **64**, 368–377.
- Marler, P. & Tamura, M.** 1964. Culturally transmitted patterns of vocal behavior in sparrows. *Science*, **146**, 1483–1486.
- Marsland, S., Priyadarshani, N., Juodakis, J. & Castro, I.** 2019. AviaNZ: A future-proofed program for annotation and recognition of animal sounds in long-time field recordings. *Methods in Ecology and Evolution*, **10**, 1189–1195.
- Martin, J. P., Doucet, S. M., Knox, R. C. & Mennill, D. J.** 2011. Body size correlates negatively with the frequency of distress calls and songs of Neotropical birds. *Journal of Field Ornithology*, **82**, 259–268.
- Mayr, E.** 1963. *Animal Species and Evolution*. Cambridge (MA): Harvard University Press.
- McGregor, P. K. & Krebs, J. R.** 1982. Song Types in a Population of Great Tits (*Parus major*): Their Distribution, Abundance and Acquisition by Individuals. *Behaviour*, **79**, 126–152.
- McGregor, P. K. & Krebs, J. R.** 1989. Song learning in adult great tits (*Parus major*): effects of neighbours. *Behaviour*, **108**, 139–159.
- McGregor, P. K., Krebs, J. R. & Perrins, C. M.** 1981. Song Repertoires and Lifetime Reproductive Success in the Great Tit (*Parus major*). *The American Naturalist*, **118**, 149–159.
- McInnes, L., Healy, J. & Astels, S.** 2017. hdbscan: Hierarchical density based clustering. *The Journal of Open Source Software*, **2**, 205.

- McInnes, L., Healy, J. & Melville, J.** 2018. UMAP: Uniform Manifold Approximation and Projection for Dimension Reduction. *The Journal of Open Source Software*, **3**, 861.
- Mercader, J., Barton, H., Gillespie, J., Harris, J., Kuhn, S., Tyler, R. & Boesch, C.** 2007. 4,300-Year-old chimpanzee sites and the origins of percussive stone technology. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 3043–3048.
- Mesoudi, A., Chang, L., Dall, S. R. X. & Thornton, A.** 2016 March. The Evolution of Individual and Cultural Variation in Social Learning. **31**, 215–225.
- Mets, D. G. & Brainard, M. S.** 2019. Learning is enhanced by tailoring instruction to individual genetic differences. *eLife*, **8**, 1–15.
- Mets, D. G. & Brainard, M. S.** 2017. Genetic variation interacts with experience to determine interindividual differences in learned song. *Proceedings of the National Academy of Sciences of the United States of America*, **115**, 421–426.
- Mets, D. G. & Brainard, M. S.** 2018. An automated approach to the quantitation of vocalizations and vocal learning in the songbird. *PLoS Computational Biology*, **14**, e1006437.
- Mikula, P., Valcu, M., Brumm, H., Bulla, M., Forstmeier, W., Petrusková, T., Kempenaers, B. & Albrecht, T.** 2020. A global analysis of song frequency in passerines provides no support for the acoustic adaptation hypothesis but suggests a role for sexual selection. *bioRxiv*, 2020.06.30.179812.
- Moon, K. R., Dijk, D. van, Wang, Z., Gigante, S., Burkhardt, D. B., Chen, W. S., Yim, K., Elzen, A. van den, Hirn, M. J., Coifman, R. R., Ivanova, N. B., Wolf, G. & Krishnaswamy, S.** 2019. Visualizing structure and transitions in high-dimensional biological data. *Nature Biotechnology*, **37**, 1482–1492.
- Morin, O.** 2016. Reasons to be fussy about cultural evolution. *Biology and Philosophy*, **31**, 447–458.

- Nelson, D. A.** 2000. A preference for own-subspecies' song guides vocal learning in a song bird. *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 13348–13353.
- Nottebohm, F., Stokes, T. M. & Leonard, C. M.** 1976. Central control of song in the canary, *Serinus canarius*. *Journal of Comparative Neurology*, **165**, 457–486.
- Nowicki, S., Searcy, W. A. & Peters, S.** 2002. Quality of song learning affects female response to male bird song. *Proceedings of the Royal Society B: Biological Sciences*, **269**, 1949–1954.
- Nunn, C. L., Thrall, P. H., Bartz, K., Dasgupta, T. & Boesch, C.** 2009. Do transmission mechanisms or social systems drive cultural dynamics in socially structured populations? *Animal Behaviour*, **77**, 1515–1524.
- Odom, K. J., Hall, M. L., Riebel, K., Omland, K. E. & Langmore, N. E.** 2014. Female song is widespread and ancestral in songbirds. *Nature Communications*, **5**, 1–6.
- Paxton, K. L., Sebastián-González, E., Hite, J. M., Crampton, L. H., Kuhn, D. & Hart, P. J.** 2019. Loss of cultural song diversity and the convergence of songs in a declining Hawaiian forest bird community. *Royal Society Open Science*, **6**,
- Payne, R. B.** 1982. Ecological Consequences of Song Matching: Breeding Success and Intraspecific Song Mimicry in Indigo Buntings. *Ecology*, **63**, 401–411.
- Päckert, M.** 2018. Song: The Learned Language of Three Major Bird Clades. 75–94.
- Perrins, C. M.** 1965. Population Fluctuations and Clutch-Size in the Great Tit, *Parus major* L. *Journal of Animal Ecology*, **34**, 601–647.
- Perry, S., Baker, M., Fedigan, L., Gros-Louis, J., Jack, K., MacKinnon, K. C., Manson, J. H., Panger, M., Pyle, K. & Rose, L.** 2003. Social conventions in wild white-faced capuchin monkeys: Evidence for traditions in a neotropical primate. *Current Anthropology*, **44**, 241–268.

- Pike, T. W. & Laland, K. N.** 2010. Conformist learning in nine-spined sticklebacks' foraging decisions. *Biology Letters*, **6**, 466–468.
- Podos, J.** 2001. Correlated evolution of morphology and vocal signal structure in Darwin's finches. *Nature*, **409**, 185–188.
- Podos, J. & Warren, P. S.** 2007. The Evolution of Geographic Variation in Birdsong. *Advances in the Study of Behavior*, **37**, 403–458.
- Podos, J., Southall, J. A. & Rossi-Santos, M. R.** 2004. Vocal mechanics in Darwin's finches: Correlation of beak gape and song frequency. *Journal of Experimental Biology*, **207**, 607–619.
- Renoult, J. P. & Mendelson, T. C.** 2019. Processing bias: Extending sensory drive to include efficacy and efficiency in information processing. *Proceedings of the Royal Society B: Biological Sciences*, **286**, 20190165.
- Richerson, P. J. & Boyd, R.** 2005. *Not by Genes Alone: How Culture Transformed Human Evolution*. Chicago: University of Chicago Press.
- Ritchie, G. R. S., Kirby, S. & Hawkey, D. J. C.** 2008. Song learning as an indicator mechanism: Modelling the developmental stress hypothesis. *Journal of Theoretical Biology*, **251**, 570–583.
- Rivera-Gutierrez, H. F., Matthysen, E., Adriaensen, F. & Slabbekoorn, H.** 2010. Repertoire sharing and song similarity between great tit males decline with distance between forest fragments. *Ethology*, **116**, 951–960.
- Ríos-Chelén, A. A., Salaberria, C., Barbosa, I., Macías Garcia, C. & Gil, D.** 2012. The learning advantage: Bird species that learn their song show a tighter adjustment of song to noisy environments than those that do not learn. *Journal of Evolutionary Biology*, **25**, 2171–2180.
- Ryan, M. J. & Brenowitz, E. A.** 1985. The Role of Body Size, Phylogeny, and Ambient Noise in the Evolution of Bird Song. *The American Naturalist*, **126**, 87–100.
- Sainburg, T., Theilman, B., Thielk, M. & Gentner, T. Q.** 2019. Parallels in the sequential organization of birdsong and human speech. *Nature Communications*

nlications, **10**,

- Sasaki, T. & Biro, D.** 2017. Cumulative culture can emerge from collective intelligence in animal groups. *Nature Communications*, **8**, 15049.
- Searfoss, A. M., Pino, J. C. & Creanza, N.** 2020. Chipper: Open-source software for semi-automated segmentation and analysis of birdsong and other natural sounds. *Methods in Ecology and Evolution*, **11**, 524–531.
- Seddon, N.** 2005. Ecological adaptation and species recognition drives vocal evolution in neotropical suboscine birds. *Evolution*, **59**, 200–215.
- Slabbekoorn, H. & Smith, T. B.** 2002. Bird song, ecology and speciation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **357**, 493–503.
- Slater, P. J. B.** 1986. The cultural transmission of bird song. *Trends in Ecology and Evolution*, **1**, 94–97.
- Slater, P. J. B.** 2003. Fifty years of bird song research: A case study in animal behaviour. *Animal Behaviour*, **65**, 633–639.
- Slater, P. J. B. & Lachlan, R. F.** 2003. Is Innovation in Bird Song Adaptive? In: *Animal innovation*, (Ed. by S. M. Reader & K. N. Laland), pp. 117–135. Oxford: Oxford University Press.
- Smaldino, P. E. & Epstein, J. M.** 2015. Social conformity despite individual preferences for distinctiveness. *Royal Society Open Science*, **2**,
- Spurgin, L., Bosse, M., Adriaensen, F., Albayrak, T., Barboutis, C., Belda, E., Bushuev, A., Cecere, J., Charmantier, A., Cichon, M., Dingemanse, N., Doligez, B., Eeva, T., Erikstad, K. E., Fedorov, V., Griggio, M., Heylen, D., Hille, S., Hinde, C., Ivankina, E., Laine, V., Kempenaers, B., Kerimov, A., Krist, M., Kvist, L., Mänd, R., Matthysen, E., Nager, R., Nikolov, B., Norte, A. C., Orell, M., Ouyang, J., Petrova-Dinkova, G., Richner, H., Rubolini, D., Slagsvold, T., Tilgar, V., Török, J., Tschirren, B., Vágási, C., Yuta, T., Groenen, M., Visser, M., Oers, K. van, Sheldon, B. & Slate, J.** 2019. The great tit HapMap project: a continental-scale analysis of genomic variation in a songbird. *bioRxiv*, 561399.

- Suthers, R. A.** 2004. How birds sing and why it matters. In: *Nature's music: The science of birdsong*, (Ed. by P. Marler & H. Slabbekoorn), pp. 272–295. New York.
- Tchernichovski, O., Feher, O., Fimiarz, D. & Conley, D.** 2017. How social learning adds up to a culture: From birdsong to human public opinion. *Journal of Experimental Biology*, **220**, 124–132.
- Thorpe, W. H.** 1958. The Learning of Song Patterns By Birds, With Especial Reference To the Song of the Chaffinch Fringilla Coelebs. *Ibis*, **100**, 535–570.
- Tobias, J. A. & Seddon, N.** 2009. Signal design and perception in hypocnemis antbirds: Evidence for convergent evolution via social selection. *Evolution*, **63**, 3168–3189.
- Tobias, J. A., Aben, J., Brumfield, R. T., Derryberry, E. P., Halfwerk, W., Slabbekoorn, H. & Seddon, N.** 2010. Song divergence by sensory drive in amazonian birds. *Evolution*, **64**, 2820–2839.
- Tobias, J. A., Cornwallis, C. K., Derryberry, E. P., Claramunt, S., Brumfield, R. T. & Seddon, N.** 2014. Species coexistence and the dynamics of phenotypic evolution in adaptive radiation. *Nature*, **506**, 359–363.
- Van Boheemen, S. J., Diblíková, L., Bílková, J., Petrusek, A. & Petrusková, T.** 2019. Extraordinary variation in a simple song: No geographical patterns in initial phrase variation of the Yellowhammer, a passerine with pronounced dialects. *Auk*, **136**, 1–18.
- Vehtari, A., Gelman, A. & Gabry, J.** 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing*, **27**, 1413–1432.
- Verzijden, M. N., Cate, C. ten, Servedio, M. R., Kozak, G. M., Boughman, J. W. & Svensson, E. I.** 2012. The impact of learning on sexual selection and speciation. *Trends in Ecology and Evolution*, **27**, 511–519.
- Whitehead, H. & Richerson, P. J.** 2009. The evolution of conformist social learning can cause population collapse in realistically variable environ-

- ments. *Evolution and Human Behavior*, **30**, 261–273.
- Whiten, A.** 2019a. Cultural Evolution in Animals. *Annual Review of Ecology, Evolution, and Systematics*, **50**, 1–22.
- Whiten, A.** 2019b. Cultural Evolution in Animals. *Annual Review of Ecology, Evolution, and Systematics*, **50**, 1–22.
- Whiten, A., Ayala, F. J., Feldman, M. W. & Laland, K. N.** 2017. The extension of biology through culture. *Proceedings of the National Academy of Sciences*, **114**, 7775–7781.
- Williams, J. M. & Slater, P. J. B.** 1990. Modelling bird song dialects: the influence of repertoire size and numbers of neighbours. *Journal of Theoretical Biology*, **145**, 487–496.
- Williams, H., Levin, I. I., Norris, D. R., Newman, A. E. M. & Wheelwright, N. T.** 2013. Three decades of cultural evolution in Savannah sparrow songs. *Animal Behaviour*, **85**, 213–223.
- Yeh, D. J. & Servedio, M. R.** 2015. Reproductive isolation with a learned trait in a structured population. *Evolution*, **69**, 1938–1947.
- Zirin, R. A.** 1980. Aristotle's Biology of Language. *Transactions of the American Philological Association*, **110**, 325–347.