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**École doctorale 139 :
Connaissance, langage,
modélisation
Laboratoire Éthologie
Cognition
Développement (LECD)**

Tifany VOLLE

Ontogenèse et fonctions du partage vocal chez un oiseau chanteur, le rougequeue noir, *Phoenicurus ochruros*

Thèse présentée et soutenue publiquement le 26 juin 2024

en vue de l'obtention du grade de docteur en Neurosciences,

spécialité Ethologie et Cognition

sous la direction de Sébastien DEREGNAUCOURT et Tudor Ion DRAGANOIU

Membres du jury:

Elodie Floriane Mandel-Briefer	Rapporteure	PR-HDR, University of Copenhagen
Clémentine Vignal	Examinatrice et Présidente	PR-HDR, Université Sorbonne Université
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Under the supervision of

Sébastien DEREGNAUCOURT & Tudor-Ion DRAGANOIU

FOREWORD

This PhD project has been made possible by a grant from the Université Paris Nanterre and the Doctoral School ED 139.

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ACKNOWLEDGMENTS / REMERCIEMENTS

Je remercie les membres du jury, Elodie Floriane Mandel-Briefer, Hans Slabbekoorn, rapporteurs, Nicole Geberzahn et Clémentine Vignal, examinatrices, d'avoir accepté de prendre le temps de lire et d'évaluer mon travail ; ainsi que mon comité de suivi de thèse : Charlotte Curé, Nicolas Mathevon et Fanny Rybak, qui m'ont suivie et conseillée tout au long de mon parcours.

Merci à Sébastien Derègnaucourt et Tudor Draganoiu, mes directeurs de thèse, pour m'avoir confié ce projet et permis d'étudier un sujet qui me passionne. Ils m'ont poussé à acquérir de nombreuses connaissances et ont su nourrir mon autonomie. Ils m'ont également fait confiance pour encadrer les projets scientifiques d'étudiants de Master et pour présenter mes travaux à de nombreux colloques.

Je tiens à exprimer toute ma gratitude aux personnes sans qui cette thèse n'aurait pas pu aboutir. Je tiens surtout à remercier tous ceux qui par leur soutien m'ont fait murir et faire que ces dernières années resteront pour moi une expérience marquante.

Tout d'abord merci à l'équipe du LECD (Laboratoire d'Ethologie, Cognition, Développement). Les enseignants et plus particulièrement Nicole Geberzahn pour sa bienveillance. Ce fut un plaisir d'échanger avec elle. J'adresse une pensée à Laurent Nagle pour sa visite sur le terrain durant mon master et des premiers filets que j'ai aidés à poser pour le bagage des oiseaux. Je remercie Sandra Boyer qui m'a permis d'acquérir les compétences en gestion et administration nécessaires au métier de chercheur. Pour ses conseils avisés et petits remontants sucrés, pour l'attention qu'elle porte aux doctorants je la remercie sincèrement.

J'adresse toute ma gratitude aux docteures qui m'ont précédé, brillantes jeunes femmes, modèles de persévérance à toutes épreuves, sources d'inspiration, notamment Alice Araguas pour sa lucidité et sa capacité à transmettre ses connaissances, Lucille Le Maguer, Uyen Tran, Charlotte De Mouzon. Elles m'ont montré leur détermination et leur bienveillance.

Merci à mes compagnons de bureau, doctorants ou stagiaires : Camille Le Gal et Clara Damage pour nos sorties culturelles ou gastronomiques et vos conseils judicieux. Julie Bosca pour partager son savoir en statistiques et son précieux Caillou. Julie et Camille, merci pour nos moments de gloire partagés en conférences. Romain Di Stasi, compagnon de liste blanche, pour nos débats et nos paris que j'ai toujours (presque) gagnés ! Marie Huet et Lucas Batory pour leur infinie gentillesse et leur accueil. Marion Burtey, d'un courage exemplaire, pour qui j'ai une pensée ce jour. Juliette Aychet et Juliana Lopez Marulanda pour m'avoir rassuré au cours de mes dernières années de doctorat. Bon courage aux derniers arrivés Timon Lebaron-Kherif et Océane Cossu-Doye. Surtout, merci à tous pour avoir supporté mon humour et pour votre réconfort dans les moments ardus.

Avoir partagé et voir avancer tous ceux que j'ai croisés au LECD a été un plaisir partagé ; en particulier Chloé O'Neill et Elise Gauthier, qui je suis sûre, seront de fantastiques chercheuses. A ceux qui ont été avec moi sur le terrain, Nicolas Coron et Léa Brun, dans des conditions parfois difficiles. Merci aux stagiaires, Rémi Chambon, Elodie Schloesing, Amanda Cocquelet, Samuel Desvisgnes, Manon Nourdin, que je n'ai pas eu la chance de tous rencontrer et qui ont contribué, de 2015 à 2018, à agrandir le jeu de données utilisées pour ma thèse.

Merci à Rémi Chambon pour son expertise en statistiques et le temps précieux qu'il m'a accordé. Son soutien et ses encouragements m'ont motivé, sa patience et sa pédagogie m'ont fait énormément progresser. Je garde en mémoire ta rigueur de travail et tes conseils avisés.

Merci à tous les bagueurs qui m'ont permis de réussir mon permis spécialiste avec une mention toute particulière pour Sébastien Gauthier, tout comme moi passionné, pour son investissement. Il a su m'encourager dans les moments difficiles et me faire gagner en assurance, il a su me transmettre ses valeurs éthiques et ses compétences. Un grand merci à sa famille de m'avoir accueilli. « ET BIM ! »

Merci à tous les habitants de La Valla-sur-Rochefort, village dans lequel j'ai passé quatre saisons de terrain, pour la confiance accordée lors de mes passages matinaux avec mon micro, mes jumelles et ma tenue de Mère Noël. Plus particulièrement, les familles Charles, Rebourg, Rolland pour le confort que je leur dois : la tasse de café ou le verre de cassis et tant d'autres attentions (conversations, légumes du jardin, logement) qui fond chaud au cœur, pour leur présence réconfortante lors des périodes de confinement Covid.

A ceux qui m'ont montré le chemin, Joël Attia et Will Swaney. Le premier que je remercie de son accueil et sa disponibilité pour une première visite à l'ENES (Equipe de Neuro-Ethologie Sensorielle) en 2012. Il m'a transmis sa passion pour la recherche en éthologie et en bioacoustique. Le second pour son suivi longitudinal d'une universitaire de 2014 à ce jour. Il a été mon tuteur de première année de Bachelor et reste un conseiller précieux avec son œil d'expert lors de nos rencontres en conférences.

Pour ses grandes capacités d'écoute et d'analyse et pour avoir cru en moi, merci à Philippe Pouget. Il m'a aidé à tenir le cap. Merci à Philippe Solal pour sa disponibilité et ses conseils.

A mes amis les plus proches et leur moitié : François-Xavier Brun, Dihia Ikene Maller, Victoria Sauvage, Leila Yildirim, Daniel Taylor, un grand merci d'avoir été présents aux bons moments, pour toutes vos attentions à mon égard, votre grande patience et la force que vous m'apportez.

Merci à ma famille, Clémence Bourcet et Emmanuel Bovari pour avoir gardé le lien et apporté leur soutien au fil de ces années. A mes parents source infinie et indéfectible de soutien en tous genres. Merci à mon frère, Arthur, d'avoir pris soin de moi à distance.

Merci à ceux que j'ai peut-être oubliés ou restés anonymes pour tous les mots d'encouragements que vous m'avez adressés. A tous ceux qui ont pris de mes nouvelles et leur patience à attendre ma réponse Pour tous vos messages bienveillants, merci infiniment.

Et pour finir, aux chanteurs des concerts matinaux, les rougequeues noirs de La Valla-sur-Rochefort. En particulier au doyen nommé George de l'Orme : merci pour être revenu à chacune de mes périodes de terrain, pour ta présence réconfortante et indéfectible. A jamais ma mascotte. Un exemple, qui m'a inspiré à persévérer au cours de mon voyage de doctorat. En effet : que de battements d'ailes pour faire toutes ces migrations huit ans durant !

« Soyez comme l'oiseau posé pour un instant sur des rameaux trop frêles qui sent plier la branche, et qui chante pourtant, sachant qu'il a des ailes. »

Victor Hugo

NOTES TO READERS

This PhD project is constituted of several scientific papers written independently, each paper representing a chapter of the thesis. Therefore, the reader might find some redundancies from one chapter to another. References of the general introduction and general discussion were merged and placed at the end of this manuscript.

Paper 1

“Lifetime evolution of vocal repertoires in a songbird, the black redstart: a longitudinal field approach

Tifany Volle, Sébastien Derégnaucourt, Tudor-Ion Draganoiu

Prepared for submission to *Animal Behaviour*

Paper 2

“Foreign-local microdialect discrimination in a songbird, the black redstart”

Tifany Volle, Sébastien Derégnaucourt, Rémi Chambon, Tudor-Ion Draganoiu

Published in *Animal Behaviour*

TABLE OF CONTENTS

GENERAL INTRODUCTION

1. Vocal learning

Vocal communication is used by many vertebrate species during interactions such as courtship, mating, territorial defence, offspring care and sharing emotional state (Garcia & Favaro, 2017; Rohrmeier et al., 2015; Seyfarth & Cheney, 2003, 2010). Studying animal vocal communication helps us to better understand how these animal societies are organised (Freeberg et al., 2012) and identify the evolutionary bases, the ontogenesis and the neurological processes behind human language (Fitch, 2010). Vocal learning is necessary for the acquisition of speech in Humans. Vocal learning is only shared with a few other groups of animals (Doupe & Kuhl, 1999; Janik & Knörnschild, 2021).

1.1 What is vocal learning?

Vocal learning is defined as the ability to learn and modify vocal signals by imitating conspecifics or other species and is, therefore, strongly linked to an individual's auditory experience (Boughman & Moss, 2003; Janik & Slater, 2000). It is an evolutionary rare trait that only appeared in a few groups of the animal kingdom. Vocal learning has been observed in humans (Bruner, 1981; Hauser et al., 2002), cetaceans (Janik, 2014), elephants (Stoeger & Manger, 2014), pinnipeds (Reichmuth & Casey, 2014), bats (Boughman, 1997, 1998) and three bird orders: Psittaciformes (parrots), Apodiformes (hummingbirds), and Passeriformes (perching birds) (Janik & Knörnschild, 2021; Searcy & Nowicki, 2019). Its presence in an Anseriform species, the Australian musk duck, *Biziura lobata*, has been observed but remains in need of more research (ten Cate, 2021; ten Cate & Fullagar, 2021).

1.2 Vocal learning in Passeriformes

Birdsong is one of the most studied communication systems both in the field and in the laboratory (Brenowitz & Beecher, 2005; Kipper & Kiefer, 2010). Birds have two types of vocalisations: calls, which are simple, and songs, which are more complex. Although these two categories exist, it is sometimes difficult to classify the vocalisations of certain species into one of them, and ultimately the classification can be done arbitrarily (Catchpole & Slater, 2008). Here we will use the definition given by Smotherman et al., (2016) which is based on those of Marler and Slabberkoorn (2004), Catchpole and Slater (2008) and Bradbury and Vehrencamp (2011): " Calls are short discreet vocalizations uttered irregularly or in isolation in support of specific social functions such as alarm calls, contact calls and begging calls, which are typically used within close range of conspecifics to coordinate intraspecific social behaviors. Songs are longer, more complex stereotyped call sequences that are repeated frequently and spontaneously following discrete daily and seasonal emission patterns typically associated with courtship and territorial behaviors". In order to make an inventory of the different signals that an individual can produce, these are grouped together in what is known as a song or call repertoire. In Passerines, oscines have been widely studied for their ability to learn their songs while one of its sister groups, the suboscines have been considered as non-vocal learners. Yet evidence of vocal learning has been found in two suboscines, the three-wattled bellbird, *Procnias tricarunculata* and the bare-throated bellbird, *Procnia nudicollis* (Kroodsma et al., 2013; Saranathan et al., 2007). Still more research is needed to fully appreciate the vocal learning abilities of suboscines which are an underrepresented taxa in this research area (Loo & Cain, 2021; ten Cate, 2021).

GENERAL INTRODUCTION

Oscines have been a model of choice in the study of vocal learning and decades of studies allowed the identification of neural pathways and genes involved in vocal learning, to shed light on the diversity of vocal development strategies and factors influencing the content learned by individuals (Lattenkamp & Vernes, 2018). The different steps involved in song learning are: the sensory phase, during which juveniles will hear and memorize songs, followed by the sensory motor phase, at this time pupils practice and modify their songs using auditory feedback. During this phase songs are referred to first subsong and then plastic songs; after this step learned songs will crystallise into their final form (Brainard & Doupe, 2002; Konishi, 1965, 1985; Rundstrom & Creanza, 2021; Soha, 2017; Thorpe, 1958). These steps have variable durations and number of occurrences throughout a bird's lifetime depending on the species (Hyland Bruno et al., 2021). For example, species like the zebra finch, *Taeniopygia guttata,* are only able to learn during the first months of life (sensitive phase) before their song crystallises while species like the European starling, *Sturnus vulgaris,* are able to learn new songs throughout their lifetime (Adret-Hausberger et al., 1990; Chaiken et al., 1994; Mountjoy & Lemon, 1995; Zann, 1996). These discoveries gave rise to the following dichotomic categorisation of closed-ended learners on one side and open-ended learners on the other (Brenowitz & Beecher, 2005). Nowadays, this dichotomic view of learning programs has been refined and replaced by a continuum along which species can be placed, reflecting better the diversity of learning programs observed. Despite more than 50 years of focus on the matter of song learning out of the 4000 plus species of oscines, only a few have been studied (Searcy et al., 2021) . Furthermore research on oscine songs has mostly been focused on males but it has now been shown that female singing is a widespread phenomenon, especially among tropical songbirds and it is believed that singing of both sexes is the ancestral condition (Odom et al., 2014). The study of female songs has consequently been affected by this bias and has therefore received less attention (Riebel, 2016; Riebel et al., 2019).

1.3 A parallel between birds and humans

The success of oscines as a model in the study of vocal learning, is partly due to the similarity in the process of vocal learning found with humans. Indeed, both go through a sensory phase and a sensorimotor phase with variable vocalisations before they produce proper species-specific vocalisations (babbling in humans and subsongs in birds) (Kuhl, 2004). In addition, oscine and humans have comparable neuroanatomical structures (Chakraborty & Jarvis, 2015; Zhang et al., 2023). Comparing the oscine neural control brain regions and pathways associated with vocal learning has helped to guide our understanding of human brain structures using a simpler model (Brainard & Doupe, 2002; Doupe & Kuhl, 1999). Finally, birds are easy to keep and breed in the laboratory compared to other species. Another characteristic common to both songbirds and humans is the presence of learned geographically restricted “dialects” (Marler, 1970; Nettle, 1999; Trudgill, 1983). This is because vocal learning can lead to the emergence of vocal cultures in humans as well as in other vocal learners.

2. Vocal culture in non-humans

Vocal learning plays an important role in the apparition of dialects as this type of learning is based on imitation. Vocal learning enables the accurate transmission of local patterns that can last for hundreds of generations (Lachlan et al., 2018) and can also facilitate novel patterns of vocalisations, issued from copying error or innovation to spread through a population (McGregor et al., 1997). A wide range of vocal learning taxa present vocal dialects (also known as “vocal cultures”). Vocal culture is not the only type of culture found in the animal kingdom, as culture was observed on behaviours such as tool use, sexual behaviours, foraging behaviours and migration itineraries to name a few (Whiten, 2021). Here, we will only focus on vocal cultures.

2.1 Definition of dialects

Dialects (also known as “vocal cultures”) are defined as vocal variations among populations, at different geographic scale delineated from each other by boundaries (Baker & Cunningham, 1985; Mundinger, 1982). Dialectal boundaries are generally sharp, yet in some population they are less abrupt, as individuals at this boundaries can display bilingualism (Henry et al., 2015). A wide range of vocal learning taxa demonstrate vocal dialects and research concerning the latter is the largest source of evidence for culture in the animal kingdom. Besides humans and birds, dialects have also been described in mammals, mainly in bats (Boughman, 1997; Davidson & Wilkinson, 2002; Esser & Schubert, 1998) and cetaceans (Ford, 1991; Rendell & Whitehead, 2001; Schulze et al., 2022; Weilgart & Whitehead, 1997; Whitehead & Rendell, 2015).

2.2 Dialects in cetaceans

The phenomenon of humpback whale song dialects stands out as a prominent example of vocal culture within the various clades of cetaceans. However, it is not the only one, as dialects have also been documented in killer whales and sperm whales

(Ford, 1991; Rendell & Whitehead, 2003). The song of a male humpback whale, *Megaptera novaeangliae,* is long, complex, stereotyped, has a hierarchical structure and is used as a sexual display (Herman & Tavolga, 1980; Payne & McVay, 1971). Males from the same population sing the same song at any point in time, showing strong cultural conformity (Payne et al., 1983; Payne & Payne, 1985). In addition, song evolution is constant and the song will progressively change within and between years (Cerchio et al., 2001; Garland et al., 2011; Payne & Payne, 1985). Males' song can also be rapidly changed to a completely novel one, this process is called song revolution and has only been documented in this non-human animal as of today. This process has been observed multiple times over decades in the south pacific populations (Garland et al., 2011, 2012, 2013, 2015, 2017). It takes around two years for a song variant to be horizontally transmitted east across the populations in the South Pacific, from the east Australian population across to French Polynesia population (Noad et al., 2000). Song evolution renders a song more complex as time passes but once the song has fully changed to a new version or a novel song is learned, then the song is simpler (Allen et al., 2018; Garland et al., 2021; Tyarks et al., 2022).

2.3 Dialects in birds

At first, vocal dialects research was focused mostly on the song of oscines and the other two vocal learning bird taxa, parrots and hummingbirds were left aside. More recently, geographical variation in parrots calls have been reported (Wright & Dahlin, 2018). Indeed, contact calls dialects have been observed at a regional and a roost site level (Baker, 2000; Bradbury et al., 2001; Wright, 1996; Wright & Dahlin, 2018). Additionally, laboratory experiments have shown that groups of parrots tend to display convergence towards shared calls, with newcomers adopting the vocalizations of the groups they join (Bartlett & Slater, 1999). Furthermore, song dialects were also reported in several species of hummingbirds including, for example, the little Hermit, *Phaethornis longuemareus*, the long-tailed hermit hummingbird, *Phaethornis superciliosus* and the long-billed hermits, *Phaethornis longirostris*, (Araya-Salas et al., 2019; Araya-Salas & Wright, 2013; Stiles & Wolf, 1979; Wiley, 1971). In Costa Rica, the latter, which is a lek-mating hummingbird has distinctive acoustic signatures at a small geographical scale. More precisely males showed acoustic signature at the lek and song-neighbourhood level (sub units of a lek)(Araya-Salas et al., 2019). Despite the previous examples given, research on both parrot and hummingbirds dialect is still lacking and requires more research efforts. Song dialects have been extensively studied in songbirds over the last 50 years and are discussed thereafter.

2.4 Dialects in songbirds

Studying geographic variation in vocal signals in songbirds, dialects (Podos & Warren, 2007), has captured scientific interest for over 50 years and continues to do so. Since the seminal work carried out by Marler & Tamura (1962) on white-crowned sparrows, *Zonotrichia leucophrys*, which compared three populations of white-crowned sparrows, separated on average by 10 km, along the San Francisco bay and reported only few song variations between males of the same population but great differences in the song structure between populations, researchers focused on how dialects appeared and are maintained as well as their adaptive significance.

2.5 Characteristics and examples of birdsong dialects

There is great variation among the 4000-plus species of oscines in the number of different species' song versions, also referred to as song types, they are able to sing. Indeed song repertoire size can range from 1 to over 2000 song types (Macdougall-Shackleton, 1997). All together these different song types compose the song repertoire of an individual (Catchpole & Slater, 2008). An example of this variation in song repertoire size between species can be illustrated when comparing birds such as the orange-crowned warbler, *Vermivora celata,* (Yoon et al., 2012) and the white-crowned sparrow (Nelson & Poesel, 2011) which possess only one song type to the tropical mockingbird, *Mimus gilvus*, with 133 song types (Price & Yuan, 2011) and the brown thrasher, *Toxostoma rufum*, which as a repertoire of more than 2000 song types (Kroodsma & Parker, 1977). Nowadays a wide range of songbirds species have been observed to display song dialects (reviewed in Krebs & Kroodsma, 1980; Podos & Warren, 2007).

2.5.1 Geographical scale and boundaries

In songbirds, dialects have been observed at different geographical scales, and Podos and Warren (2007) proposed the following classification based on the geographical spread and / or the number of individuals sharing similar songs. Dialects range from microgeographic, when found at distances inferior to 2 km and shared by less than 10 individuals to large dialects spread over 100 km and more than 1000 individuals (see **Table 1** for all categories). Microdialects have been described in Eurasian skylarks, *Alauda arvensis* (Briefer et al., 2011), Savannah sparrows, *Passerculus sandwichensis* (Hensel et al., 2022; Thomas et al., 2021), while a well-studied example of dialects over large spatial scales can be found in the yellowhammer, *Emberiza citrinella,* over central Europe (Diblíková et al., 2023; Petrusková et al., 2015; Wonke & Wallschläger, 2009). Even though boundaries between dialects are usually sharp, in areas where they meet, bilingual individuals singing elements of adjacent dialects can be observed (see **Table 2** in Podos & Warren, 2007, and Päckert, 2018). It is also important to acknowledge that pattern of song sharing might apply to specific populations but not to the entire species. It is the case for ortolan buntings, *Emberiza hortulana*, in which neighbouring males in the populations of central and southern Europe display similar final phrase of a song though in a small isolated population of Norway males do not express this pattern of sharing (Osiejuk et al., 2007). For the population of Norway, the absence of dialect was suggested to be caused by various ecological factors (Osiejuk et al., 2007). Male biased sex ratio promotes males to disperse further than their initial natal dispersal distances. Combined to an extended learning period towards a large number of tutors followed by selective attrition this leads males to have a repertoire size twice the one found in central European males. Dispersal, learning strategies and isolation seem to drive songs variations which leads to the loss of dialect cues significance and presence in the Norwegian population (Osiejuk et al., 2007).

Table 1. Characteristics of the four different sizes of dialects as described by Podos and Warren (2007)

Dialect sizes	Spread (km)	Number of individuals sharing
Microgeographic	< 2 km	< 10
Small	2 -10 km	< 100
Medium	10 - 100 km	< 1000
Large	< 100 km	> 1000

2.5.2 Timeframe

Years of research on the matter of vocal geographical variation coupled with longitudinal studies of populations revealed the different durations during which they are maintained. Although dialects can be maintained over several decades, as it is found in the white-crowned sparrow where they lasted for 40 years (Marler and Tamura 1962; Nelson et al. 2004), they can also quickly change from year to year. Indeed, in corn buntings, *Miliaria calandra*, all males concurrently gradually modify elements of their local song to another common version (McGregor et al., 1997). This gradual modification of elements gives a new version of the local song every breeding season and also leaves noticeable resemblances between songs from different years (e.g. Holland et al., 1996; McGregor et al., 1997; McGregor & Thompson, 1988). Different land use by humans, resulted in different patterns in dialect evolution in this species. Indeed, in Cornwall, within an area which underwent a rapid change in land use, dialect from 14 years apart showed no similarity (Holland et al., 1996) while in a population located in agricultural land in Oxfordshire, which use did not change, it was found that despite some elements gradually changing, dialect stayed stable for eight years (McGregor & Thompson, 1988).

2.5.3 Dialects' importance for conservation

Nowadays conservation of species is a rising concern, and several researchers have brought up the importance of dialects' research in this issue. Actually, changes in populations dialect systems can reflect habitat loss or degradation causing a change in the population structure (Laiolo & Tella, 2007; McGregor et al., 1997). Regent honeyeaters, *Anthochaera phrygia*, are critically endangered Australian songbirds, their population has declined to an estimated 200-400 birds distributed over a 300 000 km² range *(see National Recovery Plan for the Regent Honeyeater., 2016*). This decrease in the population size is mainly due to habitat loss caused by human activity. In this population, 27 per cent of males did not sing the regional dialect (Crates et al., 2021). In addition, the song complexity of the regent honeyeater has declined in the past decades. In areas of very low-density 12 per cent of males sang other species' songs. This is due to the restricted access to tutors young males experience during their song-learning phase, which is triggered by the low population density. In this species habitat loss and the declining population density lead to the erosion of local dialects and song complexity which has repercussions on male fitness (Crates et al., 2021). The effect of habitat fragmentation on vocal traditions has been shown in other species such as the Dupont’s lark, *Chersophilus duponti* (Laiolo & Tella, 2007) and the orange-billed sparrow, *Arremon aurantiirostris* (Hart et al., 2018). Birdsong evolution can be strongly impacted by human activities (e.g. habitat modification, noise, chemical pollution…), affecting both the acoustic and physical environment of birds (Brumm & Slabbekoorn, 2005) as demonstrated by the past examples. Consequently, birdsong evolution can be revealed to be a great indicator of changes in the population density or pending extinction, making the study of vocal signals a great tool for conservation. Furthermore, dialects are cues used by both females and males during their interactions and the use of the proper dialect by a reintroduced individual could facilitate its integration in the group and at a larger scale the success of a conservation operation (Crates et al., 2021; Lewis et al., 2021; Martins et al., 2018; Wright & Dahlin, 2018).

2.6 Origins and function of dialects

Podos and Warren (2007) highlight the importance of species' dispersal pattern and song learning role into dialect evolution as well as the potential fitness benefits vocal sharing could provide. Three broad categories of hypotheses have been proposed to explain dialect evolution.

2.6.1 The epiphenomenon hypothesis

The epiphenomenon hypothesis is considered as the null hypothesis for dialect evolution. It was briefly introduced by Andrew (1962) and suggests that dialects arise as by product of specific learning programs and dispersal patterns, both of which undergo evolutionary changes driven by selective pressures unrelated to dialect formation. For example, dialects could evolve as a result of selection for optimal transmission of songs through the habitats, leading to an adaptation to the acoustic environment (Doutrelant et al., 1999; Hunter & Krebs, 1979; Slabbekoorn & Smith, 2002b). Consequently, dialects systems arise when populations reside in distinct habitats. But habitats properties are not the only driver of vocal variation; indeed, morphological constrains could also lead to the evolution of different dialects. Podos and Warren (2007) noted that contrary to the other two following functional hypothesis, it does not require negative selection against foreign dialect singers.

2.6.2 The genetic or local adaptation hypothesis

The "local adaptation hypothesis" was formalized by Nottebohm (1969) and posits that females preferentially mate with males from their natal region, compared to males from other regions as they can gain fitness advantages (Marler & Tamura, 1962).

A consequence of such selective pairing for the offspring of the pair is the likelihood of showing adaptation to the local ecological conditions. Four predictions are made under the local adaptation hypothesis: 1) young birds learn their song early, before they disperse from their natal area, this is referred to as pre-dispersal learning; 2) During dispersion birds preferentially settle in localities where other birds sing similar songs to them, compared to an area occupied by birds singing a “foreign” dialect; 3) As a result of assortative mating populations with different dialects eventually end up to genetically diverge/ differentiate; 4) Female evolve preferences for males of their natal dialect during mate choice. The third assumption of this hypothesis, that dialects could reduce gene flow between population and promote speciation through assortative mating is still an area of debate (Toews, 2017). Even though it seems to hold true for some species (Helbig et al., 2001; Lipshutz et al., 2017; Shipilina et al., 2017 but see Soha, 2020). Wheatcroft et al. (2022) also demonstrate a bias towards local dialect in nestlings pied flycatchers, *Ficedula hypoleuca.* They hypothesize that this discrimination could result in pre-mating reproductive barriers with foreign dialect singers and with a closely related species, the collared flycatcher, *Ficedula albicollis*.

2.6.3 The social adaptation hypothesis

The social adaptation hypothesis posits that male singing songs similar to other males of their region gain fitness advantages while males singing nonlocal songs face social penalties (Payne, 1981). This hypothesis predicts that males learn local songs post-dispersal and that dialects result from an adjustment to local song conditions (Payne, 1981). As previously mentioned, exhibiting the local song could be advantageous to males, in both intra- and inter-sexual interactions. For example, one year-old males indigo buntings, *Passerina cyanea*, that match the local microdialect exhibit higher levels of mating success and fledging rates compared to those that do not match the dialect (Payne, 1982). In song sparrows, *Melospiza melodia*, song sharing with neighbouring males was positively correlated to lifetime territory tenure (Beecher et al., 2000). Also, the more a young male shares songs with an older male from which he learned, the longer both individuals will survive (Beecher et al., 2020). Furthermore, song similarity with other males could serve as a social password (Feekes, 1977) and as a marker of long-term residency (Rothstein & Fleischer, 1987). As a consequence, the number of aggressive interactions between males sharing the same dialect decrease while more aggression is directed towards foreign dialects singers (Briefer et al., 2010; Thomas et al., 2021). Another benefit of song sharing between individuals, is the use of shared songs during territorial interactions to regulate the level of aggression. For example a territory owner can match the song type used by the intruder (song type matching), and increase the level of aggression, or use a song present in both its and the rival's repertoire but not presently sung (repertoire matching) to decrease it (Akçay et al., 2013; Vehrencamp, 2001; Vehrencamp et al., 2007 reviewed in Logue, 2021 and Todt & Naguib, 2000).

Dialect systems are rare and their features present important variations between species (Podos & Warren, 2007). Therefore, there is a consensus that several of the hypotheses previously presented are necessary to explain dialects evolution in a population (Soha, 2020). To date, relatively scarce research efforts were directed towards the function of microdialects (e.g. Briefer et al., 2010; Payne, 1982; Thomas et al., 2021).

2.7 Local and foreign dialects discrimination

A subject that has passionated researchers is the ability birds have to discriminate between the different dialects (Fracas et al., 2023; Hudson et al., 2019; Williams et al., 2019). A common method used to test this ability in individuals is the playback. Playback is a method by which researcher broadcast different sound stimuli, here local and foreign songs, to observe and compare the aggressive responses of the tested subject to the two stimuli.

2.7.1 Local-foreign discrimination

Parker et al. (2018) in their review report that in the majority of studies on local versus foreign dialect discrimination, a stronger response to the local dialect compared to the foreign dialect was observed (Fracas et al., 2023; Hudson et al., 2019; Williams et al., 2019). This large body of research however is focused on species with wide dialects leaving a paucity of research on smaller scale dialects (Briefer et al., 2010; Leader et al., 2002). A population with such characteristics can behave differently from a population with wide-spanning dialects. In the European skylark, focal males responded less aggressively to the song of distant neighbouring males, which shared song elements with them, compared to the song of stranger males, which they did not share song elements with (Briefer et al., 2010). To test properly for dialect discrimination, it is important to use songs of unfamiliar birds as stimuli; otherwise, there is a risk of testing for the “dear enemy effect” (Fisher, 1954), the ability tested would consequently be the discrimination between a familiar neighbour and a stranger.

2.7.2 *Hypotheses*

In order to explain this pattern of a stronger aggressive response to the local compared to a foreign dialect two hypotheses have been drafted. Firstly, on an ultimate level, according to the "*relative threat hypothesis"* (Rothstein & Fleischer, 1987; Wright & Dorin, 2001) a territorial male will perceive a new intruder as more dangerous if it displays the local rather than a foreign dialect. This is because a rival singing the local dialect might reflect its knowledge of the territory which might facilitate its ability to acquire a territory and a mate. Secondly, on a proximate level, the "*recognition hypothesis*" states that birds will exhibit a strong response to a song that closely matches with their internal representation of the species' typical song (Dabelsteen & Pedersen, 1992; Nelson, 1998). Indeed, assortative mating based on dialects can result in genetic divergence, potentially causing foreign dialect singers to go unrecognized as conspecifics.

3. Drivers of birdsong evolution

3.1 Morphology

Morphology is an important factor that affects signal production and can act as a driver of song evolution (Podos et al., 2004). Morphological traits can have multiple functions aside from their role in vocal signalling and are themselves under divergent natural selection (Nowicki et al., 1992; Tinbergen, 1952). Consequently, as a side effect, these morphological traits can contribute to reproductive isolation and even speciation (Rundle & Nosil, 2005). They are referred to as "magic traits", as under divergent selection pressure they can lead "as if by magic" to signal divergence and consequently to non-random mating (Gavrilets, 2004; Servedio et al., 2011). Bills are involved in foraging and thermoregulation (Tattersall et al., 2017) and are used to modify sounds at the end of the vocal tract (Bradbury & Vehrencamp, 2011). As the beak shape and size adapted to the diet requirements under natural selection (Benkman, 2003; Pigot et al., 2016, 2020; Smith, 1990), the consequences of such adaptations have been shown to impact song output in some species. For example, Friis et al. (2022) investigated how both bill and body sizes affected songs across more than 1000 taxonomically diverse passerines. They found that both were equally negatively related to the sound frequency of songs. More precisely, larger bill and body size species tend to produce lower sound frequency. In addition to this finding body size alone was observed to be related to sound frequency bandwidth; authors suggest that this might be due to larger bills allowing greater modulation of frequency but as a trade-off, it also hinders fast bill movements (Friis et al., 2022). Controlling for overall size, the sound frequency was found to be associated with bill shape in honeyeaters (family Meliphagidae; Friedman et al., 2019), vireos and allies (family Vireonidae; Mejías et al., 2020). In tanagers bill size was associated with trill rate (family Thraupidae; Demery et al., 2021).

In honeyeaters, the adaptation of the bill to climate, as a means of thermoregulation, was investigated to assess the fallbacks on song evolution (Friedman et al., 2019). The results showed both foraging ecology and climate affected beak size and shape. Foraging ecology had also a strong effect on beak shape while climate adaptation had a strong effect on beak size. This led to changes in song behaviour for example species with more elongate beaks tended to have lower maximum frequencies compared to species with shorter beaks. Furthermore, species with large beaks produced songs at a slower pace in comparison to species with smaller beaks (Friedman et al., 2019). A recent analysis of 163 species of honeyeaters revealed that body size constrained song frequency and pace in this avian family (Hay et al., 2024). In addition, habitat type and environmental temperature had an indirect effect on song most likely via the effects of environmental variation on body size (Hay et al., 2024). This conclusion reminds us that disentangling the effect of morphology and habitat can be tricky. Body and bill size have been extensively reported on in the context of song evolution (Ballentine, 2006; Demery et al., 2021; Derryberry, 2009; Derryberry et al., 2012, 2018; Friedman et al., 2019; Friis et al., 2022; Podos, 2001; Podos et al., 2004). Song plays an important role in mating and its evolution has potential fallbacks on mate choice and reproductive isolation potentially leading to speciation (Uy et al., 2018). Nonetheless, morphology is not the only evolutionary driver of song. In several articles, investigating how morphological traits influence the evolution of birdsong, authors agree that habitat properties are also an important factor that needs to be included or controlled for even though the effects of this factor can be indirect (Derryberry et al., 2018; Friedman et al., 2019; Hay et al., 2024).

3.2 Habitat

Habitats' properties have been identified as a driver of song evolution, as sound transmission varies with the physical properties of the environment (Morton, 1975). The acoustic adaptation hypothesis predicts that in habitats where vegetation is denser the sound frequency used should be lower and the note rate slower compared to a more open vegetation area to avoid signal degradation (Hunter & Krebs, 1979; Morton, 1975). Boncoraglio & Saino (2007) showed in a meta-analysis that there was only a weak effect of habitat structure (vegetation density) on oscines song evolution suggesting the inclusion of other relevant explanatory factors in the future. A more recent analysis has however deemed the acoustic adaptation hypothesis not applicable to passerines when looking at variables reflecting vegetation types (Friis et al., 2021; Mikula et al., 2021). Apart from vegetation type variables, the habitat presents ambient and anthropogenic noise which have been identified as main drivers in song evolution (Ryan & Brenowitz, 1985). Song structure might be adapted to the local habitat as it impacts sound transmission (Hansen, 1979). A study by Moseley et al. (2019) investigated the cultural evolution of the white-crowned sparrow, *Zonotrichia leucophrys nuttalli*, over nearly 50 years in the San Fransisco CA area. They found that the population exposed to anthropogenic noise had shifted up the minimum frequency of its song which was consistent with previous studies carried out on the same system (Derryberry et al., 2016; Luther & Baptista, 2009; Luther & Derryberry, 2012). Despite this shift in frequency in the early stages and performance constraints from urban noise, males were able to increase both vocal performance and syllable complexity through decades. When comparing the song performance evolution, over 50 years, between the urban and the rural populations, it was shown to have increased only in the urban population (Moseley et al., 2019). This study clearly shows the impact of urban noise on song evolution. The effect of urban noise on birdsongs has been heavily reported on (Duquette et al., 2021; Gomes et al., 2022; Grabarczyk & Gill, 2020; Phillips & Katti, 2020; Sheldon et al., 2020; Slabbekoorn & Boer-Visser, 2006)

Urbanisation in addition to changing the soundscape of birds is also responsible for changes in the environment as it can lead to its fragmentation and habitat loss for non-human species. Indeed, we described earlier the effect of habitat loss and population decrease in the honeyeater and the Dupont lark. In both species population fragmentation due to habitat loss led to the erosion of vocal culture. Land use by humans and its consequences on birds' populations repartition are factors driving the evolution of song dialects.

3.3 Inter- and intra-sexual selection

It is well acknowledged that sexual selection, through mate choice and male – male competition plays an important role in shaping birdsong (Andersson, 1994). Females' mate choice was proven to influence parameters such as song complexity and rate, vocal performance, and song and syllable repertoire size (Alatalo et al., 1990; Searcy & Yasukawa, 1996; Wasserman & Cigliano, 1991), as these parameters reflect males' quality. Females also have a preference for larger repertoires. For example, pied flycatcher and sedge warbler*, Acrocephalus schoenobaenus,* females show a preference towards males with larger song repertoire both in the lab and in the field (Buchanan & Catchpole, 1997; Catchpole et al., 1984; Lampe & Espmark, 2003; Lampe & Saetre, 1997). However this preference is still under debate and less widespread than previously thought (Byers & Kroodsma, 2009). In the instance where dialects are present in a population, females can display preferences towards males singing the local compared to a foreign variant (Le Maguer et al., 2021; O'Loghlen & Rothstein, 1995; Searcy et al., 2002). Moreover, the female behavioural response to songs can guide male song learning (O'Loghlen & Rothstein, 2003). In the brown-headed cowbirds, *Molothrus ater*, a brood parasitic bird, young males have limited access to conspecific singing after they hatch. Therefore, during their first breeding season, these males do not or only partially sing the local dialect (O'Loghlen, 1995). Females of the population show a mating preference towards older males singing the local dialect (O'Loghlen & Rothstein, 1995, 2003). As a consequence, first-year breeders are pushed to conform to the local vocal culture to mate and they do so by changing their repertoire between the first and second breeding seasons (O'Loghlen, 1995; O'Loghlen & Rothstein, 2003). Similarly, intra-sexual selection can drive song evolution. Indeed male-male interaction and competition have been shown to influence the song retained in the repertoire as it can facilitate neighbouring relationships. For example, in the Savannah sparrows, the individuals singing the most similar songs to their neighbours experienced lower territorial aggression (Thomas et al., 2021). As a result, newly arriving males will only keep the songs similar to their neighbours and drop the others (selective attrition) (Thomas et al., 2021). Retaining or learning songs conforming to the local culture was proven to play a role in regulating aggression levels with song or repertoire matching (Peake et al., 2005; Searcy et al., 2014). This gave rise to the aggression escalation chain where the use of shared songs can increase or decrease aggressive behavioural responses between neighbours (Beecher & Akçay, 2014).

Recognising the impact of both inter- and intra-sexual selection on song evolution, Beecher & Brenowitz (2005) proposed two functional hypotheses to explain song repertoire size and composition variation and the song learning program that should be favoured depending on the aim of selection. The first is the "*repertoire hypothesis"* which is based on the assumption that females will have a preference for large repertoires, an honest signal of males' quality (Catchpole & Slater, 2008; Collins, 2004). This hypothesis posits that in this situation the song learning program should allow birds to acquire a large repertoire (Beecher, 2008; Beecher & Brenowitz, 2005; Osiejuk et al., 2019). The second is the "*sharing hypothesis"* and it is based on the importance of song sharing between males for both male-male competition and female mate choice. The "*sharing hypothesis*" assumes that song sharing with neighbours and group members triggers social advantages both during male-male interactions and mate attraction (Beecher & Brenowitz, 2005; Payne, 1981). Thus, the learning program they use ought to facilitate their ability to acclimate to their social surroundings by learning shared songs (Beecher & Brenowitz, 2005).

3.4 Song learning mechanisms

The cultural evolution of birdsong also happens through song learning as it is based on imitation of conspecifics. Despite imitation being precise, copying errors or innovation can happen (Tchernichovski et al., 2017). On one hand, precise song imitation associated with social convergence or learning biases can lead to the maintenance of dialect for several decades (Garcia & Favaro, 2017; Lachlan et al., 2018). On the other hand, copying errors or innovation can also be rapidly transmitted through the population because of imitative learning. An illustrative example of this is the corn bunting, which from year to year carries out changes in details of the local dialects (McGregor et al., 1997).

However, individual experience is not the only factor shaping birdsong evolution through vocal learning. Genetic constraints are another factor influencing vocal learning. There is a wide range of vocal learning programs in birds, as stated at the beginning of this introduction. Different species will display different sensitive periods durations and song learning periods in their life, ranging from closed-ended learners to open-ended learners (Brenowitz & Beecher, 2005). Furthermore, repertoire size shows high variation through the songbird group with species able to learn over 2000 songs while others will retain only one (Macdougall-Shackleton, 1997). An interaction of individuals' experiences' and genetic predispositions can therefore impact bird song evolution. Mets & Brainard, (2018) observed in Bengalese finches, *Lonchura striata* *domestica*, which had a different genetically determined song tempo and were exposed to different levels of tutoring, (weak: tutoring by computer and strong: tutoring by live tutor) that this acoustic parameter is genetically inherited but can be modified by individuals' experience (exposure to live tutor).

To conclude, in order to get the full picture of birdsong evolution it is important to keep in mind that several of the factors described above might be at play in song evolution. Though it is now easier to study the interplay of the different factors with the use of modelling, fully disentangling the effect of every factor remains a challenge.

4. Song learning from the lab to the field

4.1 Song learning in the laboratory

Song learning research was facilitated by the use of sound spectrograms as a means to visualize and classify songs and asses the accuracy of tutees' imitation. One of the earliest works to use this method was the one of William Thorpe, investigating vocal development in chaffinches, *Fringilla coelebs* (Thorpe, 1954, 1958). Since then, the brain's neural circuit involved in song learning and production has been identified (Jarvis et al., 2005; Nottebohm, 1977; Nottebohm et al., 1976). In addition, the involvement of certain hormones during the different learning phases has been highlighted, notably the necessity of testosterone in song crystallisation (Marler et al., 1988; Whaling et al., 1998). Furthermore, early developmental stress was found to have a negative impact on song learning and production as brain regions controlling them were underdeveloped (Dunlap & Stephens, 2016; Nowicki et al., 1998; Searcy & Nowicki, 2008). Later this underdevelopment can result in song repertoire and production differences between males which are indicative of their quality for the audience (Nowicki et al., 2000, 2002). This partly led scientists to infer that the ability to learn is costly to implement and maintain into adulthood but more research is needed to identify the associated costs (Creanza et al., 2016).

Researchers preferred to experiment in laboratories to study song learning in birds, this method is particularly advantageous as it allows to easily record individuals in a stable acoustic environment (low noise-to-signal ratio) and to isolate birds in different conditions to control what they hear. Evidence of song learning in several species was found when males isolated during early development and therefore, unable to hear conspecific songs during the sensitive phase, sang abnormal songs as adults (Kroodsma, 1977; Petrinovich, 1985; Thorpe, 1958). In addition, if isolated males were exposed to recordings of conspecific songs, they developed songs resembling natural species songs (Marler, 1970; Petrinovich, 1985). In some cases, males will learn their song better if a live tutor is present rather than a recording or the sensitive phase can be extended if a live tutor is present. These results showed the importance of social interaction during learning (Adret, 1993; Baptista & Petrinovich, 1984; Beecher, 2017; Derégnaucourt et al., 2013). Auditory feedback is important for males to develop proper song, as it allows them to compare the produced song to their auditory templates. If males are deafened after the sensory phase but before the sensory-motor phase they develop abnormal songs (Konishi, 1965; Nottebohm, 1968). Selective learning experiments where males were equally exposed to songs from their species or from another species or subspecies showed that males preferentially learn their species songs (Marler & Peters, 1987; Nelson, 2000a; Wheatcroft & Qvarnström, 2017). These experiments enlighten the presence of an innate template for their species-specific song which is genetically inherited and leads to a learning bias (Beecher, 2017; Marler & Peters, 1988).

The controlled environment provided by a laboratory experiment also allowed the establishment of detailed learning programme timeframes for several birds of the oscine clade. To establish a species is an open-ended learner, controlled laboratory studies are essential to assess the number of new songs added and when they are added, in order to validate learning ability during adulthood and invalidate the resurgence of previously learned songs (Chaiken et al., 1994; Güttinger, 1977; Marler et al., 1972). For example, common nightingales, *Luscinia megarhynchos*, which have a large vocal repertoire (around 180 song types) and display song sharing with neighbouring males (Hultsch & Todt, 1981) are considered to be open-ended learners. In a laboratory experiment, hand-reared males were tape-tutored at different periods, from a few days post-hatching and during their first season (Todt & Geberzahn, 2003). The study showed that song memorisation was not confined to the early sensitive period of song learning. Indeed, males were able to learn and immediately sang new material until the first season's song crystallization. Moreover, songs presented past the first season crystallisation phase were not found in the males' vocal repertoire until the second season. This process was referred to as delayed production (Todt & Geberzahn, 2003). In addition, a complementary study in this species enlightened the ability males had to store in memory song types (Geberzahn & Hultsch, 2003). More precisely, song types males failed to introduce in their repertoire in the first season were exclusively added in the second season compared to novel tutored songs. This bias is the result of an additional exposition to this unexpressed song types during a playback composed of these song types and novel ones therefore leading to their recall (Geberzahn & Hultsch, 2003).The functional relevance of this type of learning is the fact that it is advantageous for males to have a large repertoire partly shared with neighbours repertoire when engaging in ‘song-type matching’ (review in Todt & Naguib, 2000).

In the field, such findings cannot be fully validated as the acoustic environment cannot be controlled and therefore the resurgence of previously learned material cannot be fully dismissed. Even though laboratory experiments offer several advantages, complementing the results with field studies is necessary as differences can be observed in the different settings. Indeed song sparrows under natural conditions showed extended sensitive periods compared to observations made in the laboratory (Nordby et al., 2001), even though in both contexts once adulthood is reached no new songs are added (Nordby et al., 2002). Song sparrows learn their songs in the summer and fall following hatching and are considered age-limited learners as they sometimes display an extended learning period at the beginning of their first year spring to learn the songs of their neighbours before crystallizing their repertoire for life (Nordby et al., 2001). This case is not the only one as laboratory results are not always transposable to wild populations (McGregor & Krebs, 1989; Rivera-Gutierrez et al., 2011).

4.2 Song learning in the field

The previous results described entail that field conditions, even though less controllable, provide more biologically relevant settings. A successful combination of laboratory and field research was conducted on the brown-headed cowbirds. Research in the field on the brown-headed cowbirds showed that it takes males two years to develop their lifelong adult repertoire (O’Loghlen, 1995; O’Loghlen & Rothstein, 1993, 2002a). As a brood-parasitic species, young males have limited access to song tutors after hatching (Dufty & Wingfield, 1986). Therefore, the song-learning program of the species confers them with a new memorisation phase (sensory learning) during the first breeding season (Dufty & Wingfield, 1986) even though they already produce a crystallized song at this time (O'Loghlen & Rothstein, 2002a). These first breeding season's songs appear to be different from the local dialect present in the area males dispersed to. However, during the second breeding season the repertoire composition of these young males has changed, switching mostly to songs of the local dialect of their first breeding season locality (O'Loghlen, 1995; O'Loghlen & Rothstein, 1993). This species displays delayed production similar to the common nightingale (O'Loghlen, 1995; O'Loghlen & Rothstein, 1993, 2002a, 2002b). Laboratory experiments later confirmed the findings from the field (O'Loghlen & Rothstein, 2012)

A field approach allows researchers to study birds under natural social pressures and after dispersal and to compare different populations (Beecher, 1996; Beecher & Brenowitz, 2005; Beecher & Burt, 2004; O'Loghlen & Rothstein, 2012; Slabbekoorn & Smith, 2002a). The spatial pattern of song type sharing among individuals is influenced by the different strategies of song learning and dispersal (Slater, 1989; Wilson et al., 2000). Consequently, multiple studies used the observation of the dispersal strategies and song sharing patterns to infer the song learning programs of a species or the other way around (Niederhauser & Anderson, 2023; Ranjard et al., 2017; Vargas-Castro, 2015). These types of studies can be of great help if captive rearing is not possible and also in secretive or imperilled species. Field observation can be the only means to gather information for these species and to infer their dispersal or song learning strategies (Niederhauser & Anderson, 2023).

Even though field studies are challenging to carry out, it is still possible to successfully implement them. In addition, captive experiments can fail to provide normal song learning conditions (Beecher, 2017; Mennill et al., 2018; Payne & Payne, 1997) leading to misleading findings. Mennill et al., (2018) broadcasted songs to juvenile Savannah sparrows in the wild and males successfully learned songs from these artificial tutors (song broadcasts), preferring songs heard both in their natal summer and first spring. They observed a transmission of this experimentally introduced songs to the following generations (Mennill et al., 2018). Both laboratory and field studies shed light on the processes birds follow to modify their repertoires. The following repertoire changes were identified in different species: addition of *de novo* material, recombination, overproduction, selective attrition (the process by which the repertoire is pruned of song unshared with neighbours) (Nelson, 2000b; Nordby et al., 2007; Osiejuk et al., 2019; Thomas et al., 2021) and gradual modification of previously present material into another acoustic configuration (McGregor et al., 1997; Trainer, 1989; Vargas-Castro et al., 2015).

To conclude, a combination of laboratory and field experiments is needed to fully assess the whole spectrum of song learning abilities across the 4000-plus species of oscines (Beecher, 1996; Kroodsma, 1996). Despite the impressive amount of research already conducted on song learning, most of the research has been carried out in the laboratory and focuses principally on the first three years of a bird's life (Beecher & Brenowitz, 2005; McGregor & Krebs, 1989; Williams, 2021). In addition, changes in the repertoire size and composition have preferentially been done in large rather than small repertoire species and a cross-sectional approach is usually preferred as it is less time-consuming than a longitudinal study (Osiejuk et al., 2019). Consequently, there is a lack of longitudinal studies in the field of known individuals and their neighbours in both song learning and song repertoire changes research (Kipper et al., 2004; Rivera-Gutierrez et al., 2011).

5. The black redstart, *Phoenicurus ochruros*

5.1 General presentation: phylogeny, distribution, habitat, diet, reproduction, morphology

The black redstart (Gmelin, 1774) belongs to the order Passeriformes and to the Muscicapidae family. This species ranges over Eurasian and the north of the African continent, they are found from Norway to Ethiopia and from China to Portugal and around the Mediterranean basin (*Black Redstart (Phoenicurus ochruros) - BirdLife Species Factsheet*, n.d.). This species is a partial migrant and therefore presents both migratory and sedentary populations. Migratory populations tend to migrate to the Mediterranean basin during fall (Landmann, 1996).Their primary habitat is dry high altitude mountain rocky areas and cliffs but due to their adaptability they took advantage of human constructions and can now be found breeding in lower altitudes but also using buildings as nesting sites (Snow & Perrins, 1998; Zamora, 1991). The population size is increasing and they are a least concern species (*The IUCN Red List of Threatened Species*, n.d.) and a common species in urban environments. Black redstarts are insectivorous they also eat small earthworms and berries (Erard, 1994). Individuals which survived their first year have an average life expectancy of 1.3 -1.6 years (Nicolai, 1992b).

Males arrive on the breeding grounds in March, they establish their territory upon arrival. By the end of April the territories and their owners are set for the season.

Experienced males, in their second breeding season or older are more likely to return earlier than first year inexperienced breeders (Musseau, 2007; Weggler, 2001). Pair forming can start in March and at the beginning of April (Draganoiu, 2005). Incubation starts by the end of April and lasts on average 15 days, young will then fledge, and parents will keep feeding them for two weeks. Some pairs can have a second brood which fledges around mid-June. Breeding males will moult at the end of August. Males display delayed plumage maturation, first year breeders have a similar plumage to females and at the end of the first breeding season they moult and acquire their definitive darker plumage (**Figure 1**). Departure to the wintering grounds occurs at the end of October.

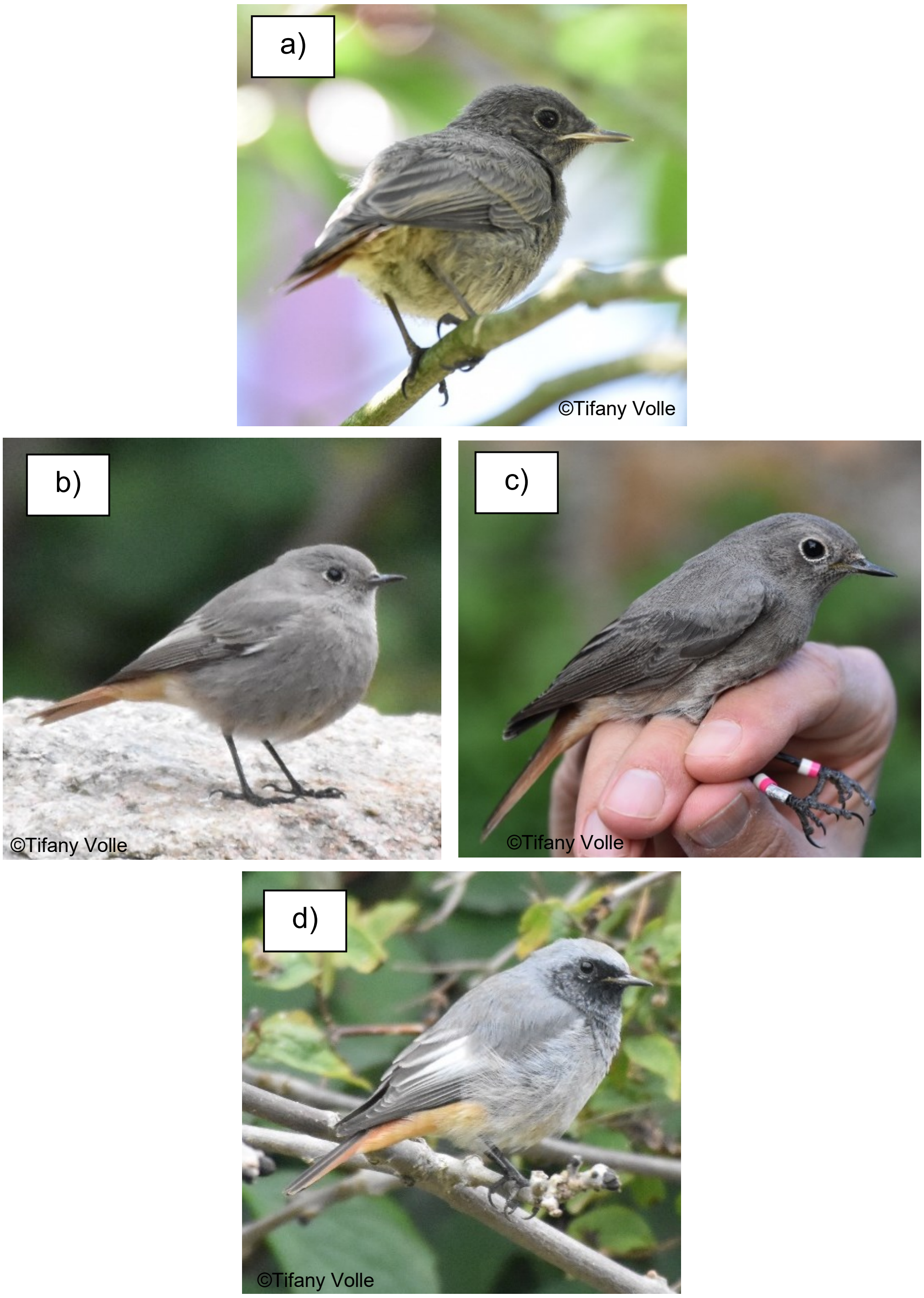

Figure 1. Plumage evolution of a male black redstart throughout three life stages: a) fledging, b) first year (Y1) for comparison, c) the female plumage and d) second year (Y2).

5.2 Singing behaviour

As of now only males are known to sing. Variations in the singing activity on the breeding grounds have been observed for the different age classes, including yearlings (bird hatched during the season) and adult breeders (Nicolai, 1992a; Schmidt, 1992; Weggler, 2000). At their return on the breeding grounds males sing from high perches (electric and fencing poles, trees, chimneys, and roofs) to defend their territory and attract mates. Males participate to the dawn choruses as they sing as soon as an hour prior to sunrise, then through the day they will have more sporadic song bouts.

During the breeding season male song activity levels are as follows (Schmidt, 1992). At the males' return, in March, song activity is at its highest, then after males are paired with their female and the first brood is ongoing male song activity will decrease slightly. Song activity will peak again when females are once again fertile for the second brood in June. Through the months of July and August song activity will decrease until it almost stops; eventually, at the onset of September, it slightly increases before decreasing again until migration. This pattern of song activity applies to breeding males (Nicolai, 1992a; Schmidt, 1992). For males that hatched during the breeding season (Nicolai, 1992a), it was observed that they start singing from mid-August, singing activity rises until mid-September and then decrease until their departure for wintering grounds. This pattern coincides with older males' song activity starting again, which led scientists to infer that this time of the season corresponds to the learning period (including both the sensitive- and sensorimotor- phase) of song in the black redstart (from 80 to 120 days post hatch) (Nicolai, 1992a; Schmidt, 1992; Weggler, 2000). Songs of spring are different from the ones in autumn in several acoustic parameters (e.g. duration, number of elements in strophes, Apfelbeck et al., 2013). These changes have been attributed to the concentration levels of testosterone which decreases between the breeding stage in April and the non-breeding stage in October (Apfelbeck & Goymann, 2011; Villavicencio et al., 2021). In addition, differences in the song of first year breeders and older males have been reported (e.g. frequencies and song part durations) but it is still an area of debate as other studies found no differences (Cucco & Malacarne, 1999; Huet des Aunay, 2016).

5.3 Song structure

Black redstart songs are composed of a beginning strophe followed by a silence then a wide frequency bandwidth harsh sound (like crumpling paper) and finally the ending strophe. Each strophe is composed of a pre-trill and a trill. Trills are composed of a repetition of smaller units called syllables, which in turn can be composed of one or several notes (**Figure 2d**). Pre-trills and trills can be composed of either one type of syllables (**Figure 2a**) or several. Generally, a strophe can either be used as solely a beginning or an ending strophe, but some males can use mobile strophes, which are strophes that can be used both as a beginning and ending strophes. Additionally, males can sing mixed strophes which are composed of the beginning of one strophe and the ending of another strophe of the repertoire (**Figure 2**, Volle, 2019). Songs can be produced complete with all parts from the beginning to the ending strophe. But sometimes males can produce either the beginning or the harsh followed by the ending strophe only; these are considered truncated songs. A males' song repertoire is defined as the number of different strophes combinations used by an individual while the strophe repertoire is defined as the number of different strophes produced. On average males have 3 strophes and 2 songs in their repertoires (Draganoiu et al., 2014)

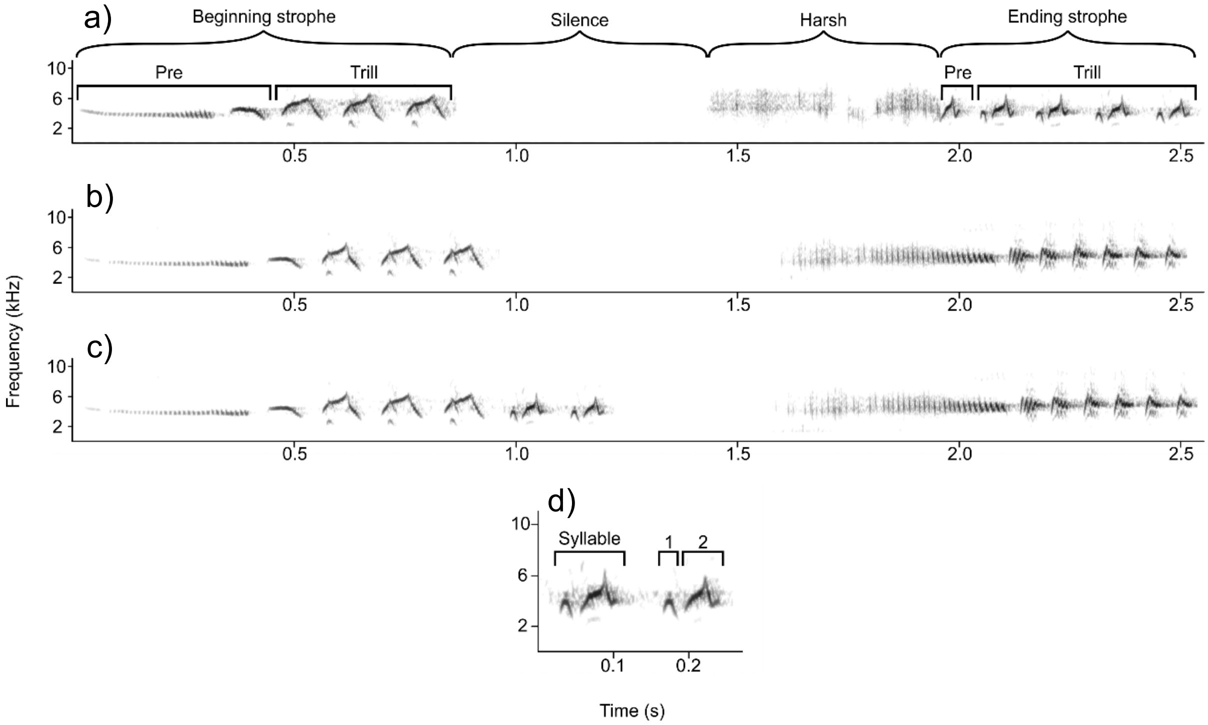

Figure 2. Complete strophe repertoire of a male black redstart (a-b). Spectrograms examples (FlatTop window; FFT length: 256; 87.5% overlap) of a) a detailed complete song b) another song sung by the same male c) a song with a mixed beginning strophe and d) of a syllable type composed of two note types 1) and 2).

5.4 Song geographic variation and microdialects

Black redstart distribution spreads over a large geographic span and it was previously found that song patterns differed between an Asian population in the Tibet plateau and different populations across Europe (Wang et al., 2005). In addition, song dialects on a smaller geographical scale have been observed in several populations from Asia and Europe (Draganoiu et al., 2014; Nicolai, 1992a; Wang et al., 2005).

5.5 Territorial responses

A considerable research effort was directed towards the identification of the mechanisms behind the singing activity of males notably using playback experiments during which the territorial responses of male black redstart were observed. To defend their territory males sing from high perches (e.g. rooftops, chimneys, utility poles and nearby trees). When challenged by a rival, a territorial male will first sing, then carry out patrol flights over its territory to locate the intruder to then hold ground in close proximity with the rival, and finally chase it and ultimately attack the opponent (Apfelbeck & Goymann, 2011; Landmann & Kollinsky, 1995; Schwarzová, 2010; Sedláček et al., 2006). Males' territoriality has also been shown to vary across the season (Weggler, 2000).

In addition, adult males are likely to defend territories during autumn and establish pair bonding with experienced females which proved to be beneficial in re-establishing both the territory and pair the following spring (Weggler, 2000). Regarding winter, it has been observed in a supposed sedentary population in Spain, that 11 adult males and one grey male defended territories during this period, yet most of the population was non-territorial at this time. Authors suggested that individuals defending territories during this period could improve individual fitness later as they had privileged access to resources (Cuadrado, 1995). Furthermore, Schwarzová, (2010) showed that in an habitat where there is a mosaic of territories with different qualities, males with smaller territories responded to an intrusion more strongly than males with larger territories. In this study the first-year breeders had stronger vocal responses to intrusion than did older breeders.

Territorial response in the black redstart has been shown to be subject to the "Dear enemy" effect (Draganoiu et al., 2014). As it was already mentioned, this is a process by which males discriminate between neighbours and strangers, the latter receiving more aggression. Indeed, an experienced breeder exposed to the song of its neighbour (experienced male in its second breeding season at least) and the song of a foreign individual had a stronger aggressive response to the latter. Male black restarts have been shown to respond well in several playback studies (Apfelbeck et al., 2011; Draganoiu et al., 2014; Schwarzová, 2010) making them a great model to test vocal signal significance using this method.

5.6 Studied population

My thesis focuses on a population of black redstarts studied since 1997 until 2022 and displaying microdialects. It is located in the mountainous area of the Massif Central, France (study area: 4,64 km²; mean position: 45°45'N, 3°50'E; mean altitude of 863 m) (**Figure 3**). The habitat in which our population is settled, is composed of old farming building complexes and farmhouses (the village has not been subject to many additional construction or destruction in the past 20 years) (**Figure 3)**. Consequently, the breeding habitat has stayed stable through this period hence it gave grounds for the population's stability.

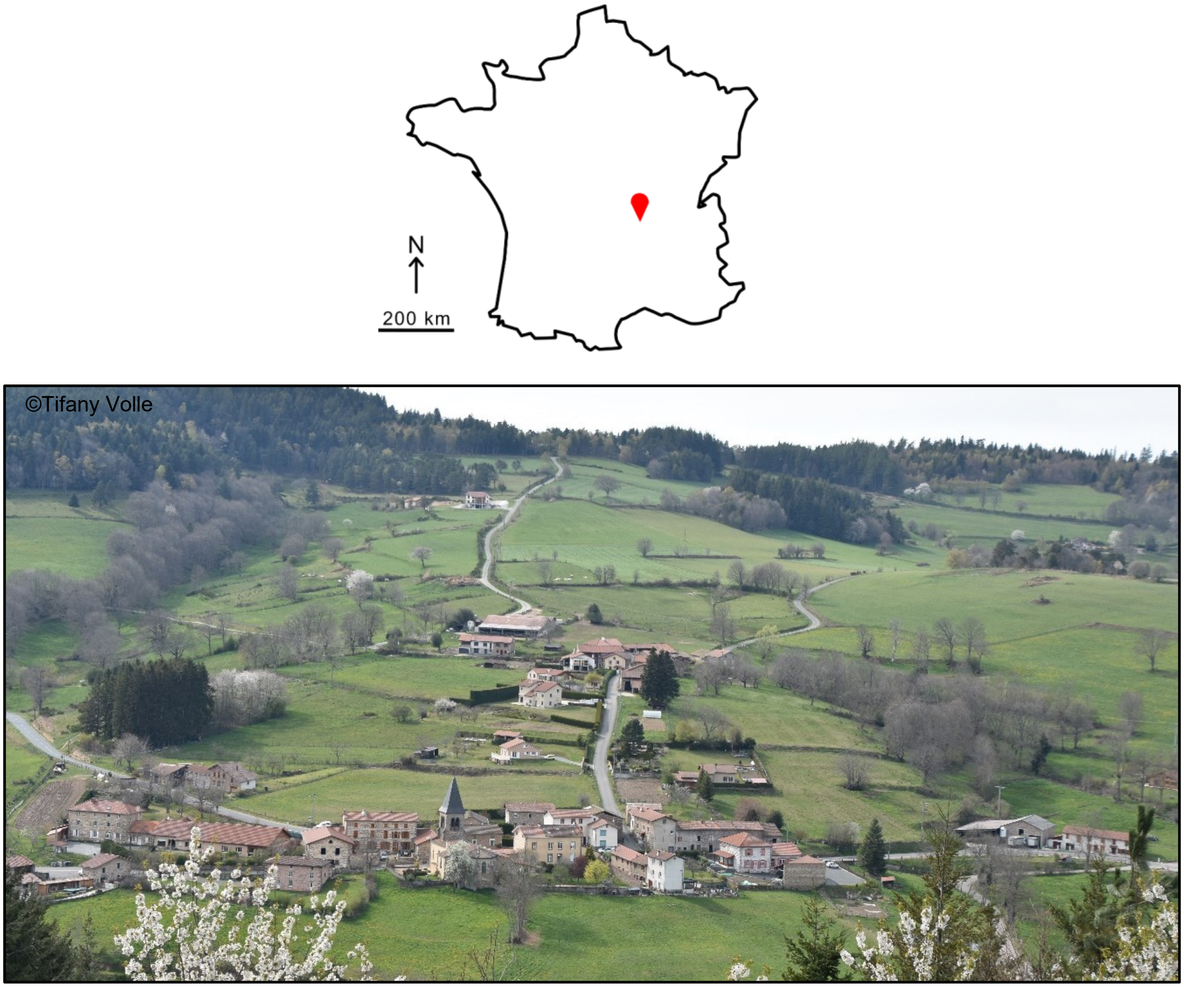

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Figure 3. Location of the studied population in France (top) and picture of the village center and surrounding hamlets (bottom).

To be identified individuals were banded during the longitudinal survey (**Figure 4**). Black redstart males of the studied population display high breeding site fidelity, with 50% of first-year breeder males returning to or close to their territory the following season (Draganoiu, 2005; Musseau, 2007). When returning first-year breeders display philopatry, indeed 3-10% of males return to the area the following year (Draganoiu, 2005; Musseau, 2007). Males past their second breeding season (+2Y) return from migration on average (± SE) on the 20th of March (± 9 days) and first-year breeders return on average on the 29th of March (± 12 days). The earliest return date is the 3rd of March in the population. Older males' (+2Y) return tends to be grouped while first-year breeders' is spread through time. The pairs build their nest exclusively within buildings. They lay their first brood on the 4th of May (± 8 days) on average and their second around the 20th of June (± 10 days) (Musseau, 2007). Females then incubate the eggs for 13 days on average. Both parents then feed the brood. Young fledge between 15 and 17 days after hatching (Draganoiu, 2005). The departure for migration starts at the beginning of September and lasts until the end of October (Musseau, 2007).

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Figure 4. Male black redstart during the banding procedure in its first breeding season (2018, left) and later in the field during its fourth breeding season (2021, right).

In the area, groups of males (2 - 8 individuals) form over clumped groups of houses, called hamlets, which are separated on average by 1275 ± 101 m (mean ±

SE) (**Figure 3 and 5**). This characteristic distribution goes hand in hand with a high song sharing between individuals living in the same neighbourhood and low sharing between neighbourhoods (Draganoiu et al., 2014), resulting microdialects lasting up to 14 years (Chambon, 2015; Schloesing, 2015). We surveyed 14 hamlets, belonging to three French neighbouring villages: La Valla-sur-Rochefort, Saint-Didier-sur-Rochefort and Saint-Just-en-Bas. Out the fourteen hamlets surveyed between 2015 and 2022, microdialects were found in 11 of them. **Figure 5** shows strophes belonging to 3 different hamlets sung by different males of the population.

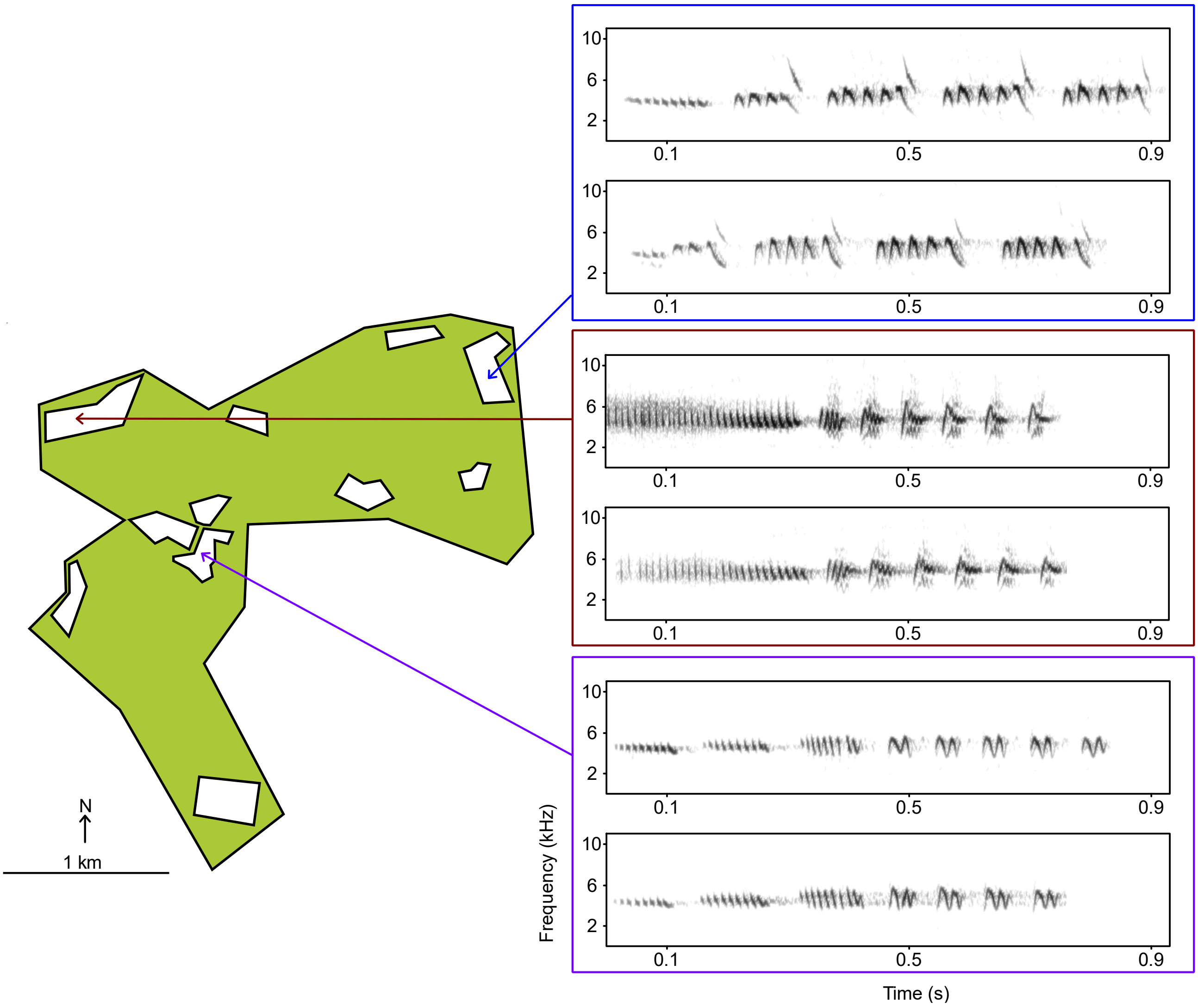


Figure 5. Studied hamlets (*N* = 11, represented in white) dispersion over the research area (in green). Examples of characteristic strophes of three hamlets' dialects sung by two neighbouring individuals (one line per individual, strophes within the same-coloured frame are shared).

Male black redstarts in the area have been shown to have vocal discriminative ability towards their neighbours' and strangers' song and also towards calls of their fledglings (Draganoiu et al., 2006, 2014). The characteristics of the population described previously led us use this population to study microdialects functions.

Furthermore, as a longitudinal survey has been carried out on this population, we have a rare opportunity to have natural non familiar shared and non-shared songs to broadcast during playbacks.

6. Aims of thesis

The black redstart with its small, stereotyped song repertoire (2-3 song types), the presence of microdialects with sharp boundaries in some populations and its characteristic territorial behaviour constitutes a suitable model to study both the ontogeny and the functions of song sharing in a songbird. Therefore, using this biological model, we studied the evolution of the strophe repertoire through life and the role of microdialects in territorial interactions. Using a longitudinal field approach, this thesis is based on both theories of song learning and dialect maintenance and functions and aims to expand our knowledge past the laboratory settings. My thesis aims to study the proximate question related to song sharing and to a larger extend microdialects. In this thesis, we aim to investigate the ontogeny of song sharing in songbirds, through the lifespan of individuals. Furthermore, we investigate the role/perception of microdialects during territorial intrusions.

6.1 Song sharing ontogeny

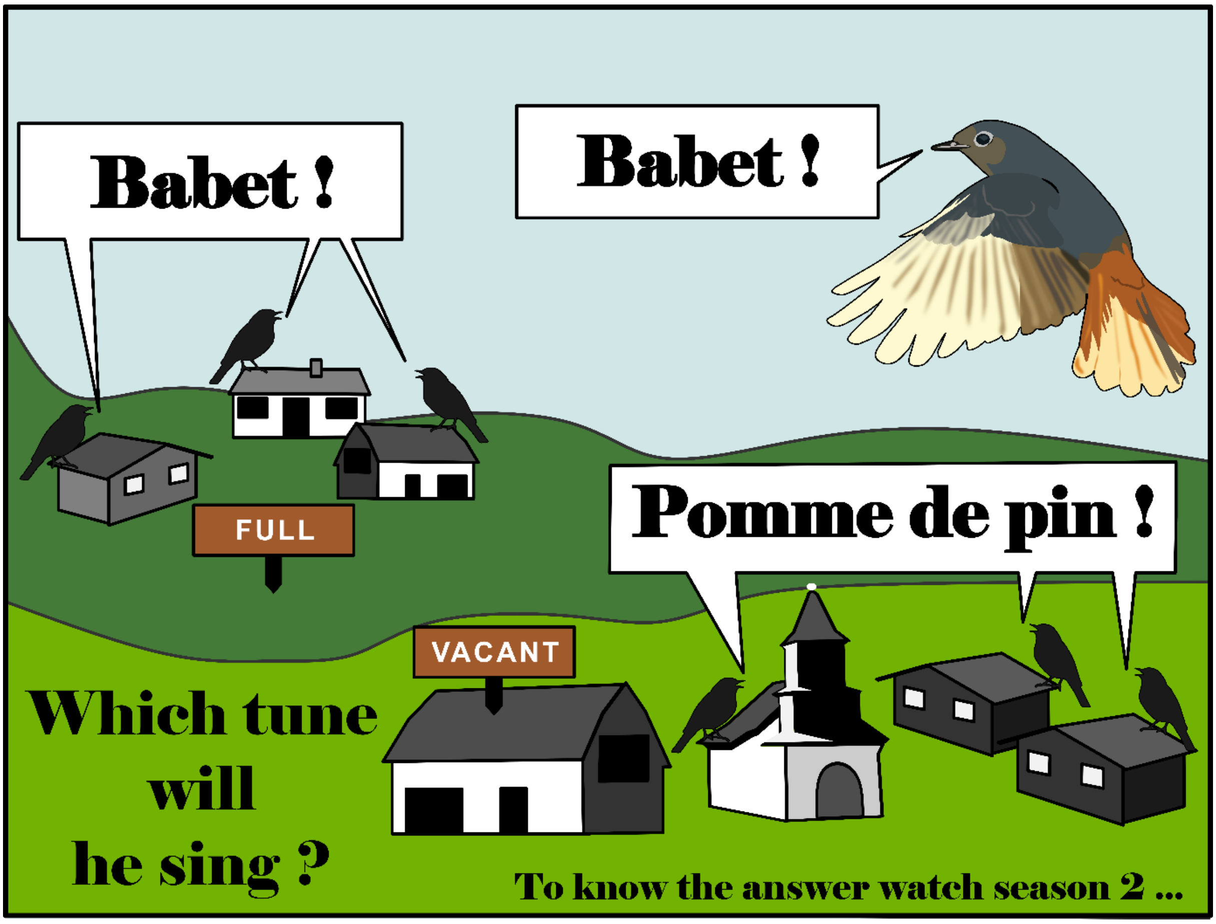
In the first chapter of this thesis, we describe the lifetime strophe repertoire evolution in a migratory population of black redstarts. We achieved this with a longitudinal survey spanning over eight breeding seasons of a population of male black redstarts displaying strong fidelity to their breeding sites (Musseau, 2007). I collected data during the last four breeding seasons (2019 to 2022). From 2020 to 2022, males were surveyed throughout the season (March to June) and during September in 2020 and 2021. Extending the survey period during my thesis provided grounds to study behavioural variation on a finer temporal scale (within the season) compared to previous years (2015 to 2018), where variation was only observed between seasons. The population resides within a small village characterized by dispersed clusters of buildings called hamlets, and the males' territories span over buildings in which they nest. Consequently, they follow the building dispersion, giving rise to small neighbourhoods of 2 to 8 males, with high song sharing within hamlets and low song sharing across hamlets, defined as microdialects, observed (Draganoiu et al., 2014). We wondered how the male learning program could facilitate the song-sharing pattern (microdialect) found in the population and which timeframe it was subject to. In regards to previous research, we predicted that males would either 1) learn their song pre-dispersal and disperse to the area where they hear the same songs as the one they learned and, therefore, be closed-ended learners (Beecher, 2017; Hensel et al., 2022; Krebs & Kroodsma, 1980; Liu & Nottebohm, 2007) or 2) have the ability to learn post-dispersal, to adapt to a new social environment, therefore, they would be able to disperse in a neighbourhood with different songs from their own if there are no territories available in the natal area, and black redstart would be considered age limited learners if learning is limited to a certain period in the lifetime (Beecher & Brenowitz, 2005)**.** Using spectrogram visual analysis of song recordings made between 2015 and 2022, we identified the strophe repertoire of first-year breeders and then tracked strophe repertoire changes through the season (March to September) and between breeding seasons (range 2 to 8 breeding season), in banded focal males to identify the learning program they followed and its timing. In addition, we assessed the level of strophe sharing between focal individuals and their neighbours comparing their repertoires. The purpose was to observe the impact of repertoire modifications on the males' strophe sharing level. This study offers valuable insights into the song learning abilities of a migratory species exhibiting microdialects by using a longitudinal field approach on banded males and their neighbours. Longitudinal field studies, through birds' lifespan are less frequently used in the study of oscines song learning, compared to laboratory approaches, as it can present methodological challenges (Rivera-Gutierrez et al., 2011). Our study aims to enrich our understanding of avian vocal learning behaviour.

6.2 Song sharing functions in territorial interactions

In chapter two, we focused on the microdialect functions in territorial interactions. Most studies on songbirds' ability to discriminate between Local versus Foreign dialects have been carried out on wide-spanning dialect species and report a stronger aggressive response to the local dialect (Fracas et al., 2023; Hudson et al., 2019; Parker et al., 2018; Williams et al., 2019). Unfortunately, there is a paucity of research on the matter in microdialect species (Briefer et al., 2010). We investigated if male black redstarts could discriminate between shared versus unshared songs independently of familiarity. The current longitudinal survey carried out on the population enabled us to obtain non-familiar natural stimuli to broadcast. We used a playback experiment to test the males' territorial response towards the Local and Foreign dialect stimuli. Based on the relative threat hypothesis (Rothstein & Fleischer, 1987; Wright & Dorin, 2001), presented earlier, we expected that males would react more aggressively to the songs of the local microdialect, conforming to the main trend observed in previous studies carried out on wide-spanning dialect species. Furthermore, we noticed a lack of exploration of the influence of several methodological factors in the past. Therefore, we also tested for the effects of the age class, the initial distance to the speaker, the relative acoustic similarity between the playback songs and songs of the tested birds and the order of the stimuli played back on the aggressive response of males. We expect more singing when birds are distant from the speaker and approaching behaviours when distant and respectively close to the speaker, based on the conceptual frame of the escalation chain of aggression (Beecher & Akçay, 2014). Also, we predicted a lower aggressiveness for first-year inexperienced males compared to older, experienced breeders (but see Garamszegi et al., 2006). In addition to the stimulus type, we explored the potential effect of the songs' similarity between the playback stimuli and the focal birds' songs (as a relative gradient). Finally, habituation to the playback was assessed by testing the effect of the stimulus order.

This thesis aims to provide a better understanding of the diversity of song learning programs in songbirds and the role they can play in dialect maintenance in the wild, using a longitudinal field study approach on identifiable individuals and their neighbours, an approach rarely used (Rivera-Gutierrez et al., 2011). Moreover, it aims to give an insight into the functions microdialects can play during social interactions. Microdialects are a relevant model to study vocal culture evolution and function due to the low number of birds sharing the same songs and the small geographical range over which they span (Garland & McGregor, 2020; Payne, 1981). A better understanding of the diversity of songbirds' learning programs and the functions of dialects in natural settings could later prove to be useful in the field of conservation (identify habitat changes and increase the successful settlement of introduced individuals (Martins et al., 2018; Wright & Dahlin, 2018)) and allow comparative studies on vocal communication with other species among which are humans.

CHAPTER 1: LIFETIME EVOLUTION OF VOCAL REPERTOIRES IN A SONGBIRD, THE BLACK REDSTART: A LONGITUDINAL FIELD APPROACH



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"Pomme de pin" means pinecone in French. In the Forez region, where the study was conducted, a regional form of French was spoken. In this dialect, a pinecone is referred to with the word "Babet".

CHAPTER 1

Lifetime evolution of vocal repertoires in a songbird, the black redstart: a longitudinal field approach

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Declaration of interest

The authors declare no competing interests.

Author Contributions

Tifany Volle: Conceptualization, Methodology, Investigation, Formal analysis, Visualization, Writing – Original draft, Writing – Review & editing. **Sébastien Derégnaucourt**: Conceptualization, Writing – Review & editing. **Tudor-Ion Draganoiu**: Conceptualization, Methodology, Investigation, Writing – Review & editing.

CHAPTER 1

ABSTRACT

Oscine songbirds learn to sing by imitating mainly conspecific adults. Song learning programs are diverse, ranging from species which can only learn during the first months of life before their songs crystallize to species that are able to learn new songs throughout their lives. There is a paucity of longitudinal studies in the field on this matter. We investigated the lifetime evolution of male strophe repertoires and strophe sharing in a migratory population of a territorial songbird, the black redstart, *Phoenicurus ochruros*, by recording colour-ringed individuals during eight consecutive breeding seasons (2015-2022). Males in our population defend breeding territories in scattered patches of buildings. We previously described the existence of microdialects between the different territorial male clusters (2-7 individuals). Three different cohorts were used to establish the timeframe and to identify the type of changes males used to modify their strophe repertoires. Males were recorded at their arrival from migration for their first breeding season (N = 52). We also followed 40 individuals during their whole life: 25 were followed within their first breeding season whereas 24 were recorded during at least two breeding seasons. Most males kept their strophe repertoires stable throughout their lifetime (2 to 8 years). Those who shared only a few or no strophes with their neighbours when they first established their territories (14/40), changed their repertoires. Three types of modifications were observed: 1) addition of shared strophes, 2) selective attrition of unshared strophes and 3) syllables' gradual modification. All the repertoire changes resulted in an increase in song sharing with neighbours. Thus, black redstarts adapt their songs to their social environment mostly during the first breeding season but also through their lifetime. More studies are needed to assess the costs and benefits of such song learning strategies.

HIGHLIGHTS

- Black redstarts learn their songs both before and after natal dispersal.
- Addition and syllable gradual modifications occur within the first breeding season.
- Males can selectively discard songs from their repertoires throughout life.
- These song modifications result in an increase of vocal sharing with neighbours.
- Song learning and social stability favour microdialects maintenance.

KEYWORDS

birdsong; black redstart; longitudinal study; microdialect; *Phoenicurus ochruros;* selective attrition*;* song learning; song sharing, sound similarity; vocal repertoire

ACKNOWLEDGEMENTS

We warmly thank Rémi Chambon, Elodie Schloesing, Amanda Cocquelet, Samuel Desvisgnes, Manon Nourdin, Nicolas Coron, Léa Brun and Georges Delorme for their help with the recordings during fieldwork. We also thank the people of La Valla-sur-Rochefort for their cooperation, especially the Charles, Rebourg, Rolland and Tholoniat families. We are grateful to Nicolas Mathevon, Fanny Rybak and Charlotte Curé for their helpful comments on the experimental procedures. T.V. was supported by a PhD grant from the University Paris Nanterre.

CHAPTER 1

INTRODUCTION

Vocal production learning enables individuals to acquire and modify their vocal signals in particular through imitation of conspecifics. It was described in several taxa: humans, cetaceans, elephants, bats, pinnipeds and three orders of birds including oscine songbirds (Janik & Knörnschild, 2021; Searcy & Nowicki, 2019). Birdsong is one of the most studied communication systems both in the field and in the laboratory (Brenowitz & Beecher, 2005; Kipper & Kiefer, 2010). Depending on the socio-sexual organization of the considered species, birdsong is used in territorial defence and mate attraction by both males and females (Catchpole & Slater, 2008; Nowicki & Searcy, 2004; Riebel et al., 2019) but also as a social signal (*e.g.* during night roosting in European starlings, *Sturnus vulgaris*: Hausberger et al., 2008). Even though songs are used in various social contexts by both sexes, scientific knowledge of birdsong learning is strongly biased towards males. In birds, vocal production learning is composed of several phases: during the sensory phase young males hear and memorize conspecific songs; during the sensorimotor phase birds practice and modify their songs based on auditory feedback. The first songs, called subsongs are followed by plastic songs before the final version of the song crystallizes (Rundstrom & Creanza, 2021; Thorpe, 1958).

The song learning process of each species follows a different schedule and research carried out over the past fifty years unravelled diverse vocal learning programs followed by songbirds (Hyland Bruno et al., 2021). Song learning programs were first divided into two categories: a closed-ended program and an open-ended program (Brenowitz & Beecher, 2005). Well-known examples of these two types of programs are exhibited respectively by the zebra finch, *Taeniopygia guttata,* which learns its song in the first three months of life before it crystallizes and by the European starling, which is able to learn new songs throughout its life (Adret-Hausberger et al., 1990; Chaiken et al., 1994; Mountjoy & Lemon, 1995; Zann, 1996). So far, most work on the timing of birdsong learning was done in the laboratory whereas fewer studies were carried out in the field. Accumulating data helped to refine this original dichotomic view on song learning programs and switch to a continuum view along which species can be placed (Osiejuk et al., 2019; García, 2019; Beecher & Brenowitz, 2005; Petkov & Jarvis, 2012; Kroodsma et al., 2013). An example of a species in between both extremes is the brown-headed cowbird, *Molothrus ater*. During the first breeding season, after reaching their post-dispersal location, males will learn a subset of songs sung by the already settled males. However, males will express fully their new repertoires, matching their neighbourhoods' songs only during the second breeding season (O'Loghlen & Rothstein, 2002, 2010, 2012).

To assess the learning programs of diverse species, a careful examination of song structure was performed. Some oscines produce only one song while other species produce a repertoire of different song types. Each song is composed of sounds separated by silent intervals usually called syllables: each syllable comprising one or more song notes (Thompson et al., 1994). Changes in repertoire size during life were examined on several levels (number of different syllables or song types produced) and the two following not mutually exclusive functional hypotheses on song learning have been proposed (Kipper & Kiefer, 2010; Osiejuk et al., 2019).

According to the *"Repertoire" hypothesis*, males with larger repertoires are preferentially selected for by females as a large repertoire may indicate individuals of higher quality. Therefore, in this situation, the song-learning program should allow birds to acquire a large repertoire (Beecher & Brenowitz, 2005; Beecher, 2008; Osiejuk et al., 2019). This hypothesis is still under debate and female preference for larger repertoires is not as widespread as previously thought as contradicting results were found for the same species between different studies (*e.g*. Great tit, *Parus major*; Red-winged blackbird, *Agelaius phoeniceus*; Byers & Kroodsma, 2009). The *"Sharing" hypothesis* posits that song sharing with neighbours and group members triggers social advantages both during male-male interactions and mate attraction (Beecher & Brenowitz, 2005; Payne, 1981). Accordingly, the learning program they follow should enable them to adapt to their social environment by learning shared song (Beecher & Brenowitz, 2005). This adaptation could lead to the emergence and the maintenance of geographical variation in the song (vocal dialects). Sharing songs with one's neighbours confers advantages such as reduced aggression (*e.g*. savannah sparrows, *Passerculus sandwichensis*, (Thomas et al., 2021), longer territory tenure (*e.g*. song sparrows, *Melospiza melodia,* Beecher et al., 2020) or higher lifetime pairing success (*e.g*. Puget sound white-crowned sparrow, *Zonotrichia leucophrys pugetensis*; Nelson & Poesel, 2013). Hence, song repertoires can be the target of different selection pressures, both sexual and social, and song learning programs may enable birds to adapt to both (Beecher & Brenowitz, 2005).

In order to increase vocal sharing between familiar individuals, birds have been shown to use several strategies. First, birds can add new material to their repertoires by producing preferentially the most popular songs or the songs of most successful individuals (Beecher, 2017; Kiefer et al., 2009). Secondly, males can exhibit overproduction of song types followed by selective attrition of unshared material (Akçay et al., 2020; Marler & Peters, 1982; Peters & Nowicki, 2017). Finally, birds can gradually transform a song component to increase its similarity with other group members (Demko et al., 2016; Vargas-Castro et al., 2015).

The present field study aimed at investigating vocal repertoires modifications in a migratory population of a territorial songbird, the black redstart, *Phoenicurus ochruros,* throughout its lifetime in order to assess the specificity of its learning program. Males in our population are philopatric and exhibit high fidelity to breeding territories (Draganoiu, 2005; Musseau, 2007). Only males sing and defend territories around farms and houses. The patchy distribution of the buildings in the study area leads to small neighbourhoods (2-8 males) with high song sharing among neighbours (microdialects) and low song sharing between different breeding patches (Draganoiu et al., 2014). Males have a strong singing activity during spring which then decreases until a mild peak in activity in autumn before migration (Cramp, 1988; Nicolai, 1992; Weggler, 2001). Males learn their songs during their first autumn (Nicolai, 1992) and vocal repertoires in our population seem to remain stable after the second breeding season (Draganoiu et al., 2014) . Most studies on song learning have been carried out in laboratory settings to control the song models birds are exposed to (Beecher & Akçay, 2021; Geberzahn & Hultsch, 2003; Kiefer et al., 2014; Todt & Geberzahn, 2003 but see Mennill et al., 2018) and there is a paucity of longitudinal studies in the field (Rivera-Gutierrez et al., 2011). Our population has been studied from 2015 until 2022 and we could identify reliably colour-ringed individuals throughout the years which makes our data set suitable to study changes across years in the vocal repertoire of an oscine songbird species.

Males' arrival dates were monitored during eight breeding seasons. Territorial males were recorded to establish their vocal repertoires and to assess the levels of song sharing between neighbours. We carried out a longitudinal survey on the evolution of their vocal repertoires during different periods: i) within the first breeding season and ii) between the breeding seasons. Based on the "*Sharing" hypothesis*, we expected birds to operate repertoire changes in order to increase song sharing with their neighbours (Beecher & Brenowitz, 2005), mainly during the first breeding season.

METHODS

Study population

We followed a population of black redstarts located in a French mountain village of Forez mountains, La Valla-sur-Rochefort and its surroundings (mean position: 45°45'N, 3°50'E; mean altitude of 863 m). Birds arrive for the breeding season during the months of March and April (10th of March to 25th of April based on observations between 2020 and 2022) and they return to their wintering grounds in late October. Males from this population settle their territories over buildings which are used as nesting sites (holes of barns and houses). Consequently, their distribution is fragmented as it follows the village layout, into hamlets (*i.e.* bunches of houses close to each other). Males followed in our study were distributed over 11 hamlets (**Appendix 1, Figure A1**). Each hamlet hosts on average 4 ± 1 (mean ± SD) and up to seven males. Males are philopatric (they return as first year breeders either to the hamlet where they hatched or to an adjacent hamlet) and exhibit a strong breeding site fidelity (Draganoiu, 2005; Musseau, 2007). Males display delayed plumage maturation: first year breeders have a similar plumage to females and at the end of the first breeding season they moult and acquire their definitive darker plumage (**Appendix 1, Figure A2**). We will refer to individuals in their first breeding season as one-year-old males

(Y1) and to birds in their second breeding season as two-year-old males (Y2). Colour banding enabled individual identification with the use of binoculars and telescopes.

Field observation periods

In 2015 and 2020 to 2022, the survey of the area started in March and ended in June apart from 2020 and 2021, when it was also carried out during September. From 2016 to 2019, the area was surveyed during April and in 2018, during March and April **(Appendix 1, Table A1)**. During fieldwork, we patrolled the hamlets daily from dawn to dusk in order to find the returning males, to define their territories, to identify their neighbours and to record them.

Song recording and repertoire analyses

Males sing from rooftops, chimneys, utility poles and nearby trees to defend their territories. We recorded males mostly during dawn choruses with Sennheiser microphones (MKH70 P48, frequency range: 50–20 000 Hz ± 2.5 dB) connected either to a NAGRA ARES-BB+ or to a Marantz PMD670. All songs were recorded in wav format (22 050 Hz sampling frequency; 16-bits accuracy)

A complete black redstart song is composed of two distinct strophes: the beginning and the ending strophe. However, truncated songs, consisting of either the beginning or the ending strophe alone, are often produced (Draganoiu et al., 2014). Each strophe is composed of one or several introductory syllables and a trill consisting of a repetition of one or more syllables. The two strophes are separated by a silence followed by a wide frequency bandwidth harsh sound (**Figure 1**). Most strophes are used exclusively at the beginning or at the end of the song, but a few strophes can be used either at the beginning or at the end of the song (mobile strophes), increasing the number of strophe combinations. Given that males can produce strophes independently of each other we focused on strophe repertoire, that we defined as the total number of strophes that a male can produce. The mean strophe repertoire in our population is 2.9 ± 0.1, ranging from 1 to 6 strophes (Draganoiu et al., 2014; Volle et al., 2024). Two of us, both having an extensive experience of analysing black redstart songs, visually analysed spectrograms of recordings with Avisoft-SASLabPro software version 5.2.15 (FlatTop window, FFT length: 256; 87.5% overlap) to determine the strophe repertoire of each male. A mean of 7.0 ± 8.1 (mean ± SD) songs were needed to establish the complete strophe repertoire of a male (Volle et al., 2024). In our population we previously documented the existence of microdialects (**Figure 1 and Appendix 1, Figure A1** (Draganoiu et al., 2014; Volle et al., 2024)), namely high strophe sharing among males settled within the same hamlet but only limited sharing among neighbouring hamlets (mean ± SE strophe-repertoire sharing score (0–1) = 0.81 ± 0.07 and 0.15 ± 0.02, respectively). Microdialects are characterised by fewer than 100 individuals sharing the same dialect and dialect groups being separated by less than two kilometres (Podos & Warren, 2007). Furthermore, some of these microdialects were stable across up to fourteen years in our population (unpublished data). Two among us visually inspected spectrograms to assess if a focal individual shared (yes/ no) one or several strophes with the other males of the neighbourhood. We calculated pairwise strophe repertoire sharing score (RS, ranging from 0 to 1) between a focal individual and its neighbours (all the other males in the hamlet) using the following formula: $RS = 2Ns / (R1 + R2)$, where Ns is the number of strophes shared between two birds, R1 and R2 being the number of strophes present in the repertoire of the first and second bird, respectively (McGregor & Krebs, 1982). These scores were then averaged to obtain the mean sharing score of a focal individual with its neighbours. The previously detailed analyses were carried on the three following cohorts.

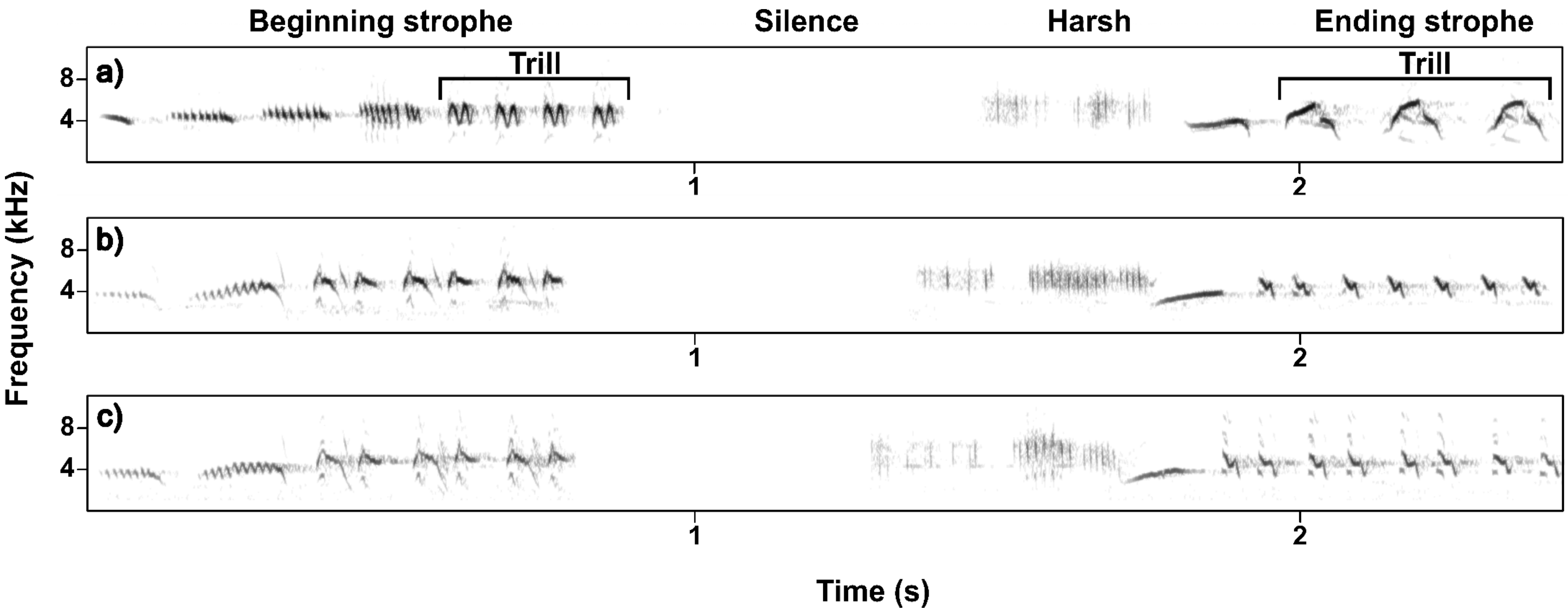

Figure 1. Spectrograms (FlatTop window, FFT length: 256; 87.5% overlap) of black redstarts songs from three different males. Song a) is issued from one hamlet ("Le Bourg") while songs b) and c) are issued from two different males of a distinct hamlet ("La Côte") that share both their strophes.

Repertoire during the first 2 months of the first breeding season (*N* = 52)

This analysis enabled us to test if first year (Y1) breeders try to settle preferentially in hamlets where they share part of their strophe repertoires with their neighbours. We considered that focal males did so if their sharing score was strictly above 0.15, which is the mean sharing level between hamlets. We retained individuals recorded for the first time within the first two months of the breeding season (1st of March – 30th of April) and had at least one neighbour (*N* = 52). Males of this cohort arrived between the 16th of March for the first one and the 18th of April for the last one and we recorded them on average 7 ± 9 (mean ± SD) days after they arrived. We analysed a mean (± SE) number of 189 ± 17 songs per focal individual. Seventy-seven neighbouring birds were included in the analysis and at least 20 songs per individual were analysed to establish neighbours' strophe repertoires. Given that 7 ± 8 songs are needed to establish the full strophe repertoire (Volle et al., 2024), we estimate that the analysis of 20 songs per individual enabled us to reliably estimate repertoire sizes.

Changes in strophe repertoire within the first breeding season (*N* = 25)

This analysis enabled us to determine the timeframe and types of changes (selective attrition, gradual modification and addition, **Table 1**) that occurred during the first breeding season (March to September) within the males' strophe repertoires. As stated in the introduction, we looked for three types of change: addition, deletion and gradual modification. We recorded 25 males in their first breeding season. These males were recorded at least twice: once between the 1st of March and 30th of April (period#1) and once between the 1st of May and 30th of June (period#2). The first recording of period#1 had to be at least 30 days apart from the last recording of period#2. We analysed 50 songs for both periods for 23 males; for the remaining two males we analysed 50 songs in the first period, but we only disposed of 22 and 16 songs for the second period. Using 50 songs per individuals per period, gave us a fair representation of the songs used by males at these times. Out of the 25 males included in the intra-annual survey eight were also followed in September.

Table 1. Summary of individuals expressing song modifications

Individuals	Modification type		
	Deletion	Addition	Gradual modification
1	**X**		
2	**X**		
3	**X**		
4	X		
5	X		
6	X		
7	X		
8	X		
9	X	X	
10		**X**	
11		X	
12		X	X
13		**X**	**X**
14			**X**

Crosses' colours indicate the time frame of the change observed for the individuals, black for intra-seasonal changes, grey for inter-seasonal changes.

Changes in strophe repertoire between breeding seasons (*N* = 24)

The purpose of this analysis was to establish the timeframe as well as the type of changes males could operate throughout their lifetime in their strophe repertoires, in particular in the context of song sharing with neighbours. From 2015 until 2022, we followed 24 males during their first and second breeding seasons. We analysed a mean (± SE) number of 219 ± 20 songs per bird in their first year and 311 ± 24 songs in their second year. We also followed eight individuals past their second breeding season, three males of 3-year-old, two males of 4-year-old, two males of 5-year-old and one male of 8-year-old, allowing us to study modifications in the long term. For sharing score calculations, a total of 108 neighbouring males were included (20 songs were analysed per individual). An inter-seasonal comparison of the strophe repertoire sizes of the focal birds (*N* = 24) was carried out on the repertoires they expressed in the first two months of each season. Males arrive on breeding grounds with a crystallised repertoire, hence the changes between seasons we refer to have occurred between May of year n and March of year n+1.

Gradual modification (N = 3)

We observed gradual modifications for five syllables produced by three different males (**Appendix 2, Table A2**). For one male, it occurred between the two periods of the first breeding season (March-April and May-June). For another one, it occurred between the beginning of the first and the second breeding seasons. For the third male, it appeared from May of the first breeding season and had ended by its return in March of the second. To assess the extent of the syllables' changes, we measured the sound similarity of the target syllables produced by the focal male in the first and second breeding seasons with the same syllable type sung by an adult neighbour of the focal male during the first breeding season (*N* = 3). For the syllable that changed between the beginning and the end of the first breeding season, we measured the similarity of the syllables produced during the March-April and the May-June period with their counterparts in the strophes of an adult neighbour (*N* = 2) (see **Appendix 2**).

Statistical analysis

We used non-parametric statistical tests (one-sided one-sample Wilcoxon signed rank test, sign test, paired sample Wilcoxon signed rank test and Wilcoxon rank sum test) for non-normal data. Otherwise, we used parametric statistical tests (paired t-test). For all statistical tests, a p value below 0.05 indicated significant results. We used R version 4.1.2 (R Development Core Team, 2021) to carry out our statistical analysis, using the rstatix and car libraries.

Ethical note

Mist netting and banding were carried out by TD and TV under the authorisation number PP548 delivered by the Centre de Recherches sur la Biologie des Populations d’Oiseaux (CRBPO) of the French National Museum of Natural History (MNHN, Paris, France). We minimized the duration of manipulation to reduce the stress of the capture and we released the birds near their territories. We ensured that each banded bird returned to its usual activities after the banding procedure. Our study followed the ASAB/ABS Guidelines for the use of animals in research.

RESULTS

Song sharing when returning from the first migration

When returning from migration Y1 breeders (*N* = 52) had a median sharing score of 0.62 (Interquartile range (IQR):0.55) with their neighbours. Y1 males had a significantly higher sharing score with their neighbours than they would if settling in another hamlet of the study area (mean ± SE, 0.15 ± 0.02 see (Draganoiu et al., 2014) (One-sided one-sample Wilcoxon test, W = 1300.5, P < 0.0001, *N* = 52). Only five males had a sharing score inferior or equal to 0.15.

Summary of males displaying changes

The majority of birds did not make changes to their repertoires. When combining individuals from the intra- and inter-annual surveys (40 different individuals), we observed 14 males (issued from 8 of the 11 studied hamlets) displaying changes. Three of them used two different types of changes (either the combination of gradual modification and addition (*N* = 2) or addition followed by selective attrition (*N* = 1). Nine of the 14 individuals used selective attrition, five displayed addition and three expressed gradual modifications of one or several syllables. As mentioned in the methods we analysed the changes both within the first breeding season and between successive breeding seasons (**Table 1**).

Intra-seasonal variability in strophe repertoires

The comparison of the Y1 individuals' strophe repertoires sizes between the first (March-April) and the second (May-June) period of the breeding season (Median 3

IQR 1 for both) did not reveal significant differences between periods (Sign test, S (3) = 3, P = 0.25, *N* = 50). Nonetheless, three out of the 25 individuals lost one or several strophes from their repertoires, not shared with neighbouring males, displaying selective attrition (**Appendix 3, Figure A5**) on average 46 ± 9 days (±SD) after they arrived on their breeding grounds. In addition, two males, despite keeping their repertoires' size stable, showed the gradual modification of two syllables of one strophe into other syllables shared with their neighbours (**Appendix 2, Figure A3-A4**). The changes operated by these five individuals induced in all cases an increase in their sharing scores with their neighbours in the May to June period of the first breeding season (mean ± SD, period 1: 0.31 ± 0.25 and period 2: 0.58 ± 0.29). Out of the 25 males of the intra-seasonal survey, eight birds were also recorded in September of the first breeding season and two of them showed changes of their repertoire composition: both added one new strophe (**Appendix 3, Figure A5**) and one male also continued to gradually modify two syllables of one strophe.

Inter-annual territory stability

All the 24 colour-ringed males that were followed for at least two years bred within the same hamlet (bunch of houses) during their whole lifespan. Seven individuals moved to an adjacent territory within the same hamlet: six did so starting with their second breeding season and one starting with his third breeding season.

Inter-annual variability in strophe repertoire

Males' (*N* = 24) strophe repertoire size did not vary significantly between the first two breeding seasons (Y1: Median 3 IQR 1 and Y2: Median 3 IQR 1) (Paired

Wilcoxon test, V = 24.5, P = 0.85, *N* = 24). Nonetheless, four males added new strophes to their repertoires before the beginning of the second breeding season and two of them also gradually modified elements of their strophes. In addition, we observed selective attrition in four males. Among the eight males that were recorded past their second breeding season, we observed selective attrition for two additional individuals until their third year and for one of them even until its fourth year. The remaining six males kept their repertoire stable throughout their lifetime (ranging from 3 to 8 years old).

Changes in sharing scores between the first and the second breeding seasons

The median sharing score was significantly higher for males in their second year, 0.74 (IQR 0.31) compared to their first year, 0.66 (IQR 0.43) (Sign test, S (21) = 3, P = 0.0015, *N* = 48) (**Figure 2**). Males exhibiting changes in their repertoires between their first and second years had a significantly lower median sharing score with their neighbours in their first year (0.56 IQR 0.31) compared to males with stable repertoires between years (0.80 IQR 0.36) (**Figure 3**) (Wilcoxon test, W = 108, P = 0.017, *N* = 24).

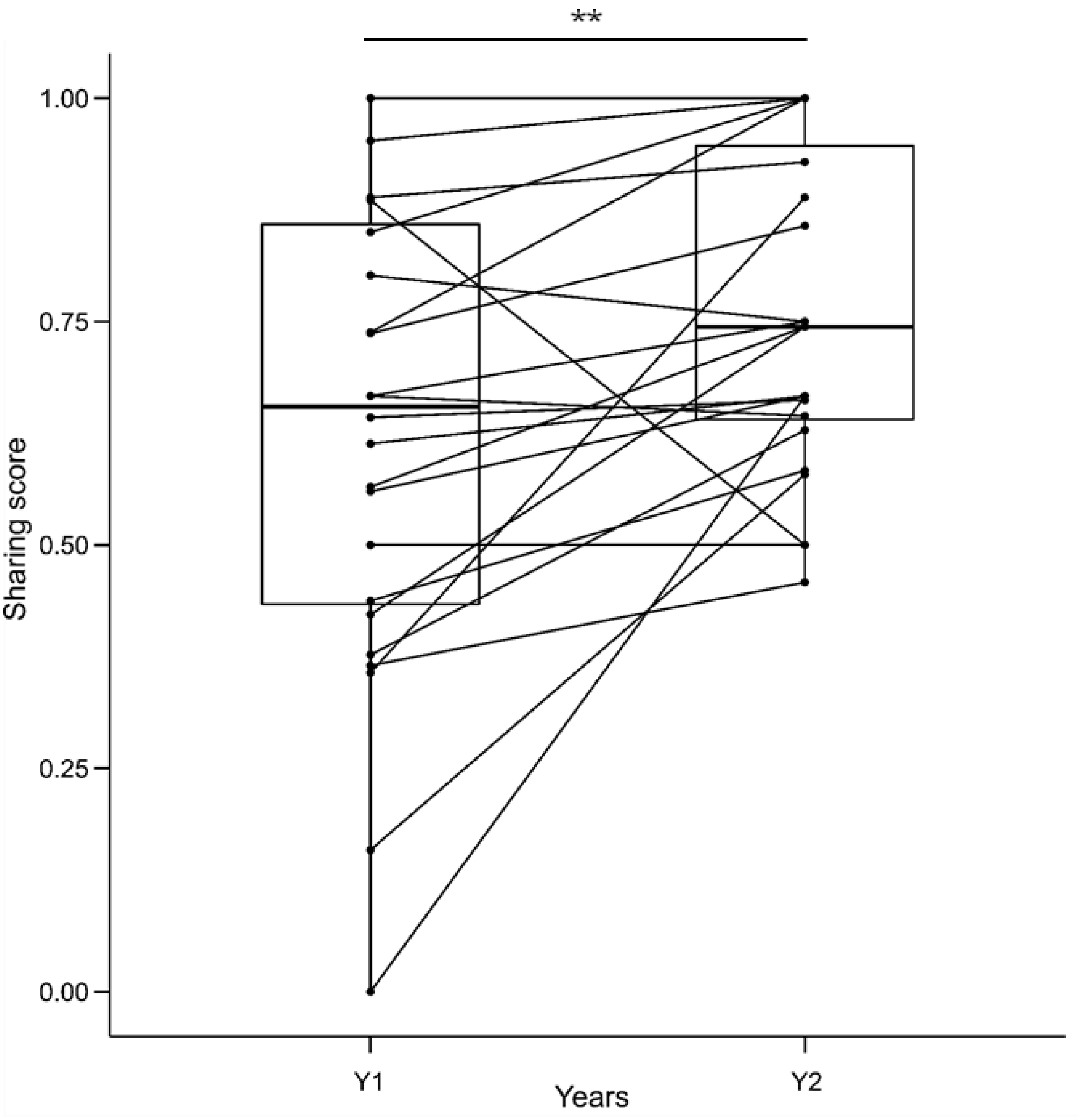

Figure 2. Evolution of the median sharing scores of focal males (*N* = 24) between their first (year 1: Y1) and their second breeding season (year 2: Y2).

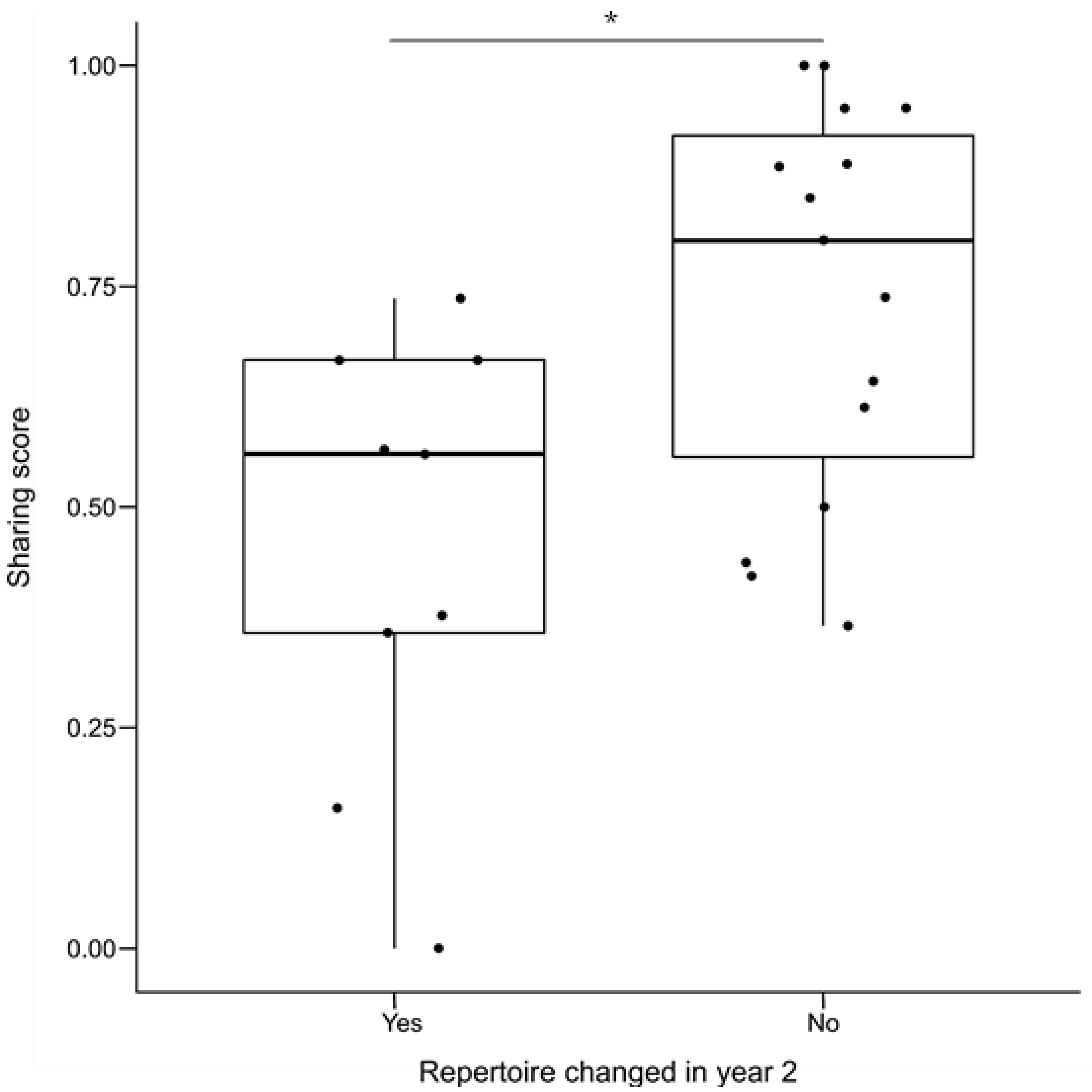

Figure 3. First breeding season strophe sharing score of males displaying either change or stability of their repertoires between the first and the second reproductive seasons.

Gradual modification

For the three males who displayed syllables' gradual modifications, the comparison of the mean acoustic similarity of the focal males' syllables (*N* = 5) in their first and second year/ season period to their neighbour model syllables during the first breeding season showed a significant difference (Paired t-test: $t_4 = -4.13$, $P = 0.0072$, *N* = 5) (**Figure 4**). The syllables produced by the focal males in their second year or their second season period were significantly more similar to the syllables of their neighbours' syllables (Mean ± SE: 0.67 ± 0.04) than the syllables the focal birds produced in their first year or their first season period (0.48 ± 0.05). Therefore, focal males increased acoustic similarity with their neighbours through gradual modification of their syllables. (**Appendix 2**, **Figure A3-A4**).

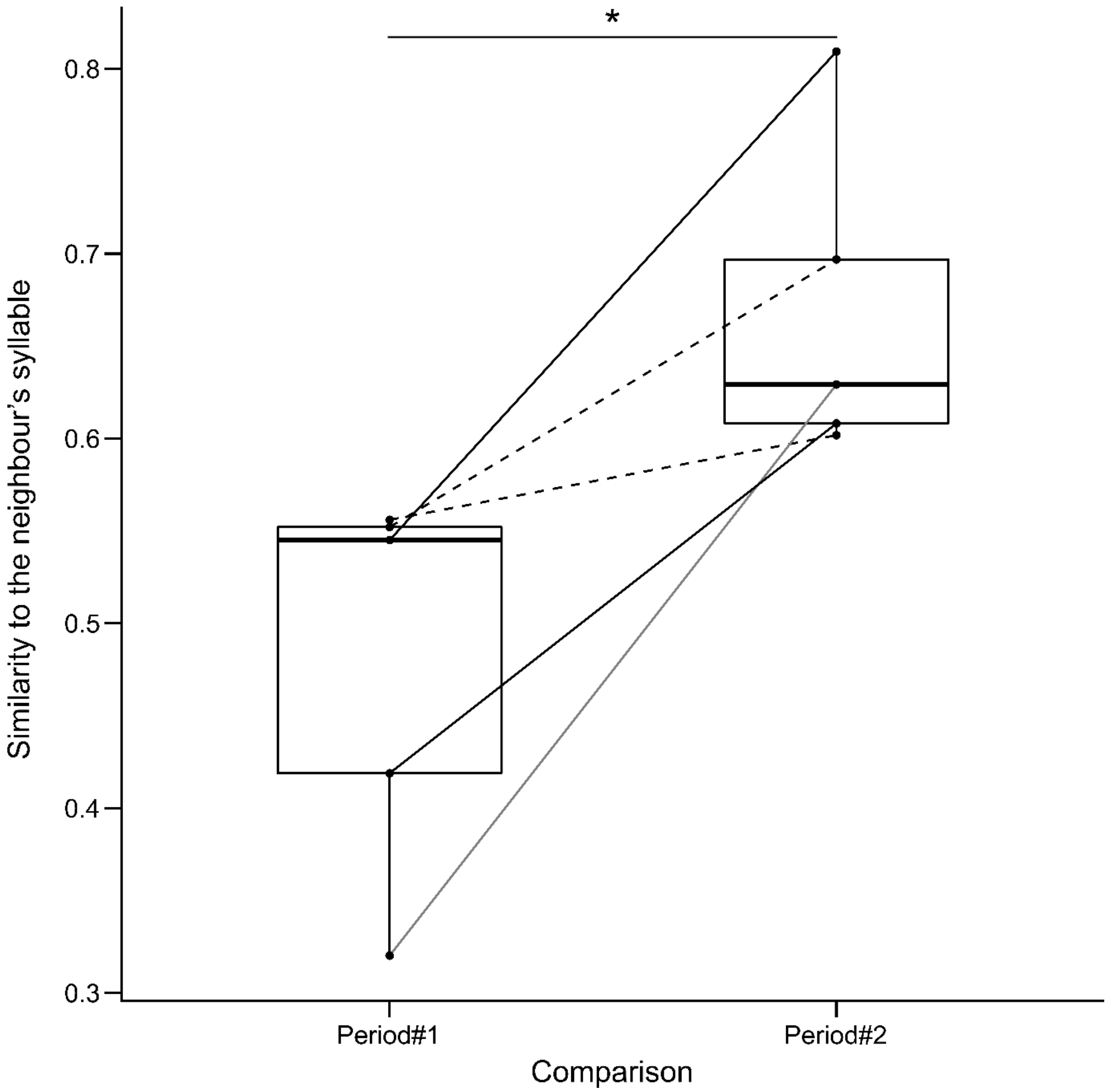

Figure 4. Effect of gradual modification on song syllables' similarity to neighbours. Evolution of the focal males' gradually modified syllables' similarity (*N* = 5) to their first-year neighbours' syllables either between breeding seasons (plain black and grey lines correspond to two distinct individuals) or within the first breeding season (dotted lines). As previously mentioned, 5 song syllables produced by 3 different males did exhibit vocal changes during the two considered periods.

DISCUSSION

In our study population, we observed that most males shared strophes with their neighbours at their arrival on their breeding sites during the first breeding season. Two thirds of the males kept their strophe repertoires stable during their whole lifespan. However, one third of the males changed their vocal repertoire composition using one or several of the three following types of change: the selective attrition of unshared strophes, the gradual modification of pre-existing syllables and the addition of new strophes. Most of these changes occurred between the middle of the first breeding season and their return for their second breeding season. Individuals who modified their strophe repertoires had on average lower strophe sharing scores with their neighbours during their first breeding season than individuals who kept their repertoires stable. These modifications resulted in an increase of their vocal sharing with their neighbours.

Pre- & post-dispersal learning

Young black redstart males start producing their songs between 80 and 120 days after hatching by copying adults singing in autumn (Nicolai, 1992). Previous studies in our study population reported that 3-10% of the males that hatched in the area returned as Y1 breeders either in their hatching hamlet or in an adjacent one (Draganoiu, 2005; Musseau, 2007). Our current results complement the previous findings as most Y1 males settled in hamlets from which they sing the local dialect but also bring to light that males can learn post-dispersal. It has been previously shown that song learning programs and dispersal patterns can lead to the appearance and maintenance of dialects (Fayet et al., 2014; Hensel et al., 2022; Podos & Warren, 2007;

Slater, 1989). Dialect boundaries are likely involved in guiding dispersal in several species where males display pre-dispersal learning and preferentially settle in areas where they sing the local song variants (Baptista & Trail, 1992; Marler & Tamura, 1962; Ranjard et al., 2017).

However, a few males settled as breeders when returning from migration for their first breeding season in hamlets where they shared a few or no strophes at all with their neighbours. We observed six of these males singing new strophes after the beginning of their first breeding season. Our field approach cannot rule out that males were exposed to these strophes during their hatching year and expressed them only in their first/second breeding seasons. These aspects can be addressed only in controlled laboratory experiments and several studies have shown that this can indeed be the case (Chaiken et al., 1994; Geberzahn et al., 2002; Hough et al., 2000). However, given the potential advantages of song sharing, it would make no sense to have memorized those strophes during the hatching year and still not express them during crucial territorial interactions as first-year breeders. In our view the most plausible explanation of our observations is the existence of a sensory learning phase during the first breeding season enabling the birds that disperse out of the area where they learned their songs in their hatching year to adapt to a new social environment (Beecher & Brenowitz, 2005).

In agreement with our previous findings (Draganoiu et al., 2014) males did not sing new strophes after the beginning of their second breeding season. These results seem to indicate that male black redstarts are age limited learners, learning their songs both in the autumn of their hatching year (Nicolai, 1992) and most likely during the first breeding season (current results). However, birds in our population live in stable social environments. In more than fifteen fieldwork seasons, we have never witnessed a male breeding in two distinct hamlets during its lifetime and territory changes within a breeding patch occurred mainly between the first and the second breeding season for around 30% of the males (Draganoiu, 2005; Musseau, 2007; current study). Interestingly, in a highly fragmented Norwegian population of ortolan buntings, *Emberiza hortulana*, with high levels of breeding dispersal, males displayed an important level of repertoire changes between years. This contrasts with a Polish population of the same species, abundant and continuous, where males did not show age related changes in their vocal repertoires (Osiejuk et al., 2019). To conclude, we cannot rule out that black redstarts may be able to learn new songs during their whole life.

In three cases we recorded the new strophes during the first breeding season (either in June or in September) while in three other cases we documented the presence of the new strophes when we first recorded the birds at the beginning of their second breeding season. However, the latter were not recorded in the autumn of their first breeding season. The new strophes were either composed of new syllables, not previously identified in the males' repertoires or resulted from gradual modifications of pre-existing syllables (Vargas-Castro et al., 2015). It took at least two months after males settled in our population before we observed the gradual modifications, while the addition of new strophes only appeared in September. This resembles to the delayed production learning as it was described in brown-headed cowbirds and common nightingales, *Luscinia megarhynchos* (O'Loghlen & Rothstein, 2010; Rothstein & Fleischer, 1987a; Todt & Geberzahn, 2003) but at a shorter time scale. Gradual syllables' modifications are difficult to detect without continuous recording as in laboratory studies (*e.g*. (Derégnaucourt et al., 2005) and could be confused with the addition of new material to the repertoire (Vargas-Castro et al., 2015). This type of change was reported only in a few field studies of songbirds, such as the clay coloured thrush, *Turdus grayi* (Vargas-Castro et al., 2015), the yellow-rumped cacique, *Cacicus cela,* (Trainer, 1989) or the corn bunting, *Miliaria calandra* (McGregor et al., 1997). In the last two species, all males in a neighbourhood gradually changed part of their songs in the same way during several years.

Selective attrition

The most frequent repertoire modification observed in our population was the overproduction followed by selective attrition, a process by which males selectively stop producing unshared songs with neighbouring males (Nelson, 1992, 2000; Nelson et al., 1996; Peters & Nowicki, 2017; Thomas et al., 2021). Selective attrition usually happens quite rapidly after a bird settles in its territory. For example, in the white-crowned sparrow, this process occurs within the first two weeks after arrival on the breeding grounds and males retain songs matching the one sung by the majority of its neighbours (Nelson, 2000). In Savannah sparrows selective attrition was observed between 4 to 21 days after arrival and males retained songs that sounded similar to most of their neighbours (Thomas et al., 2021). In our population, this process started on average 46 days after settlement but for a few individuals followed during several years it was observed only later in life (second to fourth breeding seasons). Selective attrition enables males of our population to keep vocal flexibility through life even though they seem to have lost the ability to learn new material (see also Draganoiu et al., 2014). These observations support Marler's model of memorization by instruction followed by selection in production and fulfil his prediction that action based learning should be widespread in songbird learning (Marler, 1997). The existence of a vocal repertoire turnover during several years was previously described in the field for several songbirds such as the sedge warbler, *Acrocephalus schoenobaenus,* or the ortolan bunting (Nicholson et al., 2007; Osiejuk et al., 2019) but also under controlled laboratory conditions, as described for the starlings (Chaiken 1994).

Song sharing

All these modifications led to an increase of Y1 breeders' sharing scores with the other males of the neighbourhood. Despite the increase of the strophe sharing level the repertoire size remained stable between the first and second breeding seasons as well as during their lifetime. Taken together these results support the *"Sharing" hypothesis* rather than the *"Repertoire" hypothesis*. The potential benefits of vocal sharing remain to be investigated in black redstarts. Nonetheless, on the one hand, in a playback experiment within our population, males were more aggressive towards their local *versus* a foreign microdialect both sung by unfamiliar first-year breeders (Volle et al., 2024). Such a response has been widely reported in birdsong studies on dialects. Since we used songs recorded from unfamiliar individuals, microdialect singers might be considered as more threatening local challengers. Yet on the other hand, once the relation was well established between neighbouring males, it seems to be beneficial to share. Indeed, we also found that males were less aggressive to the familiar shared songs of their neighbours than towards the unshared songs of foreign individuals (Draganoiu et al., 2014). It has been shown in several other species that sharing the local dialect can benefit the newly settled males, through improved territory acquisition, neighbouring relations, mating opportunities or reproductive success (Beecher et al., 2000; Nelson & Poesel, 2013; Payne, 1982; Rothstein & Fleischer, 1987b; Thomas et al., 2021). Thomas et al. (2021) monitored aggression experienced by first-year Savannah sparrow breeders from their neighbours at their arrival on the breeding ground as well as later, once females had arrived, based on the similarity of their songs to their neighbours. Males with less similar songs to their neighbours received more aggression than males with more similar songs. This heightened aggression might be responsible for the selective attrition of dissimilar songs in young males. Further observations could establish if song sharing in the black redstart is beneficial for newly arriving males when establishing neighbouring relationships during their first breeding season as well as for lifetime territory tenure and or pairing/reproductive success.

Conclusions

Our study brings new insights into the process of song learning and its implications for microdialect maintenance in a common yet understudied European songbird, the black redstart. Males in our study population displayed both pre- and post-dispersal learning (**Appendix 4, Figure A6**), supporting the *“Sharing” hypothesis*. A great majority of males settled in breeding patches where they share songs with the other males. While most individuals kept a stable repertoire during their lifetime, those exhibiting low song sharing with their neighbours in the first year changed their repertoires by the second breeding season, leading to an increased sharing with neighbouring birds. These non-exclusive changes included selective attrition, addition, and gradual syllable modification. If addition of new syllables and gradual modifications were not observed after the end of the first breeding season, selective attrition could exceptionally be pursued until the fourth year of life indicating a lifetime plasticity. Our results support thus the continuum view of song plasticity developed by Brenowitz and

Beecher and confirm the crucial importance of longitudinal field programs for the study of song learning.

APPENDIX 1

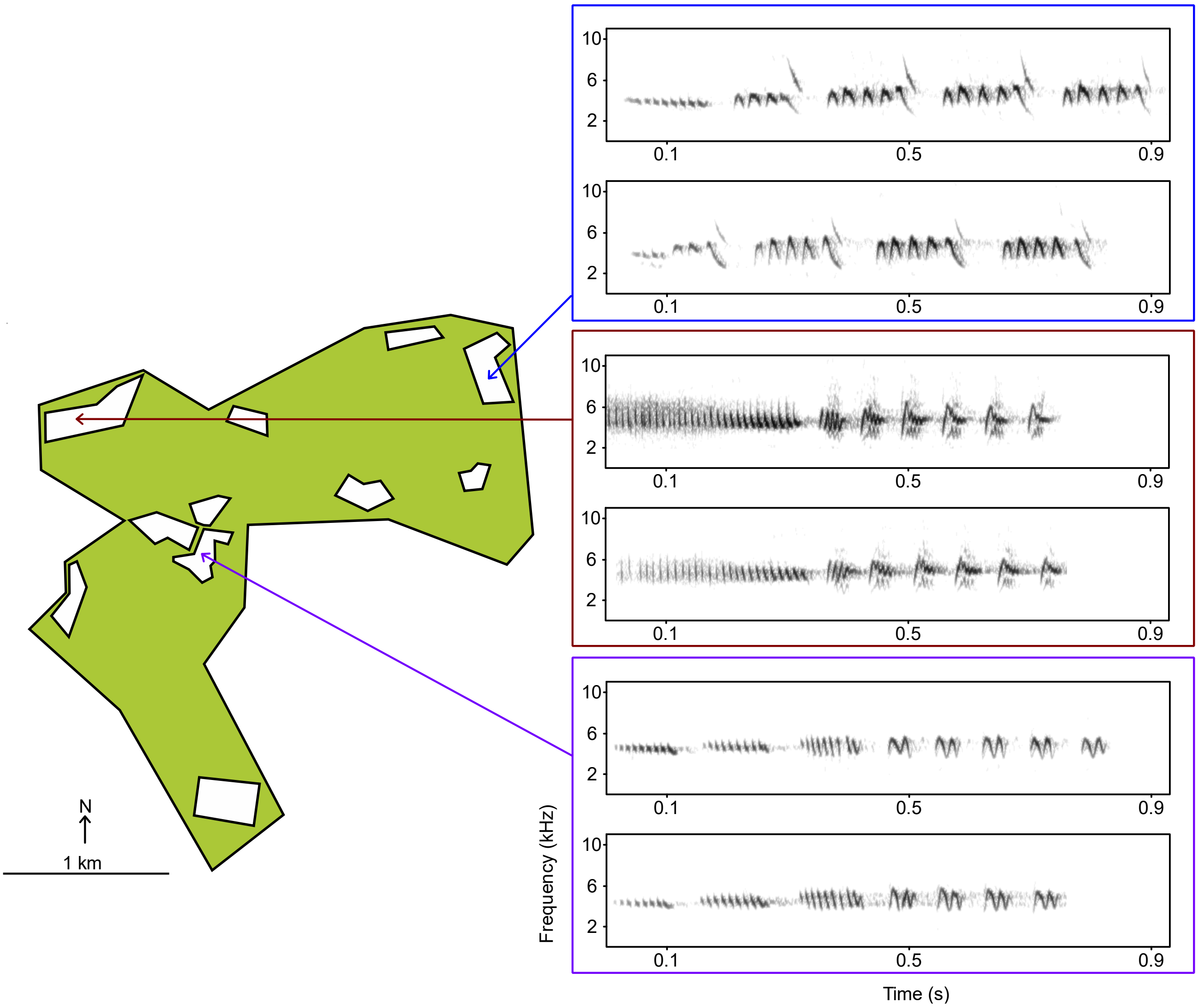

Figure A1. Studied hamlets (*N* = 11, represented in white) dispersion over the research area (in green). Examples of characteristic strophes of three hamlets' dialects sung by two neighbouring individuals (one line per individual, strophes within the same-coloured frame are shared).

Figure A2. Plumage evolution of a male black redstart thought two life stages: first-year breeder (Y1, on the left) and second year breeder (Y2, on the right).

Table A1. Periods of field work surveys (coloured cells) of the population from 2015 to 2022.

Year	March	April	May	June	July	August	September
2015	▒	▒	▒	▒			
2016		■					
2017		▒					
2018	■	■					
2019		▒					
2020	■	■	■	■			■
2021	▒	▒	▒	▒			▒
2022	■	■	■	■			

APPENDIX 2

Vocal change in the case of gradual modification

We observed gradual modification of five syllables in three males (**Appendix 2, Table A2**). To quantify these vocal changes, we calculated the similarity between the focal male syllables to the syllables of a neighbouring adult male (considered as a model to match by the focal bird) (**Appendix 2, Figure A3**). We used ten syllables' exemplars of the syllables showing gradual modification from the focal male in the two time periods as well as the "model" syllable of the neighbour (**Appendix 2, Figure A3**). In one male, we observed a gradual modification of two song syllables from May to September of its first breeding season. Throughout this period, syllables were produced with high variability (*i.e*. **Appendix 2, Figure A4b**). Therefore, we decided to focus on syllables before they started to change (March-April of the first breeding season) and after the gradual modification was carried out (March-April of the second season) rather than on the earlier variable counterparts during summer and autumn. These exemplars were extracted from spontaneous dawn singing bout recordings of each male. These syllables were of good quality (no noise or overlapping songs from other birds). The spectrograms of the second repetition of the adjusted syllables within the trills (**Appendix 2, Figure A3**, framed elements) were isolated using Avisoft-SASLabPro software version 5.2.15 (FlatTop window, FFT length: 512; 96.87% overlap). We used the Avisoft-CORRELATOR available from Avisoft-SASLabPro to compute a similarity coefficient (ranging from 0 – no overlap to 1 – complete overlap) between these syllables.

Table A2. Details on the time frame of changes for the five syllables displaying gradual modifications in three males.

Individuals	Syllables	First breeding season			Second breeding season
		Spring	Summer	Autumn	Spring
1	1				**X**
2	2		**X**		
	3		**X**		
3	4		**X**	**X**	**X**
	5			**X**	**X**

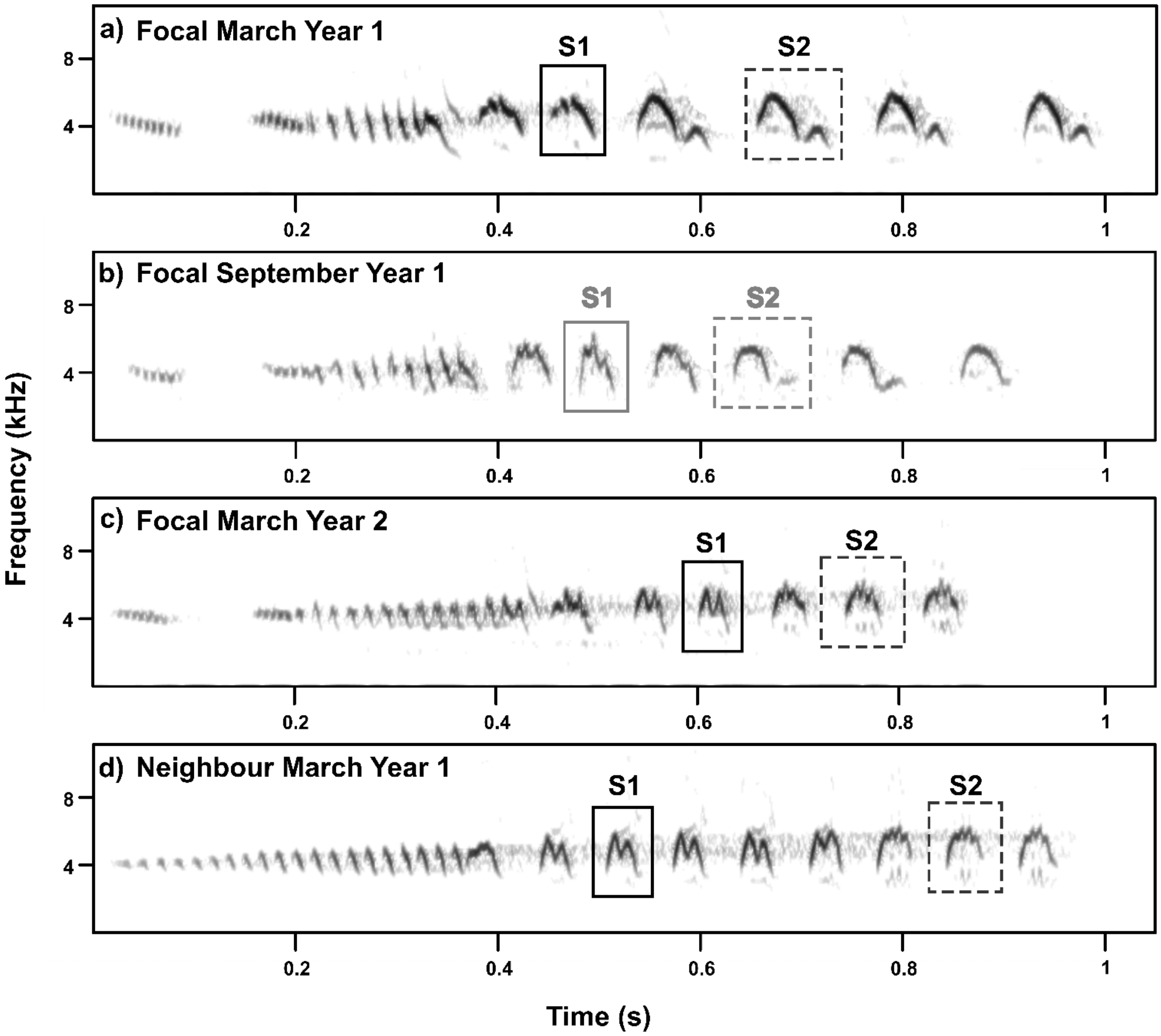

Figure A3. Spectrograms (FlatTop window, FFT length: 256; 87.5% overlap) of a beginning strophe containing modified syllables (S1 and S2) sung by the focal male during a) March of its first breeding season, b) September of its first breeding season c) March of its second breeding season and d) sung by the focal bird's neighbour during the first breeding season (model to be copied). Black-framed syllables (S1 and S2) were compared to document similarity evolution with the neighbour's song (see the text).

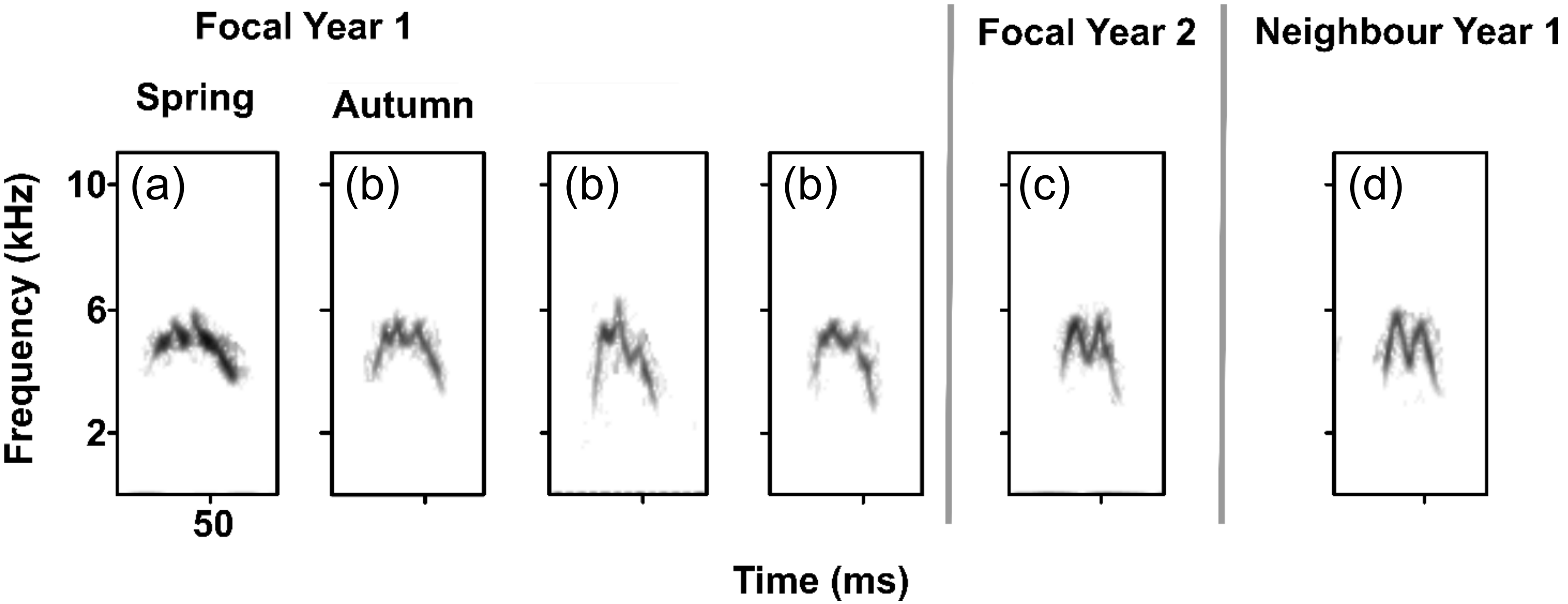

Figure A4. Spectrograms (FlatTop window, FFT length: 256; 87.5% overlap) of an adjusted syllable sung by the focal male in (a) the spring and b) the autumn of its first breeding season (syllables are from the same recording) and c) in its second breeding season compared to the same syllable sung by d) the neighbour during the first breeding season (model to be copied).

APPENDIX 3

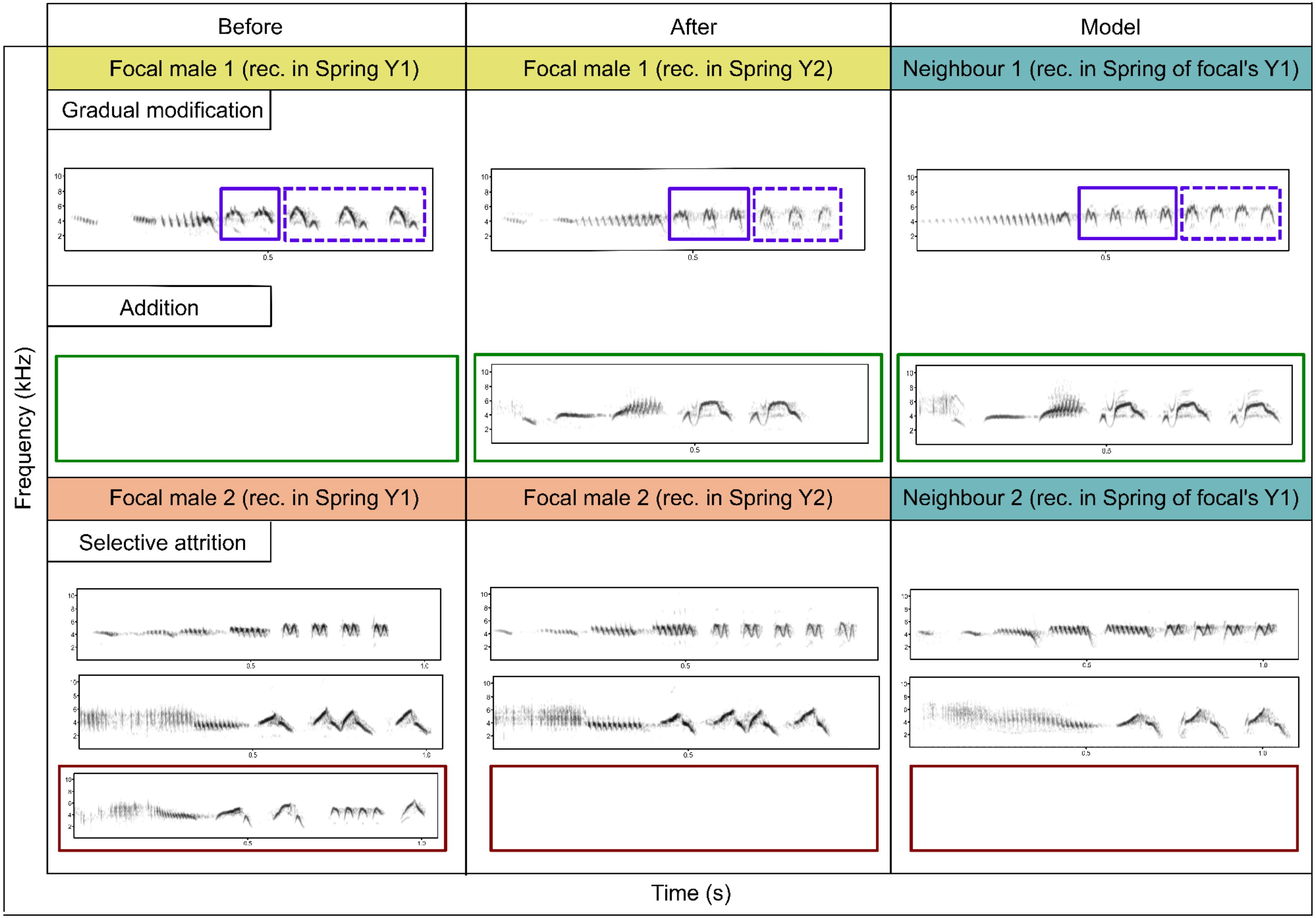
Before
After
Model
Focal male 1 (rec. in Spring Y1)
Focal male 1 (rec. in Spring Y2)
Neighbour 1 (rec. in Spring of focal's Y1)
Gradual modification
Addition
Focal male 2 (rec. in Spring Y1)
Focal male 2 (rec. in Spring Y2)
Neighbour 2 (rec. in Spring of focal's Y1)
Selective attrition
Frequency (kHz)
Time (s)
10
8
6
4
2
0.5
1.0

Figure A5. Examples of the three types of modifications of strophe repertoire between the first and second breeding seasons in two males. The repertoires of the focal males over the span of two years are put in comparison to the repertoire of their neighbours during their first breeding season (model to copy). Strophes that were added are framed in green, a strophe with gradually modified elements within is framed in purple and a strophe that the bird selectively deleted from his repertoire (not shared with any neighbour) is framed in red.

APPENDIX 4

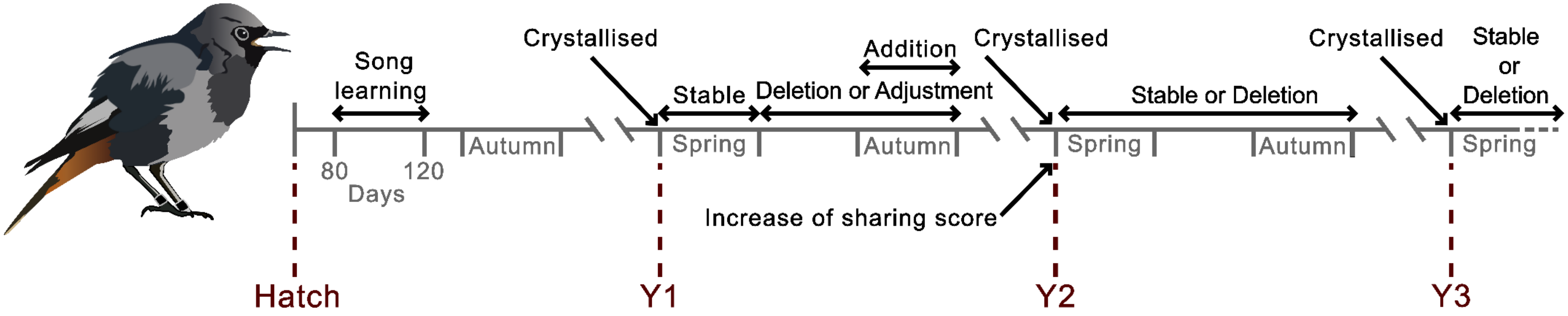

Figure A6. Timeline of strophe repertoire acquisition and modification through a black redstart lifespan. From 80 to 120 days after hatching males will most often learn the dialect of their hatching hamlet. When returning from migration the strophe repertoire is crystallised and it will stay stable during the spring of the first breeding season (Y1). For males with low strophe sharing with neighbouring males, modifications of the strophe repertoires such as gradual modification and selective attrition (deletion) begin during the summer of the first breeding season. Addition of new strophes only starts in September of their first year. Males with high strophe sharing will keep their strophe repertoire stable. By the time males return for the second breeding season (Y2) their strophe repertoire is crystallised again and an increase of strophe sharing is observed. After the return for the second breeding season most males keep their repertoires stable while a few display selective attrition through their lifetime (Y3).

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CHAPTER 1

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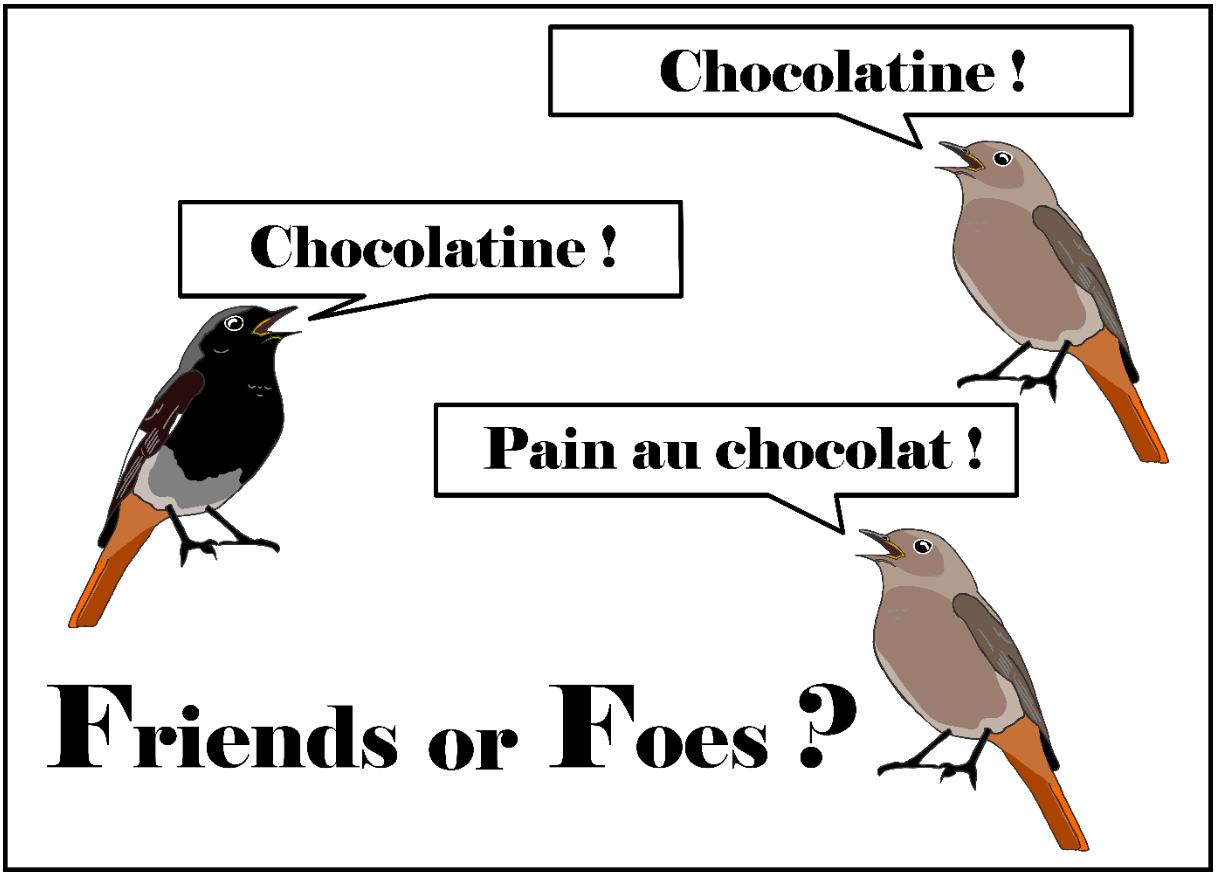
CHAPTER 2: FOREIGN-LOCAL MICRODIALECT DISCRIMINATION IN A SONGBIRD, THE BLACK REDSTART



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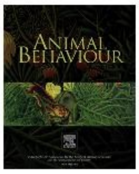
"Chocolatine" and “Pain au chocolat” both refer to the same type of pastry in French. However, "Chocolatine" is mostly used in the south-west part of France.

Animal Behaviour 210 (2024) 113–125

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Foreign–local microdialect discrimination in a songbird, the black redstart

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ARTICLE INFO

Article history:
Received 27 June 2023
Initial acceptance 2 August 2023
Final acceptance 8 December 2023

MS. number: 23-00337R

Keywords:
birdsong
black redstart
dialect discrimination
microdialect
Phoenicurus ochruros
playback
relative threat hypothesis
territorial defence
vocal communication

Dialects have been described as geographical variations of vocal signals in several taxa such as humans, cetaceans, bats and birds. Many playback studies have focused on dialect perception by territorial birds, mainly reporting a stronger aggressiveness towards local dialects in comparison to foreign ones. However, exploration of the influence of several methodological factors is lacking, and very few studies have focused on species displaying microdialects (covering distances under 2 km). We investigated these issues in a migratory population of a territorial songbird, the black redstart, *Phoenicurus ochruros*. In this species only males sing to defend their territories, and their distribution leads to several small groups of neighbours with a relatively high level of song sharing within each group. Using a playback experiment, we tested whether males were able to discriminate between the local and a foreign microdialect, while testing for the effects of their age class, the initial distance to the speaker, the relative acoustic similarity between the playback songs and songs of the tested birds and the order of the stimuli. We broadcast two acoustic stimuli (foreign and local microdialect) from unfamiliar individuals to 26 territorial males, during two breeding seasons. In line with our predictions, males showed a stronger response towards the local microdialect, spending more time in proximity to the speaker, in agreement with the escalation chain of aggression. Our results conformed to the previously reported trend in wide-spanning dialect species. We also showed that both the vocal response and the approach behaviours were influenced by the distance of tested males from the speaker at the beginning of the experiment. Males that were further from the sound source tended to sing rather than approach. More studies are needed to get a better understanding of discrimination abilities and their functions in microdialect species.

Geographical variation in vocal signals (dialects) has been widely described in humans and other animals, with a special focus on songbirds (Baker & Cunningham, 1985; Henry et al., 2015). In many oscine species living in temperate zones, only males sing, mainly during the breeding season (but see Odom et al., 2014), and song plays a major role in both territory defence and mating (Nowicki & Searcy, 2004). Accordingly, many field and laboratory studies have focused on both proximate and ultimate causes of dialects (Planqué et al., 2014; Le Maguer et al., 2021; Williams & Lachlan, 2022).

Young birds learn songs by imitating mainly adult conspecifics (i.e. parent or neighbour) heard during early stages of life (Beecher & Brenowitz, 2005), leading to the emergence and maintenance of song dialects in the case of natal philopatry (i.e. remaining or returning to the natal geographical area to breed). However, some species display a more flexible song-learning program (Beecher & Brenowitz, 2005), allowing them to adjust their vocal production to match local songs in the case of dispersal (Nordby et al., 2001; O'Loghlen & Rothstein, 2010). Two main functional hypotheses have been proposed to explain song sharing among neighbouring breeding males, although dialects could be a simple by-product of song learning and dispersal patterns previously mentioned (for a review, see Podos & Warren, 2007). The local adaptation hypothesis posits that a male singing a local dialect originates from the area and therefore represents a potential mate of quality due to its adaptations to this environment (Nottebohm, 1969). The social adaptation hypothesis was suggested for males learning local songs postdispersal and posits that dialects result from an adjustment to local song conditions (Payne, 1981).

Local–foreign song dialect discrimination has been thoroughly investigated over the last 60 years (Fracas et al., 2023; Hudson et al., 2019; Williams et al., 2019), and stronger aggressive behaviour

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https://doi.org/10.1016/j.anbehav.2024.01.020
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towards the local dialect was the most common response reported in playback experiments (Parker et al., 2018). Several complementary explanations have been suggested to explain this response pattern. At an ultimate level, the relative threat hypothesis states that a bird singing a local dialect is more competitive than a stranger singer due to its familiarity with the local environment (Rothstein & Fleischer, 1987; Wright & Dorin, 2001). At a proximate level, according to the recognition hypothesis, birds will strongly react to a song that matches closely their internal representation of the species' standard song (Dabelsteen & Pedersen, 1992; Nelson, 1998). Indeed, dialect assortative mating can lead to genetic divergence and foreign dialect singers might not be recognized as conspecifics.

However, it is important to consider several methodological factors during playback experiments such as the use of both vocal and approach behaviours to measure aggressive responses (Parker et al., 2018), the presentation order of the stimuli (i.e. habituation risk; Dong & Clayton, 2009) or the location of the speaker: territory centre versus boundaries with the neighbours (Falls & Brooks, 1975; Stoddard, 1996). Other potentially important parameters have received less attention. A few studies have pointed out the role of the initial distance of focal birds from the speaker at the beginning of playback (Armstrong, 1991; Naguib et al., 2002). More recently, the effect of the similarity between the playback stimuli and the focal birds' songs was shown to mediate territorial responses (Derryberry, 2011). Finally, the age of the tested birds is a critical biological factor due to its relations with many behaviours directly or indirectly related to territoriality (e.g. aggressiveness: Osiejuk et al., 2007; Schwarzová, 2010; pairing and mating success: Weggler, 2001).

In addition, there is an important variation in the geographical spread of dialects. While most studies have concerned widespread dialects (Benedict & Bowie, 2009; Chilton et al., 2002; Ivanitskii et al., 2023), relatively little research effort has been carried out on microdialect populations (Podos & Warren, 2007), which differ in the number of birds sharing songs (fewer than 100 individuals) and spatial sharing range (i.e. less than 2 km), as described in European wrens, *Troglodytes troglodytes* (Kreutzer, 1974a), Eurasian skylarks, *Alauda arvensis* (Briefer et al., 2011) or Savannah sparrows, *Passerculus sandwichensis* (Hensel et al., 2022; Thomas et al., 2021). For example, 1-year-old male indigo buntings, *Passerina cyanea*, that match the local microdialect have greater mating and fledging success than nonmatchers (Payne, 1982). Both the small range of geographical areas where song sharing occurs and the low number of birds sharing songs make microdialects a system model of relevance to study vocal culture (Garland & McGregor, 2020; Payne, 1981) and its potential importance in conservation biology (Laiolo & Tella, 2007; McGregor et al., 1997).

The present experimental study aimed at investigating local–foreign microdialect discrimination in a migratory population of a territorial songbird with delayed plumage maturation, the black redstart, *Phoenicurus ochruros*. Only males sing and defend territories, around farms and houses. The patchy distribution of the buildings in the study area leads to small neighbourhoods (two to eight males) with important song sharing among neighbours and low song sharing between different groups of buildings, leading to microdialects (Draganoiu et al., 2014). Male black redstarts have good discrimination abilities: they display the dear enemy effect (the ability to discriminate between the songs of their neighbours and those of strangers, Draganoiu et al., 2014) and can even discriminate between the begging calls of their different fledglings (Draganoiu et al., 2006). Neighbour–stranger discrimination studies showed that males are less aggressive to a familiar, often shared neighbour song than towards an unfamiliar unshared song of a conspecific (Temeles, 1994; Werba et al., 2022). In comparison, our study aimed to show whether males are able to discriminate shared versus unshared songs independently of the familiarity. This was enabled by our long-term survey of our studied population as both stimuli were recorded in the research area between 1 and 7 years before our experiment. Fine vocal discrimination abilities in this species combined with strong responses during playback tests (Apfelbeck et al., 2012) make the black redstart a good model to explore local versus foreign microdialect discrimination.

We broadcast two vocal stimuli from nonfamiliar birds during the breeding season to tested males: a song belonging to the local microdialect and a song from a foreign microdialect. We measured several vocal and movement behaviours during the tests to depict the global agonistic response of tested males to playback. Based on the relative threat hypothesis we expected that males would react more aggressively to the songs of the local microdialect, conforming to the main trend observed in previous studies carried out on species with widespread dialects. In addition to the stimulus type, we explored the potential effect of the similarity between the playback stimuli and the focal birds' songs (as a relative gradient). In line with the previous hypothesis, we expected a stronger territorial response for more similar stimuli. We also tested the effect of the initial distance of the birds from the speaker on their responses, expecting singing when distant from the speaker and approaching behaviours when close to the speaker, based on the conceptual frame of the escalation chain of aggression (Beecher & Akçay, 2014). We also tested the effect of age class, predicting lower aggressiveness for first-year inexperienced males compared to older, experienced breeders (but see Garamszegi et al., 2006). Finally, habituation to the playback was assessed by testing the effect of the stimulus order.

METHODS

Study Population

The population of black redstarts studied is located in hamlets (i.e. groups of houses close to each other) belonging to three French neighbouring villages: La Valla-sur-Rochefort, Saint-Didier-sur-Rochefort and Saint-Just-en-Bas (study area; mean position: 45°45′N, 3°50′E; mean altitude of 863 m). Upon their arrival from migration at the breeding grounds in March, males from this population typically establish their territories, exclusively using buildings (i.e. mainly holes in barns and houses) as nesting sites (Draganoiu et al., 2014). Since territories overlap with human constructions, male distribution is fragmented in the study area, each hamlet hosting generally three to four and up to a maximum of seven males. Overall, males breed from age 1 year, but 1-year-old breeders have a grey plumage similar to that of females due to delayed plumage maturation (Landmann & Kollinsky, 1995b).

Males actively defend their territory by singing from rooftops, chimneys, utility poles and nearby trees. When challenged by a rival, a territorial male will sing, then perform patrol flights over its territory to locate the intruder, hold ground near the rival, and finally chase and attack it. This hierarchical response pattern, based on our experience, is consistent with previous works which recorded contact as the final step of aggression in this species (Apfelbeck & Goymann, 2011; Landmann & Kollinsky, 1995a; Schwarzová, 2010; Sedláček et al., 2006).

The typical song consists of two distinct strophes: the beginning and the ending strophe. More precisely, each strophe is composed of one or more introductory syllables and a trill consisting of the repetition of one syllable. The two strophes are separated by a silence followed by a wide-frequency bandwidth harsh sound (Fig. 1a). Males also produce truncated songs, composed only from the beginning strophe or from the ending strophe preceded by the

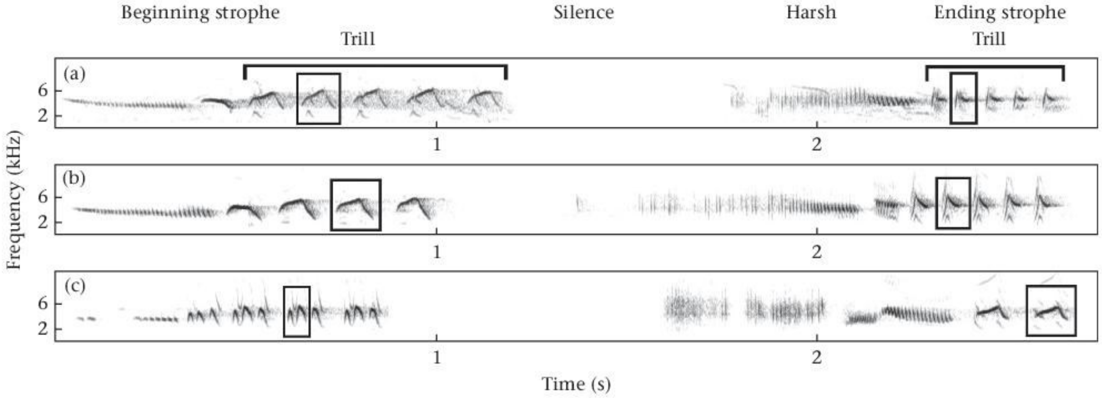

Figure 1. Spectrogram examples (FlatTop window; FFT length: 256; 87.5% overlap) of complete songs (a) from a male black redstart tested in the playback experiment (showing the different components of the song), (b) used in the local song (LS) treatment and (c) used in the foreign song (FS) treatment for this male. Each box contains the syllable used to compare these songs (see the text).

harsh sound. Each male has a strophe repertoire and a song repertoire, defined, respectively, as the total number of different strophes and the total number of strophe combinations (ca. three strophes and two songs; Draganoiu et al., 2014). In addition, in this population we documented (see Draganoiu et al., 2014) a high level of strophe repertoire sharing among males settled within the same hamlet (mean ± SE strophe repertoire sharing score (0–1) = 0.81 ± 0.07), and only limited strophe repertoire sharing between males from different hamlets (0.15 ± 0.02). In addition, some of these microdialects appear to be stable for up to 7 years in this population (Schloesing, 2015).

Song Recording and Analysis

We surveyed the study area every day during the breeding period in 2021 (from 15 March to 4 May) and 2022 (from 10 March to 26 April) to assess males' arrival time from migration and to define territorial boundaries. We recorded territorial males to establish their strophe repertoires and to measure strophe sharing between neighbouring males (see below). Songs were recorded in 2021 from 25 March to 27 May, and in 2022 from 16 March to 25 May, mostly during dawn choruses, which generally started an hour before sunrise and lasted on average 30–60 min. We used Sennheiser microphones (MKH70 P48, frequency range: 50–20 000 Hz ± 2.5 dB) connected either to a NAGRA ARES-BB + (30–20 000 Hz) or to a Marantz PMD670 (20–20 000 Hz) for song recordings (sampling frequency 22 050 Hz; resolution 16 bit; saving format: .wav).

A total of 41 males were recorded in nine different hamlets ($N = 30$ birds in 2021 and 11 birds in 2022), each hamlet hosting three to seven males (mean ± SD: 4.1 ± 1.4, $N = 9$ hamlets) over the 2 years. We used Avisoft-SASLab Pro software version 5.2.15 (https://www.avisoft.com; FlatTop window; FFT length: 256; 87.5% overlap) to establish strophe and song repertoires of these birds by visual inspection and classification of spectrograms from all recordings. On average, we analysed 126.4 ± 74.2 (mean ± SD) songs per individual (range 29–465 songs per bird, $N = 41$ birds) and a mean of 7.0 ± 8.1 songs were needed to establish the full strophe repertoire of a male. The strophe and song repertoire size (mean ± SE) in the population studied in 2021 and 2022 was 2.9 ± 0.1 different strophes (range 2–5) and 2.1 ± 0.2 different songs (1–5), respectively.

We calculated a pairwise strophe–repertoire sharing score (RS, ranging from 0 to 1) among all birds from the same hamlet (over 2021 and 2022, independently of the year) using the following formula (see McGregor & Krebs, 1982): $RS = 2N_S/(R1 + R2)$, where N_S is the number of strophes shared between two birds, R1 and R2 being the number of strophes present in the repertoire of the first and second bird, respectively. The average sharing score within a hamlet over the 2 years ranged from 0.29 to 1 (mean ± SE: 0.65 ± 0.07, $N = 9$ hamlets).

To calculate the singing rate of black redstarts from the study area (information needed to perform the playback experiment, see below), a 5 min continuous singing episode recorded during the year of the playback experiment was randomly selected from each tested (focal) bird. We counted the strophes produced during this 5 min singing period by visually inspecting the spectrograms, using Avisoft-SASLab Pro software version 5.2.15 (Hamming window; FFT length: 256; 87.5% overlap). We then calculated the singing rate per minute by dividing the total number of strophes produced by five. Birds displayed a mean (±SE) singing rate of 6.7 ± 0.5 songs/min in 2021 ($N = 804$ songs from 20 different birds) and 6.5 ± 0.7 songs/min in 2022 ($N = 227$ songs from six different birds).

Playback Experiment

We carried out the playback experiment on 26 males from nine hamlets belonging to the study area in 2021 ($N = 20$ birds) and 2022 ($N = 6$), representing approximately 30% of all males settled in this area over these 2 years. These males shared at least a combination of one beginning and one ending strophes with their local neighbours. Since this experiment required the identification of each tested bird, we identified 18 males with high certainty using their location (i.e. extensive survey of the study area allowing us to delimit each individual territory) and their plumage (grey or black plumage: inexperienced versus experienced breeders, respectively, due to delayed plumage maturation: Landmann & Kollinsky, 1995b). We used colour plastic rings to identify the remaining males (birds mist netted and banded between 2015 and 2021). We tested seven inexperienced grey males (all in 2021) and 19 experienced black males (13 in 2021 and six in 2022).

As already mentioned, a territorial male typically shares at least part of his vocal repertoire with males from the same hamlet and with males from very close hamlets to a lesser extent. Consequently, males have higher song similarity with males singing local songs compared to males from another dialect (see Appendix). In addition, each male is familiar with the specific version of the shared songs produced by their current adjacent neighbours within the hamlet, due to individual vocal microvariation (i.e. individual vocal signature; Draganoiu et al., 2014). However, given the breeding site fidelity across years (Musseau, 2007) and the very spatially restricted home range of males during breeding (Musseau, 2007) it is unlikely that birds from two distinct hamlets were familiar with the vocal signature in the shared songs of each other.

To assess the influence of the microdialects on the males' territorial responses to the simulated intrusion of an unfamiliar singing male, we played back two different types of stimuli to each focal bird, corresponding to the two treatments of its playback experiment (complete songs; Fig. 1a–c). For each focal bird, the 'Foreign Song' (FS) treatment was composed of 10 different exemplars of an unfamiliar and unshared song belonging to a bird recorded at a mean ± SD distance of 1234 ± 490 m (range 619–2340 m). The 'Local Song' (LS) treatment was composed of 10 different exemplars of an unfamiliar but shared song, selected in one of two possible ways for a given tested bird: (1) a shared song from a deceased bird which lived in the hamlet of the focal male several years ago (recorded between 2015 and 2018; for $N = 16$ focal males), or (2) a shared song from one individual recorded at least 1 year before the experiment in a distinct hamlet located at an average distance of 730 ± 404 m from the hamlet of the focal bird (recorded between 2019 and 2021; for $N = 10$ focal males). For a given treatment (FS or LS), the audio track was composed of the 10 song exemplars mentioned above (mean duration: 3.4 ± 0.5 s), successively played back for 5 min at the natural rate of one song every 10 s (see the singing-rate analysis presented above). A high-pass filter (1500 Hz) was applied to remove background noise, using Avisoft-SASLab Pro, and the song amplitudes were adjusted using the 'Equalizer' formula from Goldwave software version 6.55 (https://www.goldwave.com/) based on the root-mean-square.

To decrease pseudoreplication (Kroodsma, 1989), a total of 20 different stimuli were built and used to test the 26 males: four were used in a unique playback test (LS: 1; FS: 3), eight in two tests (LS: 7; FS: 9), six in three tests (LS: 11; FS: 7), one in four tests (LS: 2; FS: 2) and one in 10 tests (LS: 5; FS: 5). We used 16 different stimuli among them as the LS treatment (13 from males recorded 3–7 years ago in the same hamlet, and three from males recorded 1–2 years ago in a distinct hamlet), and 18 different stimuli as the FS treatment recorded 1–7 years ago in the study area. We controlled for the age of the stimuli by exclusively using songs from 1-year-old (grey) males. Hence, these stimuli represented a naturally occurring situation: inexperienced breeders newly arriving from migration and exploring the area to find a territory to settle in as breeders, often by challenging older males already installed in a territory (Musseau, 2007; Stewart et al., 2002).

We conducted the playback experiments in 2021 from 3 May to 28 May and in 2022 from 26 April to 5 May, between 0700 hours and 1200 hours (UTC). Males received the two treatments on 2 consecutive days, with a balanced treatment order randomly assigned to the 26 focal birds. When possible ($N = 12$ focal birds), we used two audio tracks for a pair of focal birds (the LS treatment for one focal bird representing the FS treatment for the other one, and vice versa). In addition, at least 3 days separated the tests of different focal birds settled within the same hamlet. Tracks were played back at a sound pressure level matching those of black redstarts (78.2 ± 1.0 SD dB measured at 1 m from the speaker using a sound level meter Voltcraft DL-1605, dBA, normal, slow, A-weighting) using an Anchor AN-Mini speaker (100–15 000 Hz ± 3 dB) connected to a Marantz PMD670 recorder with a 15 m cable.

We placed the speaker close to the birds' territory boundaries, at a height of 1–2 m (on a pole, between branches) and directed towards the centre of the territory. When possible, the boundary was not shared with a neighbour. If this was the case, a 57.5 cm diameter plastic parabola, lined with sound proofing foam 2.5 cm thick, was placed behind the speaker to avoid attracting the neighbouring male (Moser-Purdy et al., 2017). On average, the speaker was positioned at the beginning of each track playing at a distance of 33.4 ± 10.7 m (mean ± SD) and 32.4 ± 12.0 m from the focal bird (using Bosch GLM 250 VF Professional telemeter) for the FS and LS treatments, respectively, without any significant difference between them (paired t test: $t_{25} = -0.42$, $P = 0.68$). Neighbouring males did not react during the playback tests and playbacks started when the focal male was in sight, most often on a rooftop in the centre of its territory.

One observer recorded the vocal response of each bird tested using a Sennheiser microphone (MKH70 P48) connected to a NAGRA ARES-BB+, while a second observer described orally focal birds' movements using a Marantz PMD620 recorder. Both observers were blind to the type of treatment played back (FS or LS). Before the playback, a 5 m zone was delimited with natural landmarks or specific material, as the radius of a hemisphere centred on the speaker to assess close aerial or ground approaches. We took several behavioural metrics into account (i.e. latencies, durations and numbers) related to both movement and song activity of the focal birds, typically used to assess the aggressiveness level of the behavioural responses towards acoustic stimuli (Apfelbeck et al., 2013; Parker et al., 2018). All variables ($N = 14$) recorded during the 5 min of playback are presented in Table 1. Males did not produce any type of calls during the playback.

Ethical Note

Mist netting and banding were carried out by T.D and T.V under the authorization number PP548 from the Centre de Recherches sur la Biologie des Populations d'Oiseaux (CRBPO) of the French National Museum of Natural History (MNHN, Paris, France). The duration of manipulation was minimized to reduce the stress of the capture and the birds were released near their territories. These individuals ($N = 8$) were part of a longitudinal study of lifetime evolution of vocal repertoires in the black redstart (Volle et al., 2024). We ensured that each tested bird returned to its usual activities after the playback experiment. Our study followed the ASAB/ABS Guidelines for the use of animals in research.

Statistical Analyses

Most vocal behaviours in response to the playback, as well as approach behaviours, were intercorrelated (Appendix Fig. A1). The response of the tested males to playback was therefore summarized using an unrotated principal component analysis (PCA; McGregor, 1992; Table 1), built on the behavioural variables recorded for all focal males during the test period of each treatment (FS and LS). Principal components (PCA axes) to be retained were identified and interpreted (see Results) on the basis of eigenvalues (>1; Kaiser's criterion) and screen plot inspections.

To explain behavioural response variation, we computed 26 linear mixed models (LMMs) for each PCA axis, including the score of individuals on the given axis as response variable and the identity of the bird as a random effect to control for repeated measurements. A total of five predictors were considered for these models. The playback treatment (FS or LS; two-level factor) was used to test for local–foreign dialect discrimination according to the relative threat hypothesis. We used the mean similarity between the songs of the bird tested and the songs used as playback (continuous variable; see Appendix) to test for a fine and relative effect of acoustic similarity (complementary to the treatment). The order of the stimulus (first or second day of test; two-level factor) was tested for a possible habituation effect. We used the initial

Table 1
Variables recorded ($N = 14$) to describe the movements and the vocal response of the focal bird during the 5 min test period and contribution of each variable to the three principal components axes (PC1, PC2, and PC3) retained for the analyses

Behavioural type	Variable type	Variable	Variable contribution to		
			PC1	PC2	PC3
Movement	Latency (s)	First movement	0.066	−0.270	0.071
		First entry within the 5 m zone	0.498	**−0.671**	−0.012
	Duration (s)	Time spent (on the ground or perched) within the 5 m zone	−0.360	0.233	**0.711**
	Number	Entries (on the ground or perched) within the 5 m zone	−0.494	0.309	**0.599**
		Flights above the speaker within the 5 m zone	−0.153	**0.540**	**−0.697**
		Flights above the speaker and outside the 5 m zone	−0.423	0.316	−0.041
		Other flights (not within or above the 5 m zone)	−0.377	**0.486**	−0.087
	Distance (m)	Minimum distance to the speaker (m)	0.593	**−0.613**	0.072
Vocal	Latency (s)	First song (complete or truncated)	**−0.713**	−0.183	0.116
	Number	Complete songs (typical songs including two strophes)	**0.881**	0.226	0.196
		Truncated songs including only a beginning strophe	**0.772**	0.357	0.147
		Truncated songs including only an ending strophe	**0.701**	0.304	−0.079
		Songs alternating with the playback (starting between two playback songs)	**0.906**	0.268	0.117
		Songs overlapping with the playback (starting during a playback song)	**0.739**	0.393	0.134

Eigenvalues of PC1, PC2 and PC3 were 5.06, 2.21, and 1.48, respectively. High variable contributions to principal components are shown in bold. Consequently, PC1, PC2 and PC3 were mainly related to vocal response, speaker approach and close proximity to speaker behaviours, respectively. For latencies (s), if a given behaviour did not occur during the test period, a value of 300 s was used.

distance (m) of the focal bird from the speaker at the beginning of the test period (continuous variable) to test the aggression escalation chain hypothesis. Finally, we used the age class of the bird tested (inexperienced or experienced breeder; two-level factor) to test potential differences in the territorial response between these age classes. The 26 models (see Appendix Table A1) cover all possible combinations of these predictors (i.e. simple, additive and interaction effects) to a limit of two predictors in the same model for sample size issues, including a null model (i.e. containing no fixed effect). No multicollinearity between variables was detected (variance inflation factors being < 4; Dormann et al., 2013; James et al., 2013).

We used a model selection procedure for each PCA axis to determine the predominant drivers (with their potential combination) of the behavioural response of birds among several candidate predictors, exploring several biological hypotheses. For each PCA axis, we ranked the 26 models in increasing order of their Akaike information criterion value corrected for small sample sizes (AICc; Anderson & Burnham, 2003). The difference in AICc between each model and the first ranked one (ΔAICc) was computed. If no model displayed a ΔAICc lower than two points, the first ranked model was considered as the unique best model. Otherwise, each model with a ΔAICc below this threshold was also considered as best model (i.e. is supported equally by the data as the first ranked model). In this case (several models within ΔAICc < 2), we discarded models with an additional noninformative term (i.e. zero included in the 95% confidence interval of this parameter estimate) to avoid misinterpretation. Finally, for each model retained, both marginal (R^2m; variance explained only by the fixed effect(s)) and conditional (R^2c; variance explained by fixed and random effects) pseudo-*R*-squared were calculated (Nakagawa et al., 2017).

All statistical analyses were performed with R version 4.1.2 (*R* Development Core Team, 2021), using the AICcmodavg, car, lme4, MuMIn, ade4, ggeffects and RVAideMemoire libraries.

RESULTS

General Description of Males' Reactivity

All the 26 males reacted to both playback treatments. The overall mean (±SE) latency of the first movement was 27.1 ± 5.1 s, (LS: 28.5 ± 4.9; FS: 25.8 ± 9 s). A total of 21 males entered the 5 m zone (LS: 17; FS: 15; both treatments: 11), with a mean (±SE) latency of 174.5 ± 14.6 s (LS: 176.5 ± 19.3 s; FS: 172.4 ± 22.3 s). Eleven of the 21 males that entered this zone landed within it and held ground (LS: 11; FS: 5; both treatments: 5) and the mean (±SE) duration spent on the ground or perched in this zone was 61.3 ± 16.5 s (LS: 87.5 ± 26 s; FS: 35.9 ± 17.9 s). Sixteen males displayed flights above the speaker within the 5 m zone (LS: 7; FS: 13; both treatments: 4), with a mean (±SE) of 1.2 ± 1.3 flights (LS: 0.6 ± 0.2 flights; FS: 1.8 ± 0.4 flights).

A total of 19 individuals sang during at least one treatment (LS: 14; FS: 14; both treatments: 9), with a mean (±SE) song latency of 130.9 ± 21 s (LS: 125.1 ± 30.8 s; FS: 136.7 ± 29.3 s). Males that sang produced a mean (±SE) number of 5.9 ± 1.2 strophes (LS: 6.5 ± 2.1 strophes; FS: 5.4 ± 1.4 strophes) during the 5 min of the playback.

Composite Responses to Playback (PCA)

Three principal components were retained as composite responses to playbacks (Table 1). The first principal component (PC1) explained 36.16% of the variance in the measured behaviours. Behaviours related to the vocal activity of the male were strongly correlated with PC1 (Table 1). Higher positive PC1 scores corresponded to a stronger vocal response (i.e. subjects sang more strophes and started to sing earlier). The second principal component (PC2) explained 15.76% of the variance. Behaviours reflecting the flight approach to the speaker, which could be associated with patrolling the territory, were more strongly correlated with PC2 than other measures (Table 1). Higher positive PC2 scores corresponded to a stronger flight approach response (i.e. subjects came closer to the speaker, flew more and entered the 5 m zone quicker). Finally, the third principal component (PC3) explained 10.58% of the variance. Behaviours reflecting a close ground approach to the speaker were more specifically correlated with PC3 (Table 1). Individuals with higher scores on PC3 spent more time holding ground within the 5 m zone close to the speaker and displayed fewer flights within 5 m over the speaker.

Variation in Composite Responses to Playback

The model retained to explain variation in PC1 (vocal response) included the initial distance of the bird from the speaker as fixed effect, composite scores increasing with increasing distance ($R^2\text{m} = 0.14$, $R^2\text{c} = 0.51$; Table 2, Table A1, Fig. 2a). Concerning PC2 (speaker flight approach behaviour), the fixed part of the retained model was also only composed of this initial distance (R^2m = 0.10, R^2c = 0.23; Table 2; Table A1, Fig. 2b), composite scores decreasing with increasing distance. Two models were finally retained by the model selection procedure regarding the variation in PC3 (speaker ground approach; Table A1). The first model included the treatment and the initial distance to the speaker as additive effects, scores being on average higher for the LS (mean ± SE: 0.39 ± 0.22) than the FS (−0.39 ± 0.22) treatment, but decreasing with increasing distance (R^2m = 0.18, R^2c = 0.69; Table 2, Fig. 3a). The fixed part of the second model was composed of the additive effect of the mean song similarity between the focal birds' songs and the stimuli and the initial distance to the speaker, scores increasing with increasing similarity index, while decreasing with increasing distance (R^2m = 0.22, R^2c = 0.61; Table 2, Fig. 3b).

DISCUSSION

Our playback study revealed that male black redstarts discriminated between two unfamiliar songs belonging to the foreign and local microdialects. Ground approach behaviours were influenced by the treatment type. Males held ground close to the speaker for longer but performed fewer flights over the speaker in the zone when exposed to the LS treatment. Interestingly, model selection showed that both the vocal response and the approach behaviours were sensitive to the focal males' distance from the speaker at the beginning of the experiment. Our results are in line with previous findings described in species with more widespread dialects, that is, a stronger aggressive response against the local dialect compared to the foreign dialect (Fracas et al., 2023; Hudson et al., 2019; Parker et al., 2018; Williams et al., 2019). However, the fixed terms of the mixed models retained had overall a relatively low level of predictive power, particularly in comparison to their random term (identity of the tested bird). An important variability among birds in the behavioural responses to the playback was therefore highlighted.

The Role of the Initial Distance From the Speaker

The aggression escalation chain proposed by Beecher and Akçay (2014) suggests that the two primary steps of the defence strategy would be signalling and approaching, followed by the last step which is characterized by close proximity to and contact with the threat. These steps therefore involve different risks and costs for individuals (Diniz, 2020; Hof & Hazlett, 2010). In agreement with this escalation concept, both our observations and previous playback experiments (Sedláček et al., 2004, 2006; Apfelbeck et al., 2011; Draganoiu et al., 2014) suggest that the time spent close to the speaker is the last step of the aggressive response of black redstarts. The three steps (vocal response, flight and ground approach behaviours) were influenced by the distance of focal birds from the speaker at the beginning of the playback, independently of the treatment. These results reinforce the importance of controlling for the distance of the focal bird from the speaker at the beginning of the experiment. This variable has only rarely been taken into account in previous playback studies (see above; Armstrong, 1991; Naguib et al., 2002). They also indicate that black redstart males are inclined to engage the aggression escalation chain without fine discrimination among different threat levels related to conspecifics. In agreement with our hypothesis, we found that birds were more likely to sing when they were initially far from the speaker and more likely to approach and spend more time close to the speaker when they were initially closer to it. This pattern matches the changing of the three aggression steps, signalling being chosen more when the threat was distant. Vocalizations are indeed particularly efficient to convey territorial information among distant birds and are likely to be less costly than approaching which constitutes a stronger response but nevertheless the best compromise when the threat is close. On the other hand, the last step of the escalation chain (close proximity behaviour) was influenced by the treatment in addition to the initial distance. This advocates for a fine discrimination between microdialects and consequently for an adjustment of the strongest agonistic response type depending on treatment.

The Role of the Treatment (Local Versus Foreign Microdialect)

The effect of the treatment type in addition to the effect of the initial distance on ground approach behaviours towards the speaker supports the relative threat hypothesis (Wright & Dorin, 2001): the stronger response towards the local microdialect treatment might reflect that local singers are perceived as a higher threat. This interpretation is plausible when considering the ground approach behaviours as the last step of the aggression escalation chain described above. In addition, males from the study

Table 2
Summary of the results of the model selection procedure to explain variation in the behavioural response of males to playback

Response variable	Fixed effect(s)	β		AICc	ΔAICc	ωAICc	R^2m	R^2c
		Mean	95% CI					
PC1 (vocal response)	**Initial distance**	**0.07**	**0.02; 0.13**	**229.43**	**0.00**	**0.31**	**0.14**	**0.51**
PC2 (flight approach)	**Initial distance**	**−0.04**	**−0.08; −0.01**	**191.54**	**0.00**	**0.27**	**0.10**	**0.23**
	Initial distance+	−0.04	−0.08; −0.01	193.40	1.86	0.11	0.11	0.24
	Test order	−0.28	−1.01; 0.45					
PC3 (ground approach)	**Initial distance+**	**−0.03**	**−0.05; −0.004**	**155.41**	**0.00**	**0.23**	**0.18**	**0.69**
	Treatment	**0.78**	**0.40; 1.16**					
	Initial distance+	0.03	−0.04; 0.11	155.58	0.17	0.21	0.26	0.62
	Song similarity+	7.03	2.08; 12.28					
	Initial distance: Song similarity	−0.11	−0.25; 0.02					
	Initial distance+	**−0.03**	**−0.05; −0.004**	**155.83**	**0.42**	**0.18**	**0.22**	**0.61**
	Song similarity	**3.02**	**1.47; 4.63**					
	Initial distance+	−0.02	−0.05; 0.02	156.83	1.42	0.11	0.19	0.69
	Treatment+	1.46	0.14; 2.82					
	Initial distance: Treatment	−0.02	−0.06; 0.02					

For each principal component (PC1, PC2 and PC3), the behavioural response interpretation is specified in parentheses. AICc: Akaike information criterion corrected for small sample sizes. Only competitive models with ΔAICc < 2 are presented. The final selected models are shown in bold (discarding models with an additional noninformative term). Mean estimate and the associated 95% confidence interval (95% CI) of parameter(s) included in the competitive models (β, excluding intercept or reference level) are specified. See the text and Table A1 for more details. AICc weight (ωAICc) is given as a measure of the probability of a model being the best model (Symonds & Moussalli, 2011). R^2m and R^2c: marginal and conditional pseudo-R-squared, respectively.

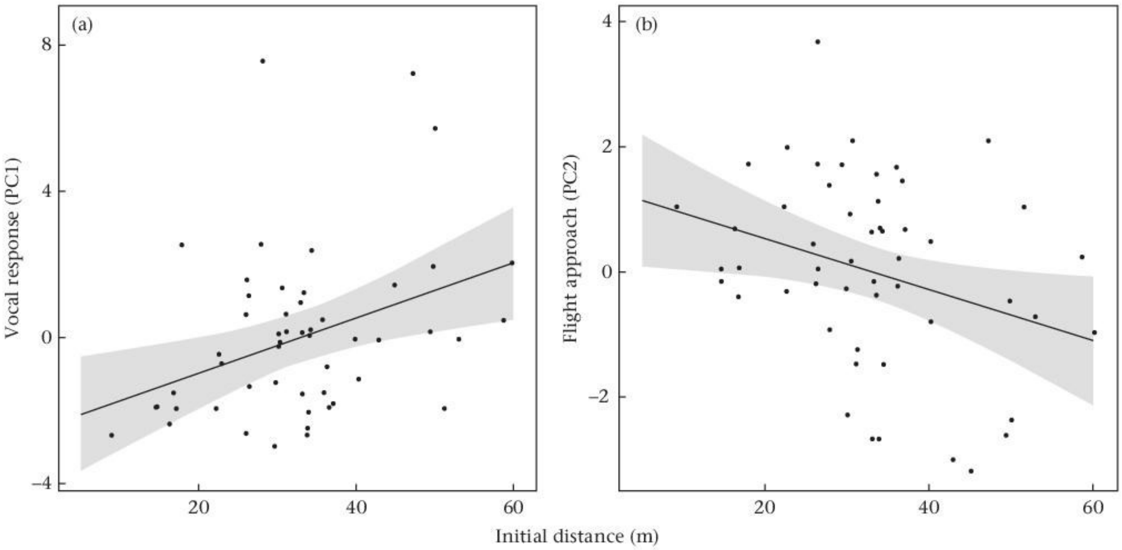

Figure 2. Variation of the estimation (mean with 95% confidence interval) of the (a) level of vocal response (PC1) and (b) flight approach to the speaker (PC2) displayed by a tested bird in relation to the distance from the speaker at which it was located at the beginning of the experiment.

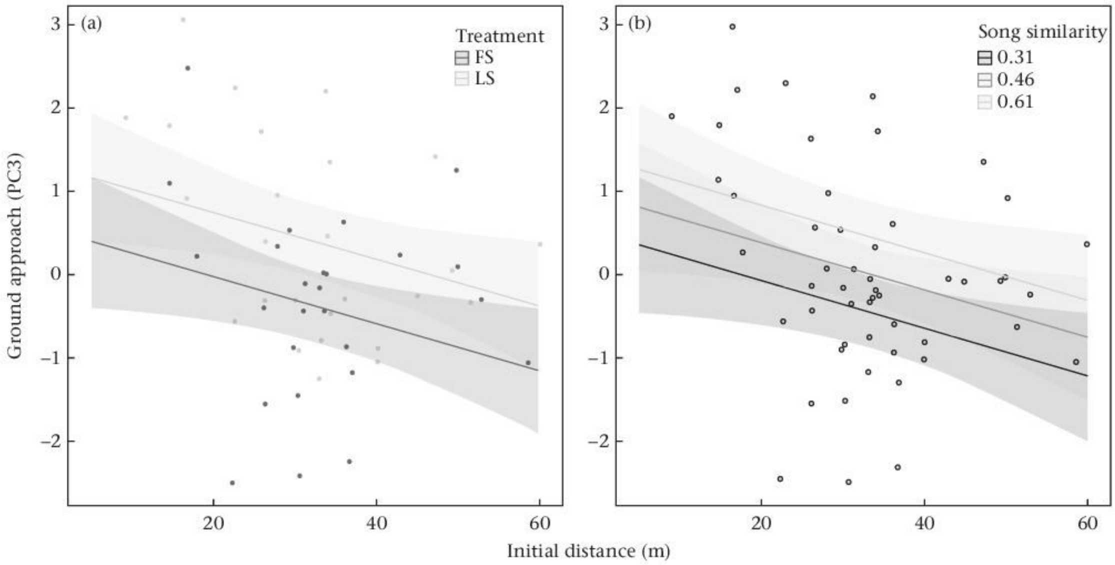

Figure 3. Estimation (mean with 95% confidence interval) of the level of males' ground approach to the speaker (PC3), according to (a) the initial distance and the treatment (LS: local song; FS: foreign song; first model retained, additive effect) and (b) the initial distance and the mean song similarity between the focal bird and stimuli (second model retained, additive effect; three values of acoustic similarities were used to represent this continuous variable, corresponding to mean minus SD, mean and mean plus SD, respectively).

population are highly philopatric, returning mainly to the breeding patch where they learned their song (Musseau, 2007; Volle et al., 2024). They either learn their songs during the first autumn as yearlings or, if newcomers, they delay the expression of the local songs until the end of the first breeding season (Volle et al., 2024). Consequently, singing the local microdialect could be an honest indicator of the simulated intruder's knowledge of the microlocal habitat and adaptation to it (Rothstein & Fleicher, 1987Rothstein & Fleischer, 1987). Moreover, it has been shown in other songbirds that having a local dialect singer settling in the adjacent territory could potentially lead to a loss of paternity for the focal bird (Forstmeier et al., 2021; but see Payne, 1982). However, our results contrast with a study reporting a lower aggressive response towards local microdialects compared to foreign ones in Eurasian skylarks (Briefer et al., 2010). A possible explanation would be the potential effect of the familiarity of focal skylarks with the songs used for the local microdialect treatment whereas this bias was methodologically ruled out in our study by using songs recorded either 3–7 years ago in the same hamlet as the tested bird or 1–2 years ago in a distinct breeding patch situated on average 730 m away.

The Role of Vocal Similarity

We found an additive effect of the initial distance from the speaker and the similarity between the focal birds' songs and the songs used as playback stimuli (see Appendix) on the close ground approach behaviours to the speaker. The model with this effect combination was considered as equally competitive as the model including the additive effect of the initial distance and the treatment type, due to partial collinearity between treatment and similarity variables. More precisely, we showed that the agonistic response increased with the vocal similarity, thus supporting the same hypothesis as the treatment effect. Our results are in line with a series of recent studies investigating dialect discrimination that considered the acoustic distance between the focal males' songs and the songs used as stimuli for playback experiments as an explanatory variable of the aggressive responses to playback. Indeed, male white-crowned sparrows, *Zonotrichia leucophrys*, responded more aggressively to the similar songs of the current dialect than to historical songs recorded in the same dialect 25 years ago (Derryberry, 2007). Furthermore, the historical songs triggered an equivalent aggressive response as the songs of a current foreign dialect (Derryberry, 2011). As already mentioned, our stimuli came equally from the past; to avoid a familiarity effect, we used songs recorded in the same patch or in neighbouring patches on average 4 years before the experiment (1–7 years ago). Our local songs from the recent past were more similar to the songs of the focal birds than the songs of the foreign dialect but in a previous experiment we found that they were less similar than the songs of the focal birds' direct neighbours (Chambon, 2015) suggesting a possible song evolution during an interval of up to 7 years. Using songs recorded in the recent past for the microlocal treatment could explain the rather subtle effect of the treatment in our experiment.

The small patch size prevented us using unfamiliar local current songs; one possibility to experimentally test the role of the similarity between the songs of the tested males and the songs used for playback would be to use synthesized signals (Mathevon et al., 2008). Another possibility would be to broadcast the bird's own song (Akçay & Beecher, 2020). This is a common procedure used both in electrophysiology and in field experiments (reviewed in Derégnaucourt & Bovet, 2016). Still, the reaction of a bird to the broadcast of its own song might be difficult to interpret since it is unnatural for a bird to be exposed to its own song and since it involves many aspects such as self-recognition and familiarity. Based on our findings, we could predict that male black redstarts would react more strongly to their own song than to the LS treatment.

Interindividual Variability

Despite methodological efforts, some variation, potential biases and responses remain to be considered further. Relatively high interindividual variation was highlighted in the models selected. Previous experimental work revealed several factors that could be responsible for interindividual variation such as personality (Amy et al., 2010; Colombelli-Négrel et al., 2022; Myers & Hyman, 2016), focal birds' social interactions prior to the playback test (Hall & Vehrencamp, 2006; Naguib et al., 2022; Schmidt et al., 2007), territory size and quality (Schwarzová, 2010; Naguib et al., 2022) as well as the density of neighbours (Yoon et al., 2012). For example, black redstarts with small territories responded more strongly to playback (Schwarzová, 2010). The breeding stage and time of day might also affect males' territorial behaviour (Briefer et al., 2008; Moser-Purdy et al., 2017; Verner & Milligan, 1971). Some experiments have indeed shown that males might be more reactive during specific time windows (e.g. early morning during the egg-laying phase in great tits, *Parus major*: Mace, 1987; Gil & Llusia, 2020). Unfortunately, we did not always have precise information about the breeding status (mated or not) and stage (egg laying, incubation or chick rearing phase) of males during the experiment and we tested them at a time of day that allowed us to carry out the standardized experimental procedure. Consistently with previous results (Apfelbeck et al., 2012; Huet des Aunay, 2016) males' vocal output during the playback test was reduced (eight times lower than that found during the dawn chorus). Therefore, also testing birds during the dawn chorus could enable investigation of their vocal response at a finer scale due to the higher singing rates. This would allow us to explore more specifically song timing (alternation or overlapping with stimuli) and matching (selection of songs matching the stimuli) as indicators of aggression escalation (Todt & Naguib, 2000; Logue, 2021). Since only a few individuals sang during the two experimental conditions, we did not explore these variables statistically. Finally, in our experiment age was not a factor present in the retained models. However, the uneven distribution of age classes might conceal a potential effect of age on the aggressive response (Poesel & Nelson, 2012; Schwarzová, 2010).

Conclusion

To conclude, our study confirms a result that is well known for bird species with a widespread dialect in a microdialect songbird population followed over a long period of time. Males were able to discriminate between two different microdialects and were more aggressive towards the local one. Our results bring new insights in this context and suggest that microdialect singers could be more threatening local challengers. We also highlighted a strong and consistent effect of the distance between the focal males and the speaker at the beginning of the experiment, a parameter that is rarely considered in playback experiments. Nevertheless, a large part of the response variability was accounted for by individual differences. We call for more playback studies in microdialect populations followed in the long term to better understand the functional value of singing the local dialect, notably by taking an acoustic similarity gradient and the dawn chorus period into account.

Author Contributions

Tifany Volle: Conceptualization, Methodology, Investigation, Formal analysis, Visualization, Writing – Original draft, Writing – Review & editing. **Sébastien Derégnaucourt**: Conceptualization, Methodology, Writing – Original draft, Writing – Review & editing. **Rémi Chambon**: Formal analysis, Visualization, Writing – Original draft, Writing – Review & editing. **Tudor-Ion Draganoiu**: Conceptualization, Methodology, Investigation, Visualization, Writing – Original draft, Writing – Review & editing.

Data Availability

Data are available in the supplementary material.

Declaration of Interest

The authors declare no competing interests.

Acknowledgments

We thank Nicolas Coron and Léa Brun for their help during fieldwork. We thank the people of la Valla-sur-Rochefort for their cooperation during fieldwork, especially the Charles, Rebourg and Tholoniat families. We are also very grateful to Nicolas Mathevon, Fanny Rybak and Charlotte Curé for their helpful comments on the experimental procedures. We thank the Editor and the anonymous referees for their advice. T.V. was supported by a Ph.D. grant from the University Paris Nanterre.

Supplementary Material

Supplementary material associated with this article is available in the online version at https://doi.org/10.1016/j.anbehav.2024.01.020.

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Appendix

In a previous work, we found that close neighbours sing more similar songs than other singers with the same local dialect (Chambon, 2015), using an index of acoustic similarity between birds' songs. We therefore considered that using such a metric might provide a finer potential driver of the aggressive response variation, complementary to the categorical spectrographic classification method (LS and FS treatments). To assess this song similarity between the stimuli and the focal birds' songs, 10 song exemplars, matching the type of song used in the LS stimulus (if males' repertoires comprised more than two strophes; Fig. 1b), were extracted from spontaneous dawn singing bouts recordings of each tested bird (Fig. 1a). These songs were of good quality (no noise or overlapping songs from other birds). The spectrograms of the second syllable within the trills of both the beginning and ending strophes of LS and FS songs and selected songs of focal birds (Fig. 1a–c, framed elements) were isolated using Avisoft-SASLabPro software version 5.2.15 (FlatTop window; FFT length: 512; 96.87% overlap). We used the Avisoft-CORRELATOR available from Avisoft-SASLabPro to compute a similarity coefficient (ranging from 0, no overlap, to 1, complete overlap) between these syllables as a proxy of similarity between songs. Consistent with the stimulus type definition, the songs of the focal bird were significantly more similar to the songs used in the LS treatment than to the songs used in the FS treatment (mean ± SD similarity coefficients: 0.57 ± 0.12 versus 0.35 ± 0.07, respectively; Fig. 1a, b, c; Mann–Whitney *U* test: $U = 3$, $N = 25$, $P < 0.001$). This result strengthens our initial categorical visual classification (local versus foreign treatment).

Table A1
Results of the model selection procedure based on AICc to explain variation in the behavioural response of males to playback

Response variable	Fixed effect(s)	AICc	ΔAICc	ωAICc
PC1 (vocal response)	**Initial distance**	**229.43**	**0.00**	**0.31**
	Initial distance+Age	231.50	2.08	0.11
	Initial distance+Test order	231.72	2.29	0.10
	Initial distance+Song similarity	231.80	2.38	0.09
	Initial distance+Treatment	231.87	2.44	0.09
	Initial distance*Age	231.90	2.47	0.09
	Initial distance*Song similarity	233.07	3.65	0.05
	Initial distance*Treatment	233.15	3.73	0.05
	Initial distance*Test order	233.48	4.06	0.04
	Null	234.64	5.22	0.02
	Age	236.79	7.36	0.01
	Song similarity	236.97	7.55	0.01
	Test order	236.98	7.56	0.01
	Treatment	236.99	7.56	0.01
	Song similarity+Age	239.20	9.78	0.00
	Test order+Age	239.23	9.81	0.00
	Treatment+Age	239.24	9.81	0.00
	Treatment+Song similarity	239.31	9.89	0.00
	Song similarity+Test order	239.42	9.99	0.00
	Treatment+Test order	239.43	10.00	0.00
	Treatment*Song similarity	240.53	11.10	0.00
	Song similarity*Age	241.10	11.67	0.00
	Treatment*Age	241.44	12.02	0.00
	Treatment*Test order	241.67	12.24	0.00
	Song similarity*Test order	241.67	12.25	0.00
	Test order*Age	241.73	12.30	0.00
PC2 (flight approach)	**Initial distance**	**191.54**	**0.00**	**0.27**
	Initial distance+Test order	**193.40**	**1.86**	**0.11**
	Initial distance+Song similarity	193.80	2.27	0.09
	Initial distance+Age	193.98	2.44	0.08
	Initial distance+Treatment	193.99	2.45	0.08
	Null	194.13	2.60	0.07
	Initial distance*Age	194.37	2.83	0.06
	Initial distance*Song similarity	195.70	4.16	0.03
	Initial distance*Test order	195.89	4.35	0.03
	Test order	196.17	4.63	0.03
	Song similarity	196.33	4.79	0.02
	Age	196.44	4.90	0.02
	Treatment	196.46	4.92	0.02
	Initial distance*Treatment	196.46	4.92	0.02
	Song similarity+Test order	198.46	6.92	0.01
	Test order+Age	198.58	7.04	0.01
	Treatment+Test order	198.58	7.04	0.01
	Song similarity+Age	198.71	7.17	0.01
	Treatment+Song similarity	198.72	7.19	0.01
	Treatment+Age	198.86	7.32	0.01
	Test order*Age	199.14	7.61	0.01
	Song similarity*Test order	200.99	9.46	0.00
	Treatment*Test order	201.01	9.47	0.00
	Song similarity*Age	201.13	9.60	0.00
	Treatment*Song similarity	201.25	9.71	0.00
	Treatment*Age	201.26	9.72	0.00
PC3 (ground approach)	**Initial distance+Treatment**	**155.41**	**0.00**	**0.23**
	Initial distance*Song similarity	**155.58**	**0.17**	**0.21**
	Initial distance+Song similarity	**155.83**	**0.42**	**0.18**
	Initial distance*Treatment	**156.83**	**1.42**	**0.11**
	Treatment	158.14	2.73	0.06

(*continued on next page*)

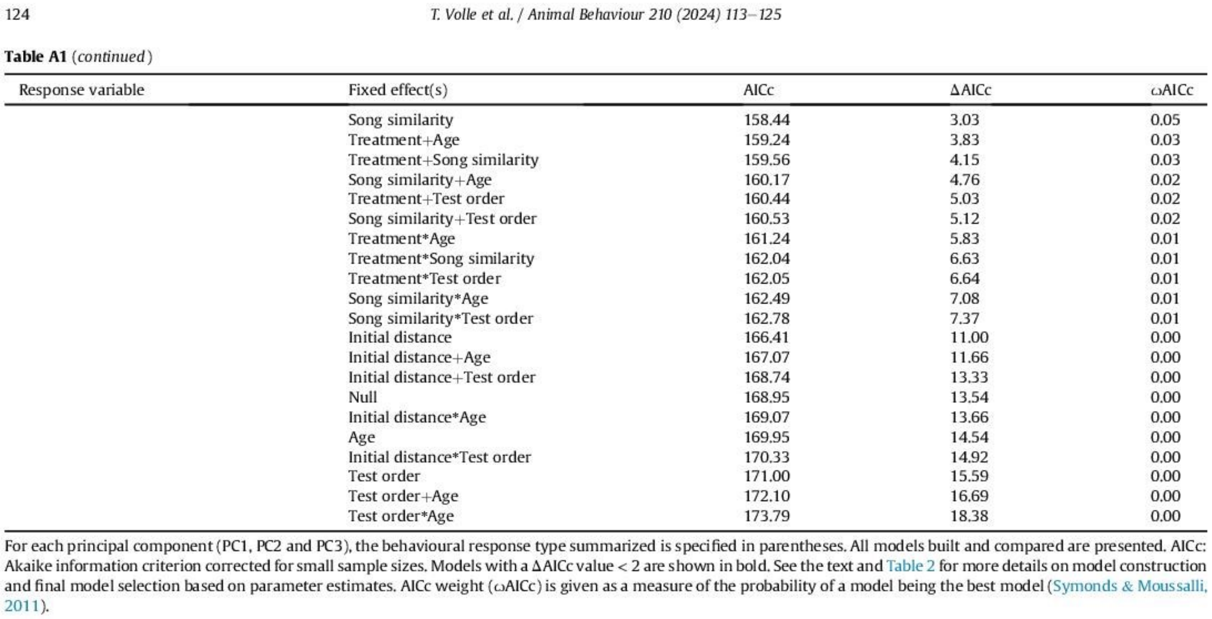

Table A1 *(continued)*

Response variable	Fixed effect(s)	AICc	ΔAICc	ωAICc
	Song similarity	158.44	3.03	0.05
	Treatment+Age	159.24	3.83	0.03
	Treatment+Song similarity	159.56	4.15	0.03
	Song similarity+Age	160.17	4.76	0.02
	Treatment+Test order	160.44	5.03	0.02
	Song similarity+Test order	160.53	5.12	0.02
	Treatment*Age	161.24	5.83	0.01
	Treatment*Song similarity	162.04	6.63	0.01
	Treatment*Test order	162.05	6.64	0.01
	Song similarity*Age	162.49	7.08	0.01
	Song similarity*Test order	162.78	7.37	0.01
	Initial distance	166.41	11.00	0.00
	Initial distance+Age	167.07	11.66	0.00
	Initial distance+Test order	168.74	13.33	0.00
	Null	168.95	13.54	0.00
	Initial distance*Age	169.07	13.66	0.00
	Age	169.95	14.54	0.00
	Initial distance*Test order	170.33	14.92	0.00
	Test order	171.00	15.59	0.00
	Test order+Age	172.10	16.69	0.00
	Test order*Age	173.79	18.38	0.00

For each principal component (PC1, PC2 and PC3), the behavioural response type summarized is specified in parentheses. All models built and compared are presented. AICc: Akaike information criterion corrected for small sample sizes. Models with a ΔAICc value < 2 are shown in bold. See the text and Table 2 for more details on model construction and final model selection based on parameter estimates. AICc weight (ωAICc) is given as a measure of the probability of a model being the best model (Symonds & Moussalli, 2011).

GENERAL DISCUSSION

GENERAL DISCUSSION

Microdialect species are scarce models in the study of dialect establishment, ontogeny and functions (Briefer et al., 2010; Hensel et al., 2022; Osiejuk et al., 2019; Parker et al., 2018). In addition, longitudinal field studies have rarely the purpose to document song ontogeny in oscines (Rivera-Gutierrez et al., 2011). Black redstarts in our study population display microdialects. They respond well to playback experiments and show discriminative abilities of vocal signals (Draganoiu et al., 2006, 2014). My thesis aimed to deepen the understanding of song learning strategies in the black redstart and to assess the role they play in microdialects' establishment. Using a longitudinal field approach covering eight breeding seasons, we showed that males can change their vocal repertoires through various means and at different timescales, matching their social environment. This work also explored the role played by microdialects during territorial interactions, relying on a specific set of behaviours and paying attention to methodological factors that have been left aside until now. Our playback experiment highlighted the males' discriminative ability towards local and foreign microdialects as well as the importance of the distance of the males relative to the speaker at the beginning of the experiment on the overall behavioural response. Finally, we provided foundational knowledge on the species, giving grounds for comparative studies. It also raised new questions to be further investigated to understand the microdialect functions and learning strategies associated with their establishment and maintenance.

1. Summary of the main findings, interpretations and limits

1.1 Ontogeny of song dialects

The first chapter of this thesis focused on the ontogeny of song sharing within a population of black redstarts, characterised by microdialects in the different neighbourhoods of the village. In addition, our longitudinal survey showed that males of the population present high fidelity to their breeding sites (Draganoiu et al., 2005, 2014; Musseau, 2007). Since 2015 and until 2022, young males in their first breeding season were ringed to be identified and followed through their lifetime. During the survey, we recorded the songs produced by the banded males as well as their neighbours. Through spectrographic analysis of the focal males' and their neighbours' songs, we established and compared strophe repertoires to assess the level of song sharing between males. In addition, we also inspected the song of focal males throughout (March to July and September) and between breeding seasons to identify if males could learn past their first year or change their repertoire and if so, what was the timeframe at which learning and changes occurred in the species.

1.1.1 Stabilty

Two thirds of the males exhibited high song sharing with their neighbours when returning from migration for their first breeding season. These individuals kept their repertoires stable throughout their lifetime. Our results, combined with the previous observations of philopatry within the population (3-10% returning first-years) (Draganoiu, 2005; Musseau, 2007) led us to infer that males express pre-dispersal learning and return to the hamlets where they learned their songs in their hatching year. Previously, song sharing patterns were used to infer the dispersal pattern of males in several species (Niederhauser & Anderson, 2023; Ranjard et al., 2017; Vargas-Castro, 2015).

1.1.2 Modification types and timeframe

The remaining third of males displayed changes in their repertoires. They had lower sharing scores with their neighbours when arriving from migration than males with stable repertoires. Males used three types of changes: selective attrition of strophes, gradual modification of syllables and addition of new strophes. A common feature of these changes is their delayed expression. Indeed, during the first breeding season, the selective attrition as well as the gradual modification only started to be expressed in May and the first signs of the addition of new material were found in September. Males did not use addition and gradual modification past their return for their second breeding season (also see Draganoiu et al., 2014). Our methodology, however, does not exclude the possibility that males encountered these strophes during their hatching year and exhibited them solely in their initial or subsequent breeding seasons. Only controlled laboratory studies could clarify this (Chaiken et al., 1994; Geberzahn et al., 2002; Hough et al., 2000). Nevertheless, considering the potential benefits of song sharing, it is unlikely that individuals would refrain from expressing strophes memorized in their hatching year during vital territorial interactions as first-year breeders.

The selective attrition and the addition of new material are vocal changes that are well described in the literature on birdsong. However, this thesis also highlighted the process of gradual syllables' modifications. This type of modification was only described in the clay-coloured thrush, *Turdus grayi* (Vargas-Castro et al., 2015), the yellow-rumped cacique, *Cacicus cela* (Trainer, 1989) and the corn bunting (McGregor et al., 1997). A similar process has been described in the calls of the red crossbill, *Loxia curvirostra*, the black-capped chickadee, *Poecile atricapillus,* and in several species from the Psittaciformes order (reviewed in Sewall et al., 2016). The functions of such changes in the calls of these species includes social cohesion, signalling social affiliation and mediation during social association (Sewall et al., 2016). Vocal convergence is defined as the collective change of the call structure to produce a novel shared variant. Gradual modification can be hard to differentiate from addition if no recordings of an intermediary version of the song undergoing the process are available (Vargas-Castro et al., 2015). Luckily during the first two breeding seasons, surveyed in the course of this thesis, we recorded the males from their arrival in March to the end of June as well as in September. This gave us the opportunity to document this gradual modification in several males.

We also revealed that males keep some vocal flexibility throughout their lifetime if they possess enough strophes in their repertoires. Selective attrition relies on previously learned and expressed material (present in the repertoire before the second breeding season). These observations support Marler's model of memorization by instruction followed by selection in production and fulfil his prediction that action-based learning should be widespread in songbird learning (Marler, 1997).

1.1.3 Purpose of changes

All changes in the vocal repertoires during the first breeding season led to an increase in song sharing between individuals of the same neighbourhood. Therefore, males black redstarts possess a learning program enabling them to match their social environment. This fits the “sharing hypothesis” predictions (Beecher & Brenowitz, 2005). We concluded that the black redstart can also learn post-dispersal if they disperse further than the area where they learned their song during their hatching year. Despite identifying the aim of repertoire changes, we could not explore the benefits males would possibly gain from such changes.

1.1.4 *Where is the black restart located on the song learning continuum?*

The longitudinal approach provides an exceptional point of view over the complete lifespan of individuals. In fact, most studies on song learning only focus on the first 2 or 3 years of an individual’s life and not after. Our results enabled us to add precisions on the black redstart song learning ability and timeframe. Due to the presence of i) a second learning phase in the first breeding season, ii) a delay before repertoire changes and iii) lifelong vocal flexibility, we would place the black redstart between the song sparrows and the brown-headed cowbirds in the song-learning continuum (**Figure 6**). Male black redstarts possess a first learning period early in life, between 80- and 120- days post-hatching (Nicolai, 1992, personal observations). Depending on the dispersal patterns followed, males can undergo a second learning period during the first breeding season after their return from migration. This new learning period seems to be triggered if males fail to return to the neighbourhood where they learned their songs and disperse in a foreign hamlet where their level of song sharing with other males is low.

The occurrence of a new or extended learning period during the first breeding season was previously described in several species. For example, in brown-headed cowbirds, a new learning period occurs during the first breeding season enabling males to learn the local song variants (O’Loghlen, 1995; O’Loghlen & Rothstein, 1993, 2002a). It is essential, as the singing activity of reproducing males ends soon after females stop laying eggs and, in some populations migration occurs earlier. Consequently, fledglings, especially late-hatchers, experience reduced exposure to song models. Therefore, they do not acquire the shared local song variants or only a few (O’Loghlen & Rothstein, 2002b). In our population, fledglings of the second broods could also experience reduced exposure to local songs and therefore be more likely to display repertoire changes.

The transition between the crystallised and changed song repertoire phenotype presents a delay and can be sudden (selective attrition and addition) or gradual (gradual modification) during the males’ first breeding season. Selective attrition can also be gradual when the strophe’s use (percentage) is compared between breeding seasons (unpublished data). For example, between seasons, a male can reduce the use of certain strophes until he totally stops producing them. Thanks to selective attrition, males still display vocal flexibility throughout their lifetime. The interval observed before males change their repertoires fits with the delayed production learning observed in the brown-headed cowbird and the common nightingale but on a much shorter timescale (O’Loghlen, 1995; O’Loghlen & Rothstein, 1993, 2002a, 2002b; Todt & Geberzahn, 2003). We identified the males’ ability to learn new material post-dispersal in the first breeding season if needed and not after (see also Draganoiu et al., 2014). Nonetheless, we cannot dismiss the possibility that males could be able to learn past the first breeding season if environmental and social conditions differed (Osiejuk et al., 2019).

Figure 6. Song learning continuum adapted from Brenowitz & Beecher (2005) with the black redstart in comparison to reference species.

1.1.5 Control of the social environment

Earlier, we evoked that the resurgence of previously learned material and learning past the first breeding season cannot be dismissed. Experiments in laboratory settings should be carried out to control for social conditions and individuals' auditory experiences. This should allow the detection of resurgence and identifying, more precisely, the song-learning program phases' durations (Todt & Geberzahn, 2003). We could also control young's auditory experience to trigger repertoire changes in them, providing us with a higher sample size than the one gathered in the field.

1.1.6 Practicing in wintering grounds

In the black redstart, the gradual change of syllables takes time and could last, at least, from May to September, with a highly variable stage in song production, known as plastic song, in September. The addition of new material only starts to appear in September. We do not know if gradual modifications or addition continue after migration in black redstart. Studies on their wintering grounds are necessary, and winter singing has yet to be reported (Nicolai, 1992a; Schmidt, 1992; Weggler, 2001). It would be interesting to study them in this context, as it was found by Souriau et al.

(2019) that male thrush nightingales, *Luscinia luscina,* can still practice in wintering grounds and have a variable song during this period. Recently, it was also reported that in wintering grounds, thrush nightingale males could either be territorial singers with crystallized songs or non-territorial males with plastic songs (Brumm et al., 2023). In addition to being territorial, males with crystallized songs were tolerant towards plastic singers settled close by, compared to the other crystallized singers, which settled further. Brumm et al. (2023) also suggest that the proximity that plastic songsters exhibit, provides them with opportunities to learn new song types from the territorial males.

1.2 Functions of song dialects

The second chapter of this thesis focuses on the functions of microdialects in the black redstarts. Using a playback experiment, we tested the discriminative abilities of the species towards the local and foreign microdialects. Male black redstarts can discriminate between neighbours and strangers and between their different fledglings (Draganoiu, 2005; Draganoiu et al., 2014). We recorded males and their neighbours and assessed the level of song sharing between them. We then tested the males by broadcasting two nonfamiliar stimuli of the local and foreign dialects. During the playback, we took into account 14 variables associated with the vocal and the approach responses in males. Several methodological factors of importance were recorded, notably the focal male’s distance relative to the speaker at the beginning of the experiment (initial distance). We carried out a principal component analysis to obtain reduced composite variables to ease the analysis. Three types of response emerged: the vocal response, the flight approach and the ground approach. To identify the factors responsible for the variation of the response variables, we performed a model selection procedure.

1.2.1 Discrimination between microdialects

We first showed that male black redstarts could distinguish between songs belonging to different microdialects. They exhibited a stronger aggressive response towards the local microdialect than towards the foreign one, concurring with findings in species with larger dialects (Parker et al., 2018). The stronger response towards the local microdialect treatment suggests that local singers may be perceived as a higher threat, possibly due to their knowledge and adaptation to the micro-local habitat fitting the “relative threat hypothesis” assumptions rather than the “recognition hypothesis” (Dabelsteen & Pedersen, 1992; Nelson, 1998; Wright & Dorin, 2001). Our findings contrast with those of a prior study which documented reduced aggression towards local microdialects in Eurasian skylarks compared to foreign ones (Briefer et al., 2010). One potential rationale for this contrast could be the familiarity of the skylarks with the songs used for the local microdialect treatment. However, in our study, we methodically addressed this potential bias by using recordings obtained around 3−7 years ago from the same hamlet as the tested bird or 1−2 years ago from a separate breeding patch situated at an average distance of 730 meters away.

Furthermore, the effect of treatment on the territorial response was evidenced on the ground approach behaviour only. The behaviours under this category are associated with the last stage of the aggressive response in the black redstart (Apfelbeck & Goymann, 2011; Landmann & Kollinsky, 1995; Schwarzová, 2010; Sedláček et al., 2006). The proximity to the potential threat could lead to contact and injuries in a real encounter (Diniz, 2020; Hof & Hazlett, 2010). The proximity to the speakers could reflect the need for birds to approach to gain more information on the threat and have finer discrimination by switching to short-range communication (Naguib et al., 2022). This approach strategy has been reported in an earlier playback study carried out on black redstarts, where birds would preferentially signal and observe first before coming near the loudspeaker (Schwarzová, 2010). Indeed, a shared song might give information on the origin of the intruder but calls or soft songs, short-range communication means, can enclose information like individuals' identity, aggressiveness and kinship (Hof & Hazlett, 2010; Kondo & Watanabe, 2009; McDonald & Wright, 2011; Ręk & Osiejuk, 2011). As black redstarts are philopatric (Musseau, 2007), new males singing the local dialect could be the offspring of the present territory owners. Territorial males could be biased towards kin and use calls to identify them (Akçay et al., 2013). Unfortunately, our study did not allow us to gain this information. However, previous findings from our team showed that black redstarts can discriminate between the begging calls of their offspring (Draganoiu et al., 2006), leaving the possibility that more information is present within other call types in this species. In addition to treatment type, the initial distance also affected the ground approach behaviours. This advocates for the fine discrimination between microdialects and the adjustment of the last step of the agonistic response type accordingly.

1.2.2 Aggression escalation chain

We shed light on the importance of the initial distance on the territorial response of males. This variable was rarely considered in previous playback studies (Armstrong, 1991; Naguib et al., 2002). Indeed, this factor affected the three behavioural response variables. This result supports the idea of an escalation chain in the aggressive response (Beecher & Akçay, 2014), as the males showed nuanced responses to the perceived threats based on the distance separating them. When birds are initially far from the speaker, they are more likely to vocalize, likely as a means of signalling their presence and territorial ownership to conspecifics over longer distances. This suggests that vocalizations are used as an initial stage in the escalation chain, particularly effective for long-range communication. When birds are initially closer to the speaker, they are more likely to approach and spend more time in its proximity. Such behaviour is associated with patrolling the territory to locate the intruder. This indicates that as the perceived threat becomes closer, the level of aggression escalates, with ground approaches being the paramount of the response. These steps involve different risks and costs for individuals (Diniz, 2020; Hof & Hazlett, 2010). Overall, the initial distance effect interacts with each step of the aggression escalation chain, influencing the strategic decisions of male black redstarts in response to playback stimuli. This highlights the importance of considering spatial dynamics and perceived threat distances in understanding territorial behaviours and aggression escalation in avian populations.

1.2.3 Inter-individual variability

We shed light on the discriminative abilities of the black redstart and the importance of taking into account the initial distance of the males at the beginning of the experiment relative to the speaker as it bears consequences on the strategy of defence chosen by males. Inter-individual variability was, however, responsible for most of the variation in the behavioural responses. This variability could be relying on factors such as personality (Amy et al., 2010; Colombelli-Négrel et al., 2022; Myers & Hyman, 2016), social interactions before the playback (Hall et al., 2006; Naguib et al., 2022; Schmidt et al., 2007) or territory size (Naguib et al., 2022; Schwarzová, 2010). We recorded other variables, including breeding stage and pairing status, but for a few males, these remained unknown. We would require a larger sample size to include these parameters in the model selection procedure.

1.2.4 Increase the sample size

The coronavirus pandemic in 2019, through the national restriction on population movement, impacted the field survey and restricted us in data acquisition on both the longitudinal survey and the playback experiment. Indeed, we could not carry out the playbacks during the Spring of 2020 as two observers were needed. Data acquisition was more challenging as it relied on only one researcher (T.V.). The ringing operation of first-year breeders was delayed until September 2020, reducing the number of captures and ringing. In addition, a natural parameter also affected our data collection. Weather conditions can dramatically impact the reproductive success of breeding couples (Mainwaring et al., 2021). In 2021 birds experienced poor weather conditions (e.g. low temperature, wind and rain) which likely reduced their brood survival. Consequently, in 2022, there was a relatively low number of first-year breeders in the area. This low number of young males impacted our data collection during the playback experiment. Indeed, we could not test any first-year male breeders during this season. Field conditions are unpredictable and are responsible for some limitations. In our case, it resulted in a lower sample size than anticipated. With more time and resources, playback experiments could be carried out to increase the sample size of both first-year breeders and older birds to study the effect of age class and other factors of interest on behavioural responses. Previously, males' age was shown to affect the territorial behavioural responses in several black redstart populations.

First-year breeders tended to have a stronger vocal response compared to older birds which tended to direct more aggressivity to the experimental intruder (dummy) (Schwarzová, 2010). If we continued the playback experiments, adding stimuli could further enlighten the acoustic parameters males focus on to discriminate between local and foreign dialects.

1.2.5 Stimuli variability in similarity

We showed that both the binary measure of the treatment type and the gradual evaluation, through the similarity score, yield similar results during the selection model procedure. We hypothesise that the similarity of the stimuli song and the song of the focal males is of importance to them. Previous findings (Chambon, 2015) showed that recent past songs were less similar than the songs of the focal birds' direct neighbours. As a result, we raise a minor concern that song evolution over seven years might reduce the efficiency of our stimuli, as shown by Derryberry's studies (2007, 2011) that also used stimuli from the past. The white-crowned sparrows responded more aggressively to the similar songs of the current dialect than to historical songs recorded in the same dialect 25 years ago (Derryberry, 2007). Furthermore, the historical songs triggered an equivalent aggressive response as the songs of a present foreign dialect (Derryberry, 2011). A potential solution to avoid these biases would be to expose males to stimuli of synthesised signals (Mathevon et al., 2008). Another possibility would be to broadcast the bird's own song (Akçay & Beecher, 2020). However, the latter method is still controversial and should be used with caution (Derégnaucourt & Bovet, 2016). Our results open the door for further investigation through other playback experiments and to the study of dialect evolution in the population.

1.2.6 Reduced vocal output

We also faced the reduction of vocal output during playback, which prevented us from looking in more detail at the vocal response of males. In several species, song matching (selection of songs matching the stimuli) reflects the aggressive intent of males. Moreover, the song timing (alternation or overlapping with stimuli) during a territorial dispute can also reveal the males' intention towards an intruder (Logue, 2021; Todt & Naguib, 2000). Common nightingales display nocturnal singing to defend their territory. Territorial defence during the night relies more heavily on singing compared to daytime defence (Schmidt et al., 2006). In this species, song timing was successfully studied in the context of night. Additionally, playback simulating various levels of aggressive intent through song timing led to different territorial responses during the day (Naguib et al., 2008). Future studies on counter singing properties in the black redstart should hence take place in the context of dawn choruses, when song output is greater, and males are more likely to rely on singing. The results of the current study are of importance, as to our knowledge this is only the second investigation of local and foreign dialects in a microdialect species to date. It provides new insights, but further research is needed to understand the functional significance of singing the local dialect in microdialect populations.

1.3 What are the benefits of sharing?

The first study of this thesis highlighted the drive males had to share with their neighbours. During dispersal, they target hamlets where they share songs with other males. When failing to settle in a hamlet with such conditions, black redstarts display a diverse toolkit of repertoire-changing means. These enable them to learn the local dialect during the first breeding season. Nonetheless, in the second study, we revealed that males react more aggressively to a simulated first-year breeder from the local dialect than to one from a foreign dialect. In addition, previous work on the population showed that males establish neighbouring relationships. Males were less aggressive towards the familiar shared songs of their neighbour than towards the unshared songs of a foreign individual (Draganoiu et al., 2014). It demonstrates the implementation of the dear enemy effect after the relationship had time to build between males. Multiple hypotheses, the “sharing hypothesis” and “social adaptation hypothesis”, suggest the presence of benefits associated with song sharing soon after arrival. For example, in several other species, sharing the local dialect was shown to benefit the newly settled males through improved territory acquisition, neighbouring relations, mating opportunities or reproductive success (Beecher et al., 2000; Nelson & Poesel, 2013; Payne, 1982; Rothstein & Fleischer, 1987; Thomas et al., 2021). Therefore, we hypothesise that song sharing might provide social advantages and fitness benefits as soon as the first breeding season but also later on. Unfortunately, during my thesis, we could not demonstrate the short-term benefits during the first breeding season or long-term benefits later in life. This subject needs to be studied further. We discussed how in the second part of the discussion.

1.4 Direction for future studies

1.4.1 Costs and benefits

Both studies conducted during this thesis lead us to a similar questioning: what are the costs and benefits of vocal sharing in the black redstart? Here we propose several leads to be investigated further in order to answer this question.

Paternity

Having a local dialect singer settling in the adjacent territory could cost mating opportunities to the resident focal bird (Beecher, 2017; Beecher et al., 2020; Beecher & Akçay, 2021).Based on the relative threat hypothesis, if females preferentially mate with males singing the local dialect, a rival singing the local dialect could cost the resident male mating opportunities. This explanation seems more than possible in the black redstarts, as Villavicencio et al. (2014) have shown in their population that males had a 30% loss of paternity to other males (but see Weggler, 1997). This rate is exceptionally high for a passerine species displaying a similar monogamous mating pattern system (Griffith et al., 2002; Kempenaers & Schlicht, 2010). If a new breeding male settles in an area with a different dialect than his own , we have seen that he can only adapt to the local dialect in time for the second breeding attempt of the season, at the end of May, or at his arrival for the second breeding season. For example, in white-crowned sparrows, first-year males who shared songs with their neighbours had higher pairing success than newcomers who did not share songs (Poesel et al., 2012) and in zebra finches, most of the extra-pair eggs were sired by males singing the dialect of the females' population (Forstmeier et al., 2021).

Aggression

Extending the learning period can be costly to newly arriving males on several aspects (e.g. energetic cost, time and mating opportunity loss) of which some are still under debate notably costs linked to the maintenance of the neural system involved in song learning (Gil & Gahr, 2002; Nowicki et al., 2002; Robinson et al., 2019). In Savannah sparrows, newly arrived males encounter comparable levels of aggression from resident neighbours, regardless of the songs they exhibit. However, after several weeks, young males showing a higher level of song similarity with the songs of their neighbours received less aggression than males with more dissimilar songs. In addition, in the studied population, young males presenting overproduction and selective attrition preferentially retained songs that maximized the song similarity level with their neighbours (Thomas et al., 2021). In our population, first-year breeder males presenting overproduction and attrition also retained songs shared with their neighbours and, therefore, have high similarity between their songs. Based on the drive to increase sharing with their neighbours present in young males and of the “dear enemy effect” in older males, we could hypothesise that the level of aggression towards first-year breeder males should vary during the season based on the song they use similarly to the Savannah sparrows. Males should become less aggressive faster towards first-year breeders sharing the local dialect compared to foreign dialect singers. In order to test this hypothesis, we should use continuous autonomous recordings similarly to Thomas et al. (2021).

Long-term benefits (survival, territory tenure and lifetime reproductive success)

In some cases, first-year breeder survival can correlate with their capacity to share songs with their neighbours. Sharing songs early into territory establishment was found to impact the survival of first-year breeders in song sparrows. Indeed, the number of years a bird survived on its territory was positively correlated to the number of songs he shared with his neighbours during their first breeding season (Beecher, 2017; Wilson et al., 2000). In Canada Warblers, *Cardellina canadensis*, song sharing was positively correlated to territory tenure (Demko et al., 2016). In Puget Sound white-crowned sparrows, *Zonotrichia leucophrys pugetensis*, males sharing songs in their first year on territory, had higher lifetime reproductive success (Nelson & Poesel, 2013). Therefore, to explore the presence of such benefits in the black redstarts, we need to continue the longitudinal survey and complement it with genetic analyses to establish reproductive success. Genetic analyses could also inform on kin relationships between birds.

1.4.2 Testing a different population

Earlier we proposed to study black redstarts in the laboratory to control for the social environment. Yet another way to assess if dialect establishment mechanisms and functions described in our population are only due to its characteristic social stability is to survey other populations in the wild. Previous studies showed differences in song-sharing levels between populations of the same species depending on various population characteristics (e.g. migratory, sedentary, density levels, isolation, stability) (Hughes et al., 2007; Osiejuk et al., 2007; Parker et al., 2022). For example, in song sparrows, both migratory and sedentary populations can be found. In a Washington state population the number of song types shared with territory neighbours was correlated with territory tenure (Beecher et al., 2000) while in a Californian population, it was associated with survival over a 1-year interval (Wilson et al., 2000). In both of these sedentary populations song sharing levels were higher in comparison to other eastern migratory populations. In the eastern migratory population sharing of whole songs or song components did not correlate with territory tenure (Hughes et al., 2007) or survival over 1 year (Lapierre et al., 2011). These results reflected the importance of a species ecology on dialect establishment and resulting benefits. The black redstart is a partial migrant and would be a great model to study the effect of this characteristic on dialect establishment. In Dickcissels, *Spiza americana*, Parker et al. (2022)

observed a faster cultural change in cropland compared to grassland populations. The cropland populations experienced higher rates of population turnover and consequently reduced site fidelity compared to more stable grassland populations. This difference in populations' stability was partly responsible for the different song evolution rates between populations (Parker et al., 2022).

1.4.3 Factors impacting song learning

Song learning after hatching

During two field seasons, we surveyed the population during September. The purpose of these observation periods was to record breeding males and fledglings' first songs. In the population of la Valla-sur-Rochefort, the singing rate is low and sporadic throughout the day in autumn making it hard to acquire song bouts for all males (personal observations). Studying them in the laboratory could permit to study song ontogeny as early as possible after hatching. In addition it could reveal the importance of the social environment in the hatching year on later learning abilities (Lehongre et al., 2009; Leitner & Catchpole, 2007). Song acquisition timing was successfully assessed in several species thanks to laboratory studies (Brenowitz & Beecher, 2005; Marler & Peters, 1987; Todt & Geberzahn, 2003). We might observe that males who fledged are at the plastic song stage in autumn and practice strophes of the local dialect. We succeeded to get one recording of a yearling male singing in September that indicates so (**Figure 7**).

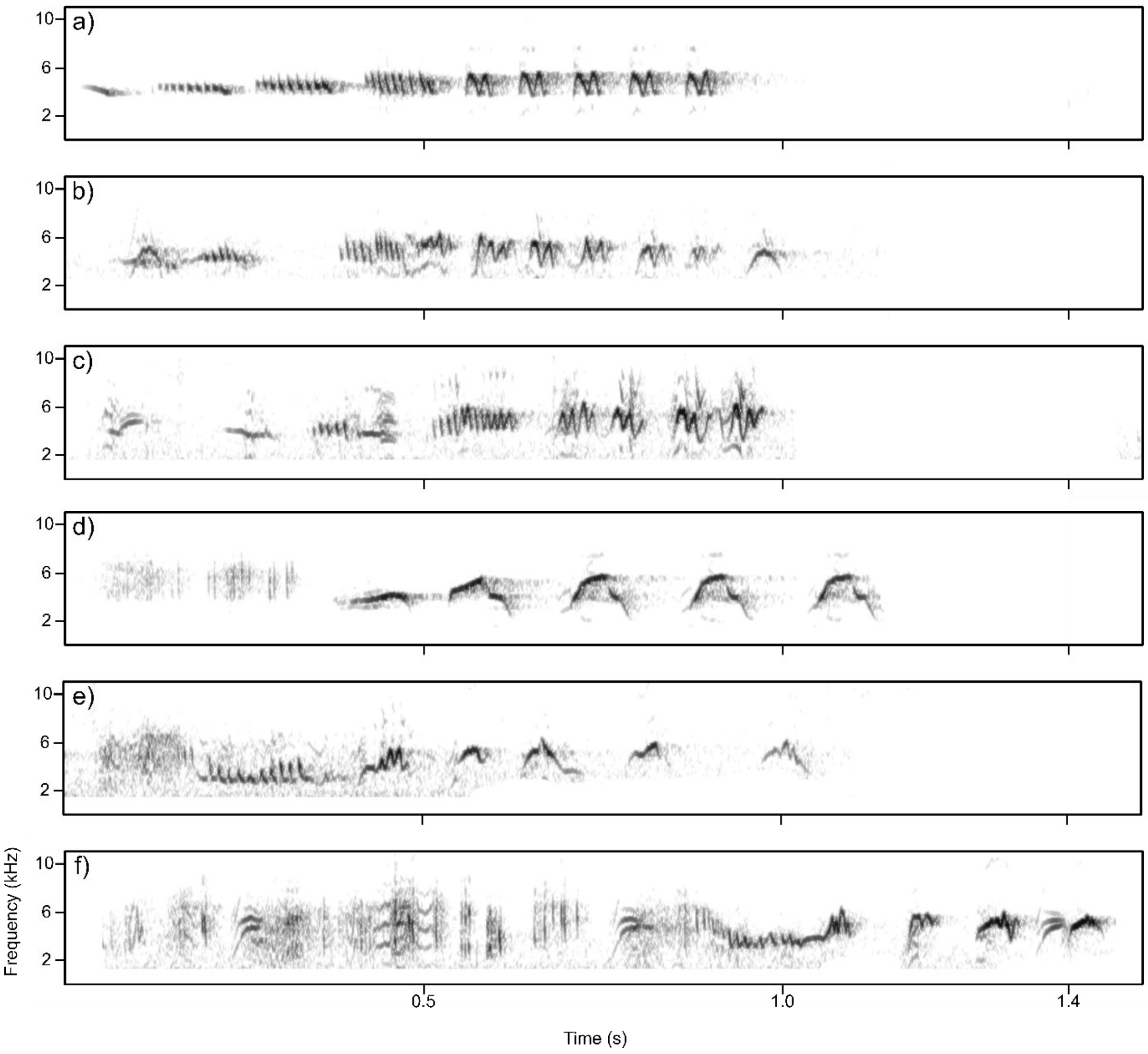

Figure 7. Comparison of local dialect strophe renditions of an adult male (a and d) and a fledging (b, c, e and f). Spectrograms examples (FlatTop window; FFT length: 256; 87.5% overlap) of the local beginning strophe sung by a) an adult male (model to match) b) and c) sung by the fledging in September. Spectrograms examples of the local ending strophe sung by d) an adult male (model to match) e) and f) sung by the fledging in September. Variability can be seen between the two renditions of the same strophe (b-c and e-f).

Testosterone

Hormones such as testosterone have been demonstrated to affect territoriality, singing behaviour and brain areas involved in song production and learning (Alward et al., 2017, 2018; Ball & Balthazart, 2010; Balthazart et al., 2010; Wingfield, 1994; Wingfield et al., 1990). Notably, high testosterone levels promote song crystallisation in several species (Brenowitz, 1997; Korsia & Bottjer, 1991; Marler et al., 1988; Templeton et al., 2012). In song sparrows and swamp sparrows, *Melospiza georgiana* both control and castrated males followed the species' typical song learning program but only control males reached full song crystallisation. Indeed, most sterilized males were stuck in the sub- and plastic song phase until they received a hormonal treatment of testosterone which led to the expression of crystallised songs (Marler et al., 1988). Testosterone levels have been shown to vary seasonally in several passerine species (Apfelbeck et al., 2013; Goymann & Landys, 2011). Black redstart testosterone levels seem to follow the same pattern with high testosterone levels during breeding and lower levels during moult and non-breeding (Apfelbeck & Goymann, 2011; Villavicencio et al., 2021). Testosterone levels could have an impact on the black redstart songs' learning and modifications in light of our results. More precisely high levels of testosterone early in the breeding stage could prevent strophe and syllable modifications until May in our population and delay the addition of new material to September when testosterone levels are low. Also, the low testosterone levels in autumn could be a reason to why variable songs are still produced at that time as males might need higher levels of testosterone to crystallise their repertoire. In the brown-headed cowbird, during the breeding testosterone levels stay high, it is believed to be the reason why males are not able to add new or modify existing songs until the end of the season (O'Loghlen, 1995; O'Loghlen & Rothstein, 1993). The inhibitory effect of testosterone was also observed in other species in a laboratory setting (Nottebohm et al., 1987; Whaling et al., 1995).

In addition, in the black redstart, on several occasions, researchers have focused on the impact of testosterone on the vocal and non-vocal behaviour involved in males' territorial response at several points of the season: breeding, moulting, and non-breeding (Apfelbeck et al., 2013; Villavicencio et al., 2021). It was found that non-vocal behaviours were not linked to testosterone levels as males display them similarly during breeding and non-breeding when testosterone levels are at their highest and lowest, respectively (Apfelbeck et al., 2013; Apfelbeck & Goymann, 2011; Villavicencio et al., 2013, 2021) while vocal behaviours seem to be impacted by testosterone levels in the specific context of territorial intrusion (Apfelbeck et al., 2012). Males were either implanted with the androgen receptor blocker flutamide and the aromatase inhibitor letrozole to inhibit the action of testosterone (referred to later as testosterone-inhibited males) and its estrogenic metabolites or received a placebo treatment (controls) at the beginning of the breeding season. The song structure of male black redstarts differed between control and testosterone-inhibited males during territorial intrusion. Control males had shorter but denser songs and song duration decreased because males shortened the silence between the beginning and the harsh part of the songs, and an increase in the frequency bandwidth of the harsh part of the song. While testosterone-inhibited males decreased the maximum frequency of the beginning strophe and did not alter the harsh part of their songs. Furthermore, in both groups, the number of elements in the two strophes increased but testosterone-inhibited males exhibited a trade-off while in controls testosterone enabled males to produce more competitive songs by the increase in the signal density (Apfelbeck et al., 2012). Apfelbeck et al., (2012) also found that treatment's affected song parameters in spring (e.g. maximum frequency of the beginning strophe and frequency bandwidth of the harsh) are acoustic parameters that have also been identified by Cucco & Malacarne (1999) to be characteristic of adult males songs in contrast with yearling songs (first-year breeder males). In addition, songs during breeding, when testosterone is high, seemed to be built for vocal performance, to be involved in both territorial defence and mate attraction, and to be an honest signal of quality (Apfelbeck et al., 2013; Cucco & Malacarne, 1999). In great tit, *Parus major*, females have been shown to eavesdrop on male-male contests to choose a mate based on songs' acoustic parameters reflecting males' quality (Otter et al., 1999). Furthermore, the black restart songs from autumn contrary to songs during breeding (spring) are believed to be directed more towards males (Apfelbeck et al., 2013). Testosterone-inhibited males had similar songs throughout the season which were similar to the autumn songs of placebo males at a time of the season when testosterone levels are low (Apfelbeck et al., 2012). In addition, in a simulated intrusion experiment testosterone-inhibited males preferentially expressed behaviour directed towards a rival, more precisely they used non-vocal behaviour while placebo males used both vocal and non-vocal behaviour (Apfelbeck et al., 2013). Based on this finding, it is conceivable to emit the hypothesis that testosterone could be involved in song crystallisation as it has already been shown to influence song output and structure in the species. This hypothesis needs to be investigated at several life stages in a laboratory setting, to induce optimal social conditions leading to strophe repertoire changes in males.

Thrush nightingales are a migratory species with a mix of territorial and non-territorial males on their wintering grounds (Brumm et al., 2023) similarly to the black redstarts (Cuadrado, 1995). Testosterone concentration can rise at the end of the wintering season, in some long-distance migrants, as birds start transitioning to the breeding stage (Ramenofsky & Wingfield, 2006; Wingfield, 2007). Brumm et al. (2023) showed that male thrush nightingales displaying crystallised songs were territorial compared to males with plastic songs on wintering grounds. Authors hypothesised that territoriality was a byproduct of the rise in testosterone levels responsible for song crystallisation at this time of the season in this species (Brumm et al., 2023). Studying testosterone levels or even song consistency in concert with territoriality in wintering grounds in the black redstart could provide answers on the timing of addition and gradual modification of song elements.

1.4.4 Data set potential

Dialect evolution from 2007 to 2022

For four years my work has contributed to building up a longitudinal data set spreading over 15 years. Therefore, information on the dialect evolution within the population is available from 2007 to 2022. The maintenance of dialects could be investigated between years to assess the duration of the presence of the different strophe types. We know that some dialects can last for 14 years but not all dialect neighbourhoods have been investigated in detail. Earlier when discussing the limitations encountered during the dialect discrimination playback experiment, we raised the possibility of dialect evolution taking its course and modifying the signals' relevance over the past seven years (Chambon, 2015; Schloesing, 2015). Therefore, analysing the data set to identify the acoustic parameters evolving and assessing the level of divergence between today's and past dialects would answer this question (Derryberry, 2007, 2011).

Syllable repertoire

In the optics of looking at our data in even more depth changing the scale at which songs are analysed could be beneficial. We studied the beginning and ending strophes' trill parts of the song in this thesis. However, syllable structure and syllable repertoire could reveal more information. Even though the analysis of strophe repertoires is relevant switching to the syllable scale could benefit us. Birds can discriminate changes at finer scales and more variation could be identified. Using the syllable repertoire has been done in other species and using it could allow further comparative studies with other species (Briefer et al., 2010; Forstmeier et al., 2002; Lipkind & Tchernichovski, 2011; Petrusková et al., 2010). Syllable repertoire would be especially relevant in the neighbourhood where the dialect is composed of one song but variation in pre-trill elements provides birds some flexibility between song variants (**Figure 8**, personal observation).

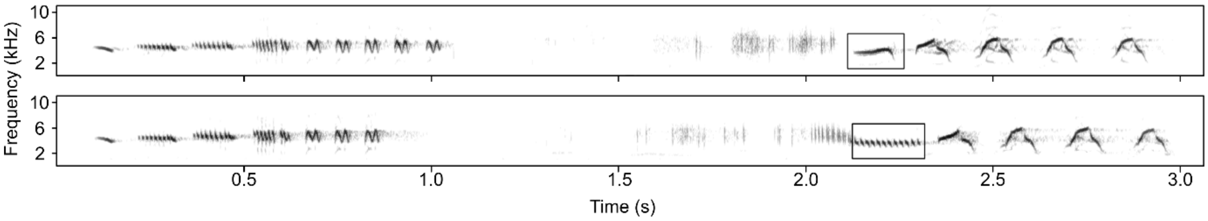

Figure 8. Spectrograms examples (FlatTop window; FFT length: 256; 87.5% overlap) of the local dialect sung by the same male with different ending strophe pre-trills (surrounded elements)

Furthermore, birds are sensitive to temporal fine structure in acoustic signals (Dooling & Prior, 2017; Fishbein et al., 2019). In dusky warblers*, Phylloscopus* *fuscatus,* Forstmeier et al. (2002) suggest that females assess males' quality over smaller units (e.g. notes) rather than by the quantity and versatility of songs. In Savannah sparrows, different song elements were found to have different signalling functions and to change at different paces, one sound called the buzz was used as a population marker and note complexes reflected identity or local affiliation. The buzz segment is maintained through time while note complexes vary (Williams et al., 2013, 2019). Therefore, segmenting the songs into smaller units than the syllables could get closer to the bird's perception of the song. Hence, this should help identify different functions for the different parts of the song and if they change at a different pace in the black redstart. Finally, the finer scale segmentation could provide ground for song senescence studies, indeed data sets similar to ours have been used in other species to investigate this aspect (Berg et al., 2020; Kipper & Kiefer, 2010; Rivera-Gutierrez et al., 2012). All this data would provide a valuable insight into the mechanisms underlying dialect maintenance and evolution as well as song learning. In future analyses, machine learning, a type of artificial intelligence, would be a great tool to further deepen the analysis of our dataset. This method is becoming increasingly popular in the study of bird songs as it facilitates the rapid and automated annotation of large audio datasets , the classification of vocal signals and the detection of acoustic variations (e.g. individual signatures and dialects) (Bocaccio et al., 2023; Wang et al., 2022; Yang et al., 2023).

Strophes frequency of use

In the first chapter of this thesis, we saw that a few males kept some vocal flexibility through life with the use of selective attrition. Males could also have flexibility through the selective production of specific strophes over others. The males who kept their repertoire stable and others who added and deleted material were found to have changes in the frequency of use of their different strophes between breeding seasons (Volle, 2019). Indeed, males seemed to produce preferentially specific strophes among others between breeding seasons. By extending the analysis of strophe frequency of use to all the neighbouring birds, we could reveal another mean by which birds can keep some flexibility to adapt to their social environment, throughout their life, by preferentially using certain strophes variants (Garamszegi et al., 2012). Also including this in future analyses, could give grounds to test the hypothesis linked to song performance and it would complement the study on the song senescence as well (Logue & Forstmeier, 2008; Poesel & Nelson, 2015)

2. Conclusion

The results of this work shed light on microdialects establishment in a population through a combination of learning and dispersal strategies. We also identified the song-learning strategies males used to conform to their social environment and the time frame under which it was conducted. Using a playback experiment we showed that during territorial interaction males were more aggressive towards the local dialect compared to foreign dialect singers. We concluded that microdialects are a base for discrimination in the species. Interestingly, we revealed the role played by the initial distance into the behavioural response and the aggression escalation chain. However, more studies are needed to investigate what are the costs and benefits of song sharing in the species as well as the acoustic parameters males focus on to discriminate. Findings from this thesis, by enlightening the process behind microdialects functions and establishment, could later participate in giving foundation to understand microdialect species behaviour and ecology which could later facilitate their reintroduction. Finally, this thesis work could potentially contribute to the field of research that investigates the origins and evolution of vocal communication across the diverse animal taxa and to an extent the specificities of human language.

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APPENDICES

Appendix 1: Substantial French summary

APPENDICES

1. Cadre théorique

1.1 Apprentissage vocal

La communication vocale est utilisée par de nombreuses espèces de vertébrés lors d'interactions telles que la défense territoriale, la parade nuptiale et les soins à la progéniture. L'apprentissage vocal est défini comme la capacité d'apprendre et de modifier des signaux vocaux en imitant des congénères ou d'autres espèces. Il a été observé chez les humains, les cétacés, les éléphants, les pinnipèdes, les chauves-souris et trois ordres d'oiseaux : Psittaciformes (perroquets), Apodiformes (colibris) et Passériformes (passereaux). Chez les passereaux, cette capacité a été décrite chez les oscines (oiseaux chanteurs) et chez deux espèces d'Arapongas (suboscines). Les vocalisations des oiseaux sont généralement classées en deux catégories : les cris, courts et simples, et les chants, plus longs et plus complexes. Le chant des oscines (oiseaux chanteurs) est le système de communication animale le plus étudié.

Le chant des oscines est un des modèles principaux d'études de l'apprentissage vocal. En effet, de nombreuses recherches ont permis l'identification des voies neurales, des gènes impliqués et de la diversité des modes de développement au cours de la vie. L'apprentissage du chant présente plusieurs étapes : une phase sensorielle, durant laquelle un juvénile mémorise des modèles de chants entendus, et une phase sensori-motrice, pendant laquelle le jeune s'exerce et modifie son chant en fonction des modèles mémorisés et un utilisant le feed-back auditif. La structure du chant se stabilise sous une forme finale dite cristallisée. Ces étapes ont des durées et une fréquence d'apparition variables dans la vie de l'oiseau et selon son espèce. Par exemple, chez le diamant mandarin, *Taeniopygia guttata*, seuls les mâles apprennent à chanter pendant une période sensible de la vie précoce (trois premiers mois) avant que le chant ne cristallise et reste le même jusqu'à la fin de la vie de l'oiseau (« apprentissage fermé »), alors que l'étourneau sansonnet, *Sturnus vulgaris,* peut modifier et apprendre de nouveaux sons tout au long de sa vie (« apprentissage ouvert »). Cette catégorisation des programmes d'apprentissage vocal d'abord considérée traditionnellement comme dichotomique (ouvert et fermé) a fait place à un continuum qui reflète mieux la diversité des programmes observés chez les espèces capables d'apprentissage vocal. Malgré plus de 50 ans de recherche sur l'apprentissage vocal, seulement quelques espèces d'oscines ont été étudiées sur environ 4000 existantes, et principalement sur le chant des individus mâles. L'engouement pour le modèle d'apprentissage vocal des oscines est en partie dû à ses similarités avec le modèle humain (exemples : période sensible et phases d'apprentissage, structures neuroanatomiques dédiées, présence de variations géographiques des signaux vocaux, dialectes).

1.2 La culture vocale

L'apprentissage vocal joue un rôle important dans l'apparition des dialectes, ou cultures vocales, grâce à un processus d'imitation précis des éléments locaux transmis sur des centaines de générations. Néanmoins, de nouveaux éléments peuvent se diffuser dans une population à la suite d'erreurs d'imitation ou d'innovation. Les dialectes se définissent comme des variations plus ou moins distinctes des signaux vocaux à différentes échelles géographiques. En effet, certains individus présentent un bilinguisme aux frontières de ces variations. Chez les oiseaux, les dialectes ont principalement été étudiés chez les oscines. Depuis les travaux pionniers de Marler and Tamura en 1962, la recherche s'est focalisée sur les processus d'apparition et de maintien des dialectes ainsi que sur leur importance évolutive.

1.3 La culture vocale chez les oiseaux

Chez les oscines, des dialectes ont été observés à plusieurs échelles géographiques, allant du microdialecte, partagé par moins de 10 individus sur moins de 2 km, au dialecte étendu à plus de 1000 individus sur plus de 100 km. Il est également pertinent de rappeler que ces variations vocales concernent certaines populations d'une même espèce. Ces dialectes peuvent se maintenir sur plusieurs décennies ou rapidement évoluer d'une année à l'autre. Des changements dans le système d'un dialecte (par ex. son érosion) peuvent refléter une modification de l'habitat (par ex. perte ou dégradation). Les dialectes sont également impliqués dans la reproduction et la défense du territoire. Ils sont ainsi capitaux pour le succès de la réintroduction d'un individu dans un groupe et primordiaux dans les efforts de conservation.

Trois grandes catégories d'hypothèses complémentaires ont été proposées pour expliquer l'évolution des dialectes. L'hypothèse explicative initiale est celle d'un épiphénomène et suggère que les dialectes sont un produit dérivé de programmes d'apprentissage et de stratégies de dispersion spécifiques. Ces derniers sont soumis à des pressions évolutives indépendantes de celles menant à la formation du dialecte.

La deuxième hypothèse est celle d'une adaptation aux paramètres locaux. Elle repose principalement sur le fait que les femelles présentent une préférence envers les mâles de leur région natale, reflétant éventuellement des avantages reproductifs liés à la connaissance de l’habitat. Cette hypothèse permet de faire 4 prédictions : 1) les jeunes oiseaux apprennent leur chant avant de se disperser depuis leur région natale 2) durant cette dispersion les oiseaux s’installent de préférence à proximité d’oiseaux au chant similaire au leur 3) l’appariement sélectif peut mener à une divergence génétique entre les populations 4) les femelles développent une préférence pour les mâles de leur dialecte natal.

Enfin, l’hypothèse d’une adaptation sociale postule qu’un mâle au chant similaire à d’autres mâles de la région aura des avantages reproductifs et sociaux (par ex. meilleur appariement, maintien du territoire, réduction de l’agressivité). Cette hypothèse implique que les mâles apprennent leur chant après leur dispersion et s’ajustent au dialecte local.

A ce jour, peu d’études ont porté sur la fonction des microdialectes. Le playback (technique de la repasse) est une méthode couramment utilisée pour tester la fonction des dialectes. Cette technique utilise la diffusion de chants familiers ou non familiers, locaux ou étrangers combinée à l’observation de la réponse comportementale de l’oiseau testé. La majorité des études sur la discrimination entre dialecte étranger et local rapporte une réponse plus intense envers le dialecte local chez les espèces à dialectes très étendus.

Afin d’expliquer cette tendance d’une réponse agressive intense envers le dialecte local, deux hypothèses ont émergé. La première hypothèse « de menace relative » est celle d’une cause ultime : les mâles territoriaux perçoivent un intrus chantant le dialecte local comme plus dangereux. En effet, un intrus présentant ce phénotype reflète sa connaissance des ressources du territoire et donc un avantage reproductif. La deuxième hypothèse de « reconnaissance » repose sur une cause proximale : les mâles territoriaux répondent plus fortement à un chant proche de leur représentation interne d’un chant typique de l’espèce. Cette hypothèse implique la reconnaissance d’un dialecte étranger comme celui d’un oiseau non conspécifique et mènerait à une divergence génétique.

1.4 Facteurs d’évolution du chant

La morphologie affecte la production de signaux et peut être un moteur de l'évolution des chants. Les traits morphologiques peuvent avoir de multiples fonctions en dehors de leur rôle dans la communication vocale et sont eux-mêmes soumis à des pressions de sélection divergente. Les propriétés des habitats sont aussi motrices de l'évolution des chants. En effet la structure du chant s’adapte pour assurer une transmission optimale du signal en fonction des propriétés physiques de l'environnement. Ainsi, la modification de l’espace sonore et de vie des oiseaux par l’activité humaine est responsable non seulement de l’évolution des chants mais aussi de l’érosion des dialectes.

Un autre facteur responsable de l’évolution des chants chez les oiseaux est la sélection sexuelle. Cette sélection peut, d’une part, être due aux préférences d’appariement des femelles avec les mâles présentant certains paramètres acoustiques dans leur chant ou avec ceux qui ont un dialecte particulier. D’autre part, les interactions entre mâles peuvent conduire à la conservation de chants qui facilitent les interactions territoriales. Ces chants permettront alors aux adversaires de réguler le niveau d’agressivité durant le conflit selon le principe de l’escalade de l’agressivité. Cette escalade est un enchainement de comportements agressifs allant du plus faible (par ex. le chant) au plus fort (par ex. un contact entre les individus), les individus adaptent donc progressivement leur comportement en fonction du déroulement de l'interaction. Deux hypothèses fonctionnelles basées sur la l'impact de la sélection sexuelle sur les chants ont été proposées. Elles visent à expliquer les variations observées dans le répertoire et les mécanismes d'apprentissage sous-jacents. La première est « l'hypothèse de répertoire » selon laquelle les femelles montrent une préférence envers les mâles ayant un grand répertoire, signe de qualité reproductrice. Selon cette hypothèse, les mâles possèdent un programme d'apprentissage qui favorise l'acquisition d'un grand répertoire. La seconde est « l'hypothèse de partage » et repose sur le principe que le partage de chant apporte des bénéfices sociaux dans les interactions mâle-mâle et lors de l'appariement. Selon cette hypothèse, les mâles possèdent un mode d'apprentissage du chant qui favorise l'acquisition de chants partagés avec les oiseaux locaux.

Le programme d'apprentissage peut également influencer l'évolution du chant, en facilitant la propagation de variations telles qu'une erreur de copie ou une innovation du chant au sein d'une population. Pour finir, les contraintes génétiques peuvent représenter un autre facteur influençant l'évolution des chants à travers les étapes et les spécificités de l'apprentissage vocal.

Pour conclure, l'évolution des chants dans une population peut être due à une combinaison de plusieurs des facteurs décrits précédemment. Bien qu'aujourd'hui l'étude de facteurs concomitants soit facilitée par l'utilisation de la modélisation, identifier l'influence propre à chaque facteur reste un défi.

1.5 L'apprentissage du chant : Du laboratoire au terrain

Les études en laboratoire, par la maîtrise de l'environnement qu'elles offrent, ont permis d'identifier avec précision certains paramètres liés à l'ontogénèse des chants. Les circuits neuronaux impliqués dans l'apprentissage et la production des chants ont ainsi été décrits et l'intervention des hormones dans leurs fonctionnements prouvée. Après un stress généré tôt dans la vie de l'oiseau, le sous-développement des aires du cerveau liées à l'apprentissage et ses répercussions sur les chants produits plus tard ont été observés. Les études en laboratoire favorisent aussi un contrôle de l'expérience auditive des individus qui a mis en évidence la nécessité d'un feedback auditif pour l'acquisition du modèle de chant même si celui-ci est en partie inné et conduit à l'apprentissage préférentiel des chants de l'espèce. Les chants appris sont également affectés si les jeunes oiseaux sont privés d'interactions sociales. Les études en laboratoire ont permis de préciser la durée des étapes de l'apprentissage vocal chez plusieurs espèces en identifiant aussi les limites de l'apprentissage de nouveaux chants.

Par contre, les études en laboratoire sont limitées à certaines espèces et ne prennent pas en compte les conditions de vie de l'espèce en milieu naturel (par ex. stratégies de dispersion, habitats…), contrairement aux études de terrain. Ces dernières sont rares du fait de leur mise en œuvre complexe. Les études en milieu naturel ont pu confirmer certains constats réalisés en laboratoire et en démentir d'autres. La diversité des études effectuées souligne les changements de répertoire chez différentes espèces : l'ajout d'éléments vocaux nouveaux, la recombinaison, la surproduction, la suppression sélective (processus par lequel les chants non partagés avec les voisins sont éliminés du répertoire vocal de l'oiseau) et la modification graduelle des éléments vocaux déjà présents dans une autre configuration acoustique. Malgré l'étendue des recherches effectuées, peu d'entre elles portent sur des espèces à faibles répertoires, ou sont conduites en milieu naturel et sont limitées aux trois premières années de vie des individus. En conclusion, une combinaison d'expériences en laboratoire et sur le terrain est nécessaire pour évaluer pleinement l'ensemble des capacités d'apprentissage des chants chez les oscines.

2. Modèle biologique : le rougequeue noir

Le rougequeue noir, *Phoenicurus ochruros*, est un oiseau insectivore appartenant à l'ordre des Passériformes et à la famille des Muscicapidae. Il est présent en Eurasie et en Afrique du Nord, de la Norvège à l'Éthiopie et de la Chine au Portugal, ainsi que dans le bassin méditerranéen. Il vit principalement dans les zones rocheuses sèches de haute altitude et dans des bâtiments pour y établir son nid. Ce sont des migrateurs partiels, avec des populations qui migrent vers le bassin méditerranéen pendant l'automne. Les mâles arrivent sur les sites de reproduction en mars, établissent des territoires et se livrent à des parades nuptiales. Ils chantent depuis des perchoirs élevés pour défendre leur territoire et attirer des partenaires. Leur activité de chant varie au long de la saison de reproduction. Cette espèce a en général deux nichées par saison. Le rougequeue noir possède un répertoire de chants stéréotypés avec en moyenne deux à trois types de chants. Les chants se composent de deux strophes séparées d'un silence et d'un harsh (son similaire à du papier froissé) (**Figure 1**). Des différences dans les chants entre les classes d'âge et les populations ont été observées. Le comportement territorial implique des chants pour défendre le territoire, des vols de patrouille et des interactions agressives avec les rivaux. Les mâles adultes défendent leur territoire au printemps et en automne. L'effet "cher ennemi" a été observé dans la population d'étude : les mâles différencient les voisins des étrangers et font preuve d'une agressivité plus intense à l'égard de ces derniers.

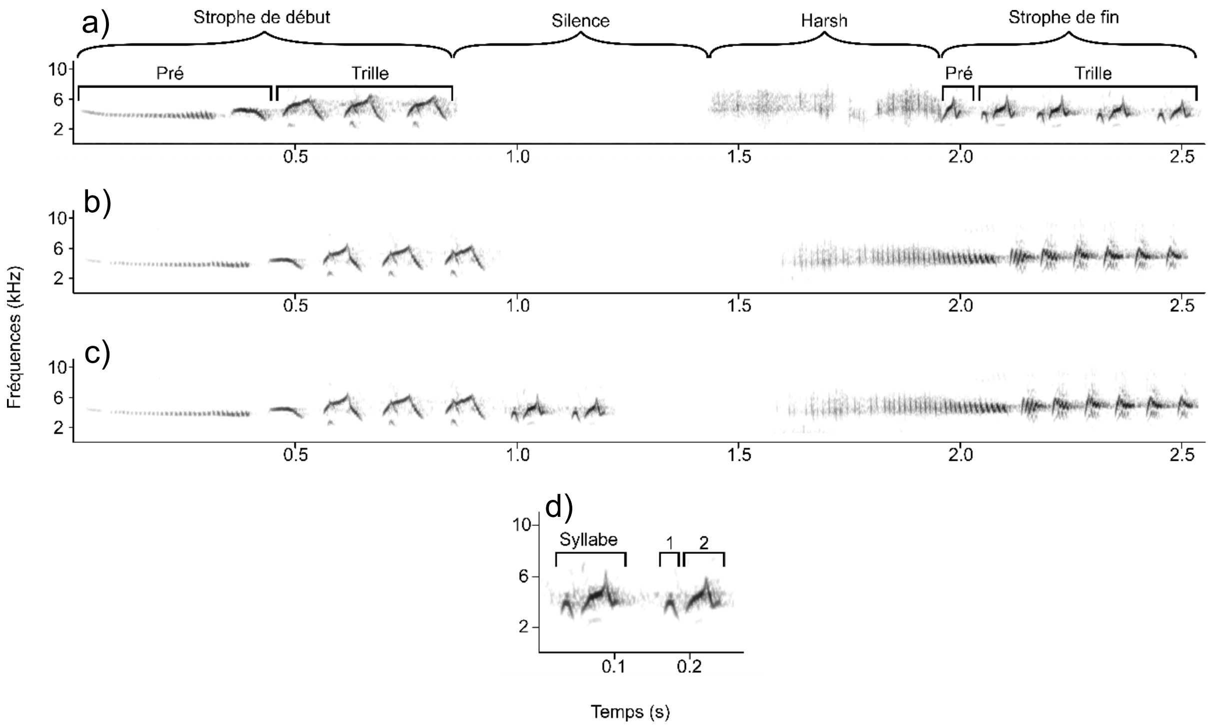

Figure 1. Répertoire complet des strophes d'un mâle rougequeue noir (a-b). Exemples de spectrogrammes (Fenêtre FlatTop ; longueur FFT : 256 ; chevauchement 87,5%) de a) un chant complet détaillé b) un autre chant produit par le même mâle c) un chant avec une strophe de début mixte et d) d'un type de syllabe composé de deux types de notes 1) et 2).

Une population spécifique de rougequeues noirs a été étudiée dans la région du Massif central en France depuis 1997 jusqu'à 2022. La zone de reproduction de cette population est stable (pas de construction ou de démolition de bâtiments) et l'étude longitudinale a permis de mieux comprendre les comportements de reproduction, la fidélité au site, la chronologie de la migration et la structure sociale de cette population. Les mâles d'un même hameau partagent leurs chants mais la distribution de la population est fragmentée et fait apparaitre la présence de microdialectes (**Figure 2**) dont certains perdurent jusqu'à 14 ans. Cette population constitue un modèle précieux pour l'étude des fonctions des microdialectes et pour observer l'importance de la communication vocale durant les interactions territoriales à l'aide d'expériences de playback.

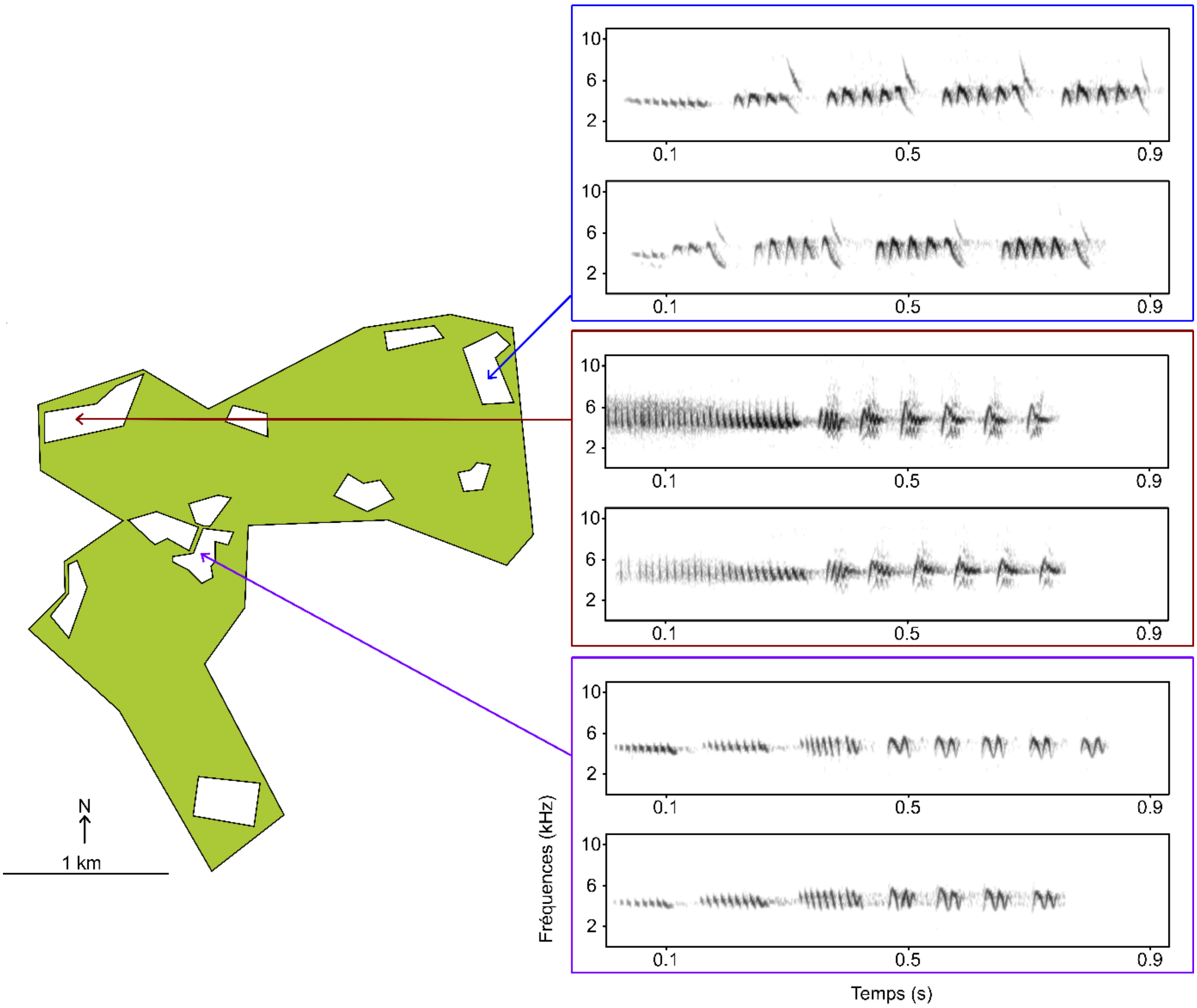

Figure 2. Répartition des hameaux étudiés (*N* = 11, représentés en blanc) dans la zone de recherche (en vert). Exemples de strophes caractéristiques de trois dialectes de hameaux chantés par deux individus voisins (une ligne par individu, les strophes dans le cadre de même couleur sont partagées).

3. Objectifs de la thèse

A travers le suivi longitudinal d’une population de rougequeues noirs, se caractérisant par sa distribution fragmentée et la présence de microdialectes, les buts de cette thèse sont d’étudier l'évolution du répertoire des strophes au cours de la vie ainsi que le rôle des microdialectes dans les interactions territoriales. Cette thèse se base sur des théories de l'apprentissage des chants, des fonctions et du maintien des dialectes. Elle vise aussi à étendre nos connaissances au-delà des environnements de laboratoire. Ma thèse a pour but d’étudier la question proximale et ultime liée au partage des chants et, plus spécifiquement, aux microdialectes. Dans cette thèse, nous nous sommes intéressés à l'ontogenèse du partage des chants chez les oiseaux chanteurs, tout au long de la vie des individus. De plus, nous avons étudié la perception des microdialectes pendant les intrusions territoriales pour mieux définir leur rôle.

4. Chapitre 1 : Évolution au cours de la vie des répertoires vocaux : une approche longitudinale sur le terrain

Le premier chapitre de cette thèse s'est intéressé à l'ontogenèse du partage des chants au sein d'une population de rougequeues noirs, caractérisée par la présence de microdialectes dans les différents hameaux du village. L’étude longitudinale de cette population a montré que les mâles présentent une grande fidélité à leur site de reproduction. Depuis 2015 et jusqu'à 2022, les jeunes mâles qui sont à leur première saison de reproduction ont été bagués afin d'être identifiés et suivis tout au long de leur vie. Au cours de l'étude, nous avons enregistré les mâles bagués ainsi que leurs voisins. Grâce à l'analyse spectrographique des chants des mâles focaux et de leurs voisins, nous avons établi et comparé les répertoires de strophes afin d'évaluer le niveau de partage des chants entre les mâles. De plus, nous avons également suivi le développement du chant des mâles focaux tout au long de la saison de reproduction (de mars à juillet et septembre) et entre les saisons de reproduction afin d'identifier si les mâles pouvaient apprendre au-delà de leur première année ou changer leur répertoire. Dans le cas échéant, nous avons cherché à savoir quel était le délai d'apprentissage et de changement du répertoire vocal chez cette espèce.

4.1 Stabilité

Deux tiers des mâles partageaient de nombreux chants avec leurs voisins lorsqu'ils revenaient de migration pour leur première saison de reproduction. Ces individus ont conservé un répertoire stable tout au long de leur vie. Nos résultats, combinés aux observations précédentes de philopatrie au sein de la population (3-10% de mâles de première année qui reviennent), nous ont permis de déduire que les mâles expriment un apprentissage pré-dispersion et reviennent dans les hameaux où ils ont appris leurs chants l’année d’éclosion.

4.2 Types et délais de modifications

Nous avons observé des changements dans le répertoire de chants chez un tiers des mâles. Ces individus avaient des scores de partage plus faibles avec leurs voisins lorsqu'ils revenaient de migration que les mâles dont les répertoires sont restés stables. Nous avons décrit trois types de changements : la suppression sélective de strophes, la modification graduelle des syllabes et l'ajout de nouvelles strophes. Une caractéristique commune de ces changements est qu’ils apparaissent sous un certain délai. En effet, au cours de la première saison de reproduction, la suppression sélective et la modification graduelle n'ont commencé à s'exprimer qu'en mai et les premiers signes d'ajout de nouveau matériel sont apparus en septembre. Les mâles n'ont pas utilisé l'addition et la modification graduelle après leur retour pour leur seconde saison de reproduction. Notre méthodologie n'exclue cependant pas la possibilité que les mâles aient entendu ces strophes au cours de leur année d'éclosion et les aient produites seulement au cours de leur première saison de reproduction ou des saisons suivantes. Seules des études contrôlées en laboratoire pourraient apporter des éclaircissements à ce sujet. Toutefois, compte tenu des avantages potentiels du partage des chants, il est peu probable que les individus s'abstiennent d'exprimer des strophes mémorisées au cours de leur année d'éclosion lors d'interactions territoriales cruciales en tant que reproducteurs de première année.

La suppression sélective et l'ajout de nouveaux éléments sont des changements bien décrits dans la littérature. Cependant, cette thèse a également mis en évidence le processus de modification graduelle des syllabes. Ce type de changement n'a été décrit que chez le merle fauve, *Turdus grayi*, le cassique cul-jaune, *Cacicus cela*, et le bruant proyer, *Miliaria calandra*. Un processus similaire a été décrit dans les cris du bec-croisé des sapins, *Loxia curvirostra*, de la mésange à tête noire, *Poecile atricapillus*, et de plusieurs espèces de l'ordre des Psittaciformes. Ce type de changements dans les cris de ces espèces pourrait faciliter la cohésion, l'affiliation et intervenir dans le processus de médiation au cours d’un changement de groupe social. La convergence vocale est définie comme le changement collectif de la structure du cri pour produire une nouvelle variante partagée. La modification graduelle peut être difficile à différencier de l'ajout si aucun enregistrement d'une version intermédiaire du chant soumis au processus n'est disponible. Heureusement, au cours des deux premières saisons de reproduction couvertes dans le cadre de cette thèse, nous avons enregistré les mâles depuis leur arrivée en mars jusqu'à la fin du mois de juin, ainsi qu'en septembre. Ceci nous a permis de documenter à l’aide d’enregistrements sonores réguliers la modification graduelle chez plusieurs mâles.

Nous avons également démontré que les mâles conservent une certaine flexibilité vocale tout au long de leur vie s'ils possèdent suffisamment de strophes dans leur répertoire. La suppression sélective repose sur le matériel déjà appris et exprimé (présent dans le répertoire avant la deuxième saison de reproduction). Ces observations soutiennent le modèle proposé par Marler de "mémorisation par l'instruction" suivie d'une sélection dans la production. Ces observations sont en accord avec la prédiction de l'apprentissage basé sur l'action (élimination d'éléments du répertoire qui se base sur l'observation du comportement des conspécifiques).

4.3 Objectifs des changements

Tous les changements dans les répertoires vocaux au cours de la première saison de reproduction ont conduit à une augmentation du partage des chants entre les individus d'un même voisinage. Par conséquent, les mâles de rougequeue noir possèdent un programme d'apprentissage leur permettant de s'adapter à leur environnement social. Ceci correspond aux prédictions de l'hypothèse du partage. Nous avons conclu que le rougequeue noir peut également apprendre après la dispersion, s'il se disperse plus loin que la zone où il a appris son chant pendant l'année d'éclosion. Néanmoins, nous n'avons pas pu mesurer les avantages que les mâles pourraient tirer en modifiant leur chant.

4.4 Où se situe le rougequeue noir sur le continuum de l'apprentissage des chants ?

L'approche longitudinale offre un point de vue exceptionnel sur l'ensemble de la vie des individus. En effet, la plupart des études sur l'apprentissage des chants ne portent que sur les deux ou trois premières années de la vie d'un individu et pas au-delà. Nos résultats nous ont permis d'avoir des précisions sur la capacité d'apprentissage des chants chez le rougequeue noir et sur la durée de cet apprentissage. En raison de la présence i) d'une deuxième phase d'apprentissage au cours de la première saison de reproduction, ii) d'un délai avant les changements de répertoire et iii) d'une flexibilité vocale tout au long de la vie, nous placerions le rougequeue noir après les bruants chanteurs et avant les vachers à têtes brunes dans le continuum d'apprentissage des chants (**Figure 3**). Les mâles de rougequeue noir possèdent une première période d'apprentissage au début de leur vie, entre 80 et 120 jours après l'éclosion. En fonction des stratégies de dispersion suivies, les mâles peuvent connaître une seconde période d'apprentissage au cours de la première saison de reproduction après leur retour de migration. Cette nouvelle période d'apprentissage semble être déclenchée si les mâles ne retournent pas dans le voisinage où ils ont appris leurs chants et se dispersent dans un hameau étranger où leur niveau de partage de chants avec d'autres mâles est faible.

La présence d'une nouvelle période d'apprentissage ou d'une période d'apprentissage prolongée au cours de la première saison de reproduction a été décrite précédemment chez plusieurs espèces. Par exemple, chez le vacher à tête brune, une nouvelle période d'apprentissage se produit au cours de la première saison de reproduction, permettant aux mâles d'apprendre les variantes des chants locaux.

Cette période est essentielle, car l'activité de chant des mâles reproducteurs se termine peu après que les femelles aient cessé de pondre des œufs et, dans certaines populations, la migration a lieu plus tôt. Par conséquent, les oisillons, en particulier ceux qui éclosent tardivement, sont moins exposés aux modèles de chants. Ainsi, ils n'acquièrent pas les variantes de chants locaux partagés ou seulement quelques-uns. Dans notre population, les oisillons de la deuxième couvée pourraient également être moins exposés aux chants locaux et donc être plus susceptibles de présenter des changements de répertoire.

La transition entre les chants cristallisés et les chants modifiés présente un délai et peut être soudaine (suppression sélective et ajout) ou graduelle (modification graduelle) au cours de la première saison de reproduction des mâles. La suppression sélective peut également être graduelle lorsque la fréquence de l'utilisation des strophes est comparée entre les saisons de reproduction successives (données non publiées). Par exemple, entre deux saisons, un mâle peut réduire l'utilisation de certaines strophes jusqu'à cesser totalement de les produire. Grâce à la suppression sélective, les mâles font encore preuve de flexibilité vocale tout au long de leur vie. Le délai de temps observé avant que les mâles ne modifient leur répertoire se rapproche de l'apprentissage retardé observé chez le vacher à tête brune et le rossignol philomèle, mais sur une échelle de temps beaucoup plus courte. Nous avons identifié la capacité des mâles à apprendre du nouveau matériel après la dispersion, au cours de la première saison de reproduction et pas après. Néanmoins, nous ne pouvons pas écarter la possibilité que les mâles soient capables d'apprendre plus tard si les conditions environnementales et sociales diffèrent.

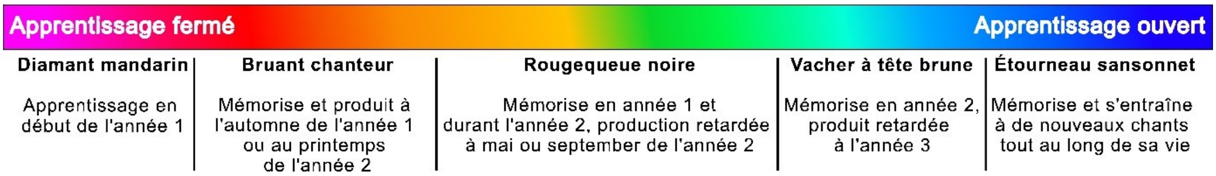

Figure 3. Continuum d'apprentissage des chants adapté de Brenowitz & Beecher (2005) avec le rougequeue noir en comparaison avec les espèces de référence.

4.5 Contrôle de l'environnement social

Plus tôt, nous avons évoqué le fait que la résurgence d'éléments déjà appris et l'apprentissage après la première saison de reproduction ne peuvent pas être écartés. Des expériences en laboratoire devraient être menées pour contrôler les conditions sociales et les expériences auditives des individus. Ceci devrait permettre de détecter la résurgence et d'identifier plus précisément les durées des phases du programme d'apprentissage des chants. Nous pourrions également contrôler l'expérience auditive des jeunes afin de déclencher chez eux des changements de répertoire, ce qui nous permettrait de disposer d'un échantillon plus important que celui recueilli sur le terrain, où les types de changements ne sont pas souvent exprimés.

4.6 Activité de chant sur les aires d’hivernage

Chez le rougequeue noir, la modification graduelle des syllabes prend du temps et peut durer, au moins, de mai à septembre de la première saison de reproduction, avec une période où la production du chant est très variable, connue sous le nom de chant plastique, en septembre. L'ajout de nouveaux éléments ne commence qu'en septembre. Nous ne savons pas si les modifications graduelles ou les ajouts se poursuivent après la migration chez le rougequeue noir. Des études sur les aires d'hivernage sont nécessaires, sachant que le chant hivernal n'a pas encore été décrit chez cette espèce. Il serait intéressant de les étudier dans ce contexte, car il a été constaté précédemment que les mâles de rossignol progné, *Luscinia luscina*, peuvent pratiquer dans les zones d'hivernage et avoir un chant variable durant cette période. Récemment, il a également été rapporté que sur les sites d'hivernage, les mâles de rossignol progné pouvaient être soit des chanteurs territoriaux avec des chants cristallisés, soit des mâles non territoriaux avec des chants plastiques. En plus d'être territoriaux, les mâles aux chants cristallisés étaient tolérants envers les chanteurs avec un chant plastique installés à proximité, par rapport aux autres chanteurs avec un chant cristallisé, qui s'installaient plus loin. Les auteurs suggèrent également que la proximité dont font preuve les chanteurs avec un chant plastique pourrait leur donner l'occasion d'apprendre de nouveaux types de chants auprès des mâles territoriaux.

5. Chapitre 2 : Discrimination des microdialectes étrangers-locaux

Le deuxième chapitre de cette thèse se concentre sur les fonctions des microdialectes chez le rougequeue noir. A l'aide d'une expérience de playback, nous avons testé les capacités de discrimination de l'espèce vis-à-vis des microdialectes locaux et étrangers. Il a été montré que les mâles de rougequeue noir peuvent discriminer entre voisins et étrangers sur la base du chant. Nous avons enregistré le chant de mâles et leurs voisins et évalué le niveau de partage entre eux. Nous avons ensuite testé les mâles (N = 26) en diffusant deux stimuli non familiers du dialecte local et du dialecte étranger. Pendant la diffusion, nous avons mesuré 14 variables associées aux réponses vocales et à l'approche des mâles. Plusieurs facteurs méthodologiques importants ont été pris en compte, notamment la distance du mâle focal par rapport au haut-parleur au début de l'expérience (distance initiale). Nous avons effectué une analyse en composantes principales pour obtenir des variables composites réduites afin de faciliter l'analyse. Trois types de réponses ont émergé : la réponse vocale, l'approche en vol et l'approche au sol. Afin d'identifier les facteurs responsables de la variation des variables de réponse, nous avons effectué une procédure de sélection de modèles.

5.1 Discrimination entre les microdialectes

Nous avons d'abord montré que les mâles de rougequeue noir pouvaient distinguer des chants appartenant à des microdialectes différents. Ils ont montré une réponse agressive plus intense envers le microdialecte local qu'envers le microdialecte étranger, ce qui concorde avec les résultats obtenus chez les espèces ayant des dialectes plus étendus. La réponse plus forte aux stimuli du microdialecte local suggère que les chanteurs locaux peuvent être perçus comme une menace plus élevée, peut-être en raison de leur connaissance et de leur adaptation à l'habitat micro-local, ce qui correspond à l'hypothèse de la « menace relative ». Nos résultats contrastent avec ceux d'une étude antérieure qui a documenté une agressivité moindre envers les microdialectes locaux chez les alouettes des champs par rapport aux microdialectes étrangers. Une possible raison de ce résultat contradictoire pourrait être la familiarité des alouettes des champs avec les chants utilisés pour les stimuli des microdialectes locaux. Cependant, dans notre étude, nous avons méthodiquement éliminé ce biais en utilisant des enregistrements obtenus il y a environ trois à sept ans dans le même hameau que l'oiseau testé ou il y a un à deux ans dans une zone de reproduction séparée située à une distance moyenne de 730 mètres.

En outre, l'effet du traitement sur la réponse territoriale a été mis en évidence uniquement sur le comportement d'approche au sol. Les comportements de cette catégorie sont associés à la dernière étape de la réponse agressive chez le rougequeue noir. La proximité avec la menace potentielle pourrait conduire à un contact et à des blessures lors d'une rencontre réelle. La proximité avec le haut-parleur pourrait refléter la nécessité pour les oiseaux de s'approcher afin d'obtenir plus d'informations sur la menace et d'avoir une discrimination plus fine en passant à une communication à courte portée. Cette stratégie d'approche a été rapportée dans une étude de playback antérieure menée sur des rougequeues noirs, où les oiseaux préféraient signaler et observer d'abord avant de s'approcher du haut-parleur. En effet, un chant partagé peut donner des informations sur l'origine de l'intrus, mais les cris ou les chants feutrés, moyens de communication à courte distance, peuvent contenir des informations telles que l'identité des individus, l'agressivité et la parenté. Comme les rougequeues noirs sont philopatriques, les nouveaux mâles chantant le dialecte local pourraient être la progéniture des détenteurs actuels du territoire. Les mâles territoriaux pourraient avoir un penchant pour les membres de leur famille et utiliser les cris pour les identifier. Malheureusement, notre étude ne nous a pas permis d'obtenir cette information (absence de cris pendant la réponse territoriale). Cependant, des résultats antérieurs de notre équipe ont montré que les rougequeues noirs peuvent discriminer entre les appels de quémande de leur progéniture, ce qui laisse la possibilité que d'autres types de cris chez cette espèce peuvent renseigner sur l’identité et la motivation des individus. Nous avons également observé que la distance initiale a influé sur les comportements d'approche au sol (l’oiseau se pose à moins de cinq mètres du haut-parleur). Cela plaide en faveur d'une discrimination fine entre les microdialectes et de l'ajustement de la dernière étape de la réponse agonistique en conséquence.

5.2 Escalade de l'agressivité

Nous avons mis en lumière l'importance de la distance initiale sur la réponse territoriale des mâles. Cette variable a rarement été prise en compte dans les études de playback précédentes. En effet, ce facteur a affecté les trois variables de la réponse comportementale. Ce résultat soutient l'idée d'une escalade de la réponse agressive, car les mâles ont montré des réponses nuancées aux menaces perçues en fonction de la distance qui les en sépare. Lorsque les oiseaux sont initialement éloignés du haut-parleur, ils sont plus susceptibles de vocaliser, probablement pour signaler leur présence à leurs congénères sur de longues distances et leur propriété sur le territoire. Ceci est en accord avec l’idée que les vocalisations sont utilisées comme une étape initiale dans la défense territoriale, et sont surtout efficaces pour la communication à longue distance. Lorsque les oiseaux sont initialement plus proches du haut-parleur, ils sont plus susceptibles de s'en approcher et de passer plus de temps à proximité. Ce comportement est associé à la surveillance du territoire pour localiser l'intrus. Ceci indique que plus la menace perçue est proche, plus le niveau d'agression augmente, les approches au sol étant la réponse la plus importante. Ces étapes impliquent des risques et des coûts différents pour les individus. Dans l'ensemble, l'effet de la distance initiale interagit avec chaque étape de l'escalade de l'agression, influençant les décisions stratégiques des mâles rougequeues noirs en réponse aux stimuli de playback. Cela souligne l'importance de prendre en compte les dynamiques spatiales et les distances perçues avec la menace pour comprendre les comportements territoriaux et l'escalade de l'agression dans les populations aviaires.

5.3 Variabilité interindividuelle

Nous avons mis en lumière les capacités de discrimination du rougequeue noir et l'importance de prendre en compte la distance initiale des mâles au début de l'expérience par rapport au haut-parleur car elle a des conséquences sur la stratégie de défense choisie par les mâles. La variabilité interindividuelle a été cependant responsable de la plupart des variations dans les réponses comportementales. Cette variabilité pourrait dépendre de facteurs tels que la personnalité, les interactions sociales avant l'écoute ou la taille du territoire. Nous avons enregistré d'autres variables, y compris le stade de reproduction et le statut d'appariement, mais pour quelques mâles, ces informations n’ont pas pu être documentées. Nous aurions besoin d'un échantillon plus important pour inclure ces paramètres dans la procédure de sélection du modèle statistique.

5.4 Augmenter la taille d’échantillon

La pandémie du coronavirus en 2019, a eu un impact sur l'enquête de terrain et nous a restreint dans l'acquisition des données à la fois sur le relevé longitudinal et sur l'expérience de playback. En effet, nous n'avons pas pu réaliser les playbacks au printemps 2020 car deux observateurs étaient nécessaires. L'acquisition des données était plus difficile car elle dépendait d'un seul chercheur (T.V.). L'opération de baguage des mâles reproducteurs de première année a été retardée jusqu'en septembre 2020, ce qui a réduit le nombre de captures et de baguages. De plus, un paramètre naturel a également affecté notre collecte de données. Les conditions météorologiques peuvent avoir un impact considérable sur le succès de la reproduction des couples reproducteurs. En 2021, les oiseaux ont connu de mauvaises conditions météorologiques (par ex. température basse, vent et pluie) qui ont probablement réduit la survie de leur couvée. Par conséquent, en 2022, le nombre de reproducteurs de première année était relativement faible dans la zone d’étude. Ce faible nombre de jeunes mâles a eu un impact sur la collecte des données lors de l'expérience de playback. En effet, nous n'avons pu tester aucun mâle reproducteur de première année au cours de cette saison. Les conditions de terrain sont imprévisibles et sont responsables de certaines limitations. Dans notre cas, la taille de l'échantillon a été plus faible que prévu. Avec plus de temps et de ressources, des expériences de playback pourraient être menées pour augmenter la taille de l'échantillon des reproducteurs de première année et des oiseaux plus âgés afin d'étudier l'effet de la classe d'âge et d'autres facteurs d'intérêt sur les réponses comportementales. Il a été démontré précédemment que l'âge des mâles affectait les réponses comportementales territoriales dans plusieurs populations de rougequeues noirs : les mâles reproducteurs de première année avaient tendance à avoir une réponse vocale plus forte que les oiseaux plus âgés qui avaient tendance à diriger plus d'agressivité vers l'intrus expérimental ("leurre"). Si nous poursuivons les expériences de playback, l’utilisation de stimuli de synthèse pourrait permettre de mieux comprendre les paramètres acoustiques sur lesquels les mâles se basent pour distinguer les dialectes locaux des dialectes étrangers.

5.5 Variabilité de la similarité des stimuli

Lors de la procédure de sélection de modèles nous avons montré que la mesure binaire du type de traitement et la mesure graduelle, par le biais du score de similarité, donnent des résultats similaires. Nous faisons l'hypothèse que la similarité entre le chant utilisé comme stimulus et le chant des mâles focaux est importante pour les oiseaux. Les résultats précédents ont montré que les chants du passé récent étaient moins similaires que les chants des voisins directs des oiseaux focaux. Par conséquent, il est possible que l'évolution culturelle du chant sur sept ans pourrait réduire l'efficacité de nos stimuli, comme l'ont montré certaines études qui ont également utilisé des stimuli enregistrés plusieurs années, voire dizaines d’années sur la zone d’étude. Par exemple, les bruants à couronne blanche ont réagi plus agressivement aux chants similaires du dialecte actuel qu'aux chants historiques enregistrés dans la même zone géographique il y a 25 ans. En outre, les chants historiques ont déclenché une réponse agressive équivalente à celle des chants d'un dialecte étranger actuel. Une solution potentielle pour éviter ces biais serait d'exposer les mâles à des signaux synthétisés. Une autre possibilité serait de diffuser le propre chant de l'oiseau. Cependant, cette dernière méthode est encore controversée et doit être utilisée avec prudence.

5.6 Diminution de la production vocale

Nous avons également observé une réduction de la production vocale pendant le playback, ce qui nous a empêchés d'examiner plus en détail la réponse vocale des mâles. Chez plusieurs espèces, la concordance des chants (utilisation de chants correspondant aux stimuli) reflète l'intention agressive des mâles. En outre, la synchronisation des chants (alternance ou chevauchement avec les stimuli) pendant un conflit territorial peut également révéler l'intention des mâles à l'égard d'un intrus. Les rossignols communs émettent des chants nocturnes pour défendre leur territoire. La défense territoriale pendant la nuit repose fortement sur le chant par rapport à la défense diurne. Chez cette espèce, la synchronisation des chants a été étudiée avec succès dans le contexte de la nuit. De plus, des playbacks simulant différents niveaux d'intention agressive par le biais de la synchronisation des chants ont conduit à des réponses territoriales différentes pendant la journée. Les études futures sur les propriétés du contre-chant chez le rougequeue noir devraient donc avoir lieu dans le contexte des chorus de l'aube, lorsque la production de chant est plus importante et que les mâles sont plus susceptibles de se fier au chant.

Les résultats de cette étude sont importants car, à notre connaissance, il s'agit seulement de la deuxième étude sur les dialectes locaux et étrangers chez une espèce à microdialectes à ce jour. Elle fournit de nouvelles informations, mais des recherches supplémentaires sont nécessaires pour comprendre les fonctions des microdialectes.

6. Quels sont les avantages du partage vocal ?

La première étude de cette thèse a mis en évidence la motivation des mâles à partager certains chants de leur répertoire avec leurs voisins. Lors de la dispersion, ils ciblent des hameaux où ils partagent des chants avec d'autres mâles. Lorsqu'ils ne parviennent pas à s'installer dans un hameau présentant de telles conditions, les rougequeues noirs font preuve d'une large panoplie de moyens pour changer de répertoire. Ceci leur permet d'apprendre le dialecte local au cours de la première saison de reproduction. Néanmoins, au cours de la deuxième étude, nous avons révélé que les mâles réagissent plus agressivement au chant d'un mâle reproducteur de première année issu du dialecte local plutôt qu'au chant d'un reproducteur avec un dialecte étranger. De plus, des travaux antérieurs sur la population ont montré que les mâles établissent des relations de voisinage. Les mâles étaient moins agressifs envers les chants familiers partagés de leur voisin qu'envers les chants non partagés d'un individu étranger. Ceci démontre la mise en place de l'effet du "cher ennemi" après que la relation ait eu le temps de se construire entre les mâles. Plusieurs hypothèses, « l'hypothèse du partage » et « l'hypothèse de l'adaptation sociale », suggèrent la présence d'avantages associés au partage des chants peu de temps après l'arrivée. Par exemple, chez plusieurs espèces d'oscines, il a été démontré que le partage du dialecte local profite aux mâles nouvellement installés en améliorant l'acquisition de territoires, les relations de voisinage, les possibilités d'accouplement ou le succès de la reproduction. Nous émettons donc l'hypothèse que le partage des chants pourrait apporter des avantages sociaux et des bénéfices en termes de succès reproducteur dès la première saison de reproduction, mais aussi plus tard. Malheureusement, au cours de ma thèse, nous n'avons pas pu démontrer les avantages à court terme pendant la première saison de reproduction ou les avantages à long terme plus tard dans la vie. Afin de décrire ces avantages des études supplémentaires seront nécessaires.

7. Conclusion

Les résultats des travaux de cette thèse mettent en lumière les processus d'apprentissage du chant et de dispersion qui mènent à l'établissement des microdialectes dans une population de rougequeue noirs. Nous avons identifié les modes d'apprentissage du chant utilisées par les mâles pour s'adapter à leur environnement social. Nous avons également déterminé les délais de mise en place de ces différents modes d'apprentissage. À la suite d'une expérience de playback simulant une interaction territoriale, nous avons observé que les mâles étaient plus agressifs lors de la diffusion du dialecte local plutôt que lors de la diffusion d'un dialecte étranger. Ceci nous permet de conclure que les microdialectes sont la base de la discrimination entre mâles chez cette espèce. Grâce à cette même expérience nous avons identifié l'importance de la distance initiale (i.e. la distance à laquelle l'oiseau testé se trouve par rapport à l'enceinte au début de l'expérience) dans la réponse comportementale et dans l'escalade de l'agressivité. Néanmoins les coûts et bénéfices rattachés au partage vocal et les paramètres acoustiques à la base de cette discrimination chez cette espèce restent à explorer. Les découvertes issues de ce travail de thèse portant sur les processus impliqués dans la mise en place et la discrimination des microdialectes, pourraient plus tard contribuer à donner une base de compréhension pour le comportement et l'écologie des espèces à microdialectes en danger, facilitant ainsi leur réintroduction. Enfin, cette recherche contribuera à alimenter les connaissances obtenues en milieu naturel qui visent à explorer les origines et l'évolution de la communication vocale chez les divers taxa d'animaux et peut-être plus largement à l'évolution du langage humain.

Appendix 2: Curriculum vitae

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EDUCATION

2024- PhD in Neurosciences - Laboratoire Ethologie Cognition Développement (LECD) - Université Paris Nanterre, France.

- PhD-title: Ontogeny and functions of vocal sharing in a songbird, the black redstart (*Phoenicurus ochruros*).

2019- Master of Sciences Ethology Ecology, *magna cum laude* - Université Lyon-Saint-Etienne Jean Monnet, France.

2018- Master of Sciences M.Sc. Evolutionary and Behavioural Ecology with Merit - University of Exeter, Great Britain.

2017- Bachelor of Science B.Sc. (Hons.) Animal Behaviour 1st class - Liverpool John Moores University, Great Britain.

TEACHING EXPERIENCES

2019-2021- Université Paris Nanterre, Département de Psychologie, France.

2019- Teaching Assistant in Psychobiology practical sessions (64 hours).

2021- Teaching Assistant in Biology (36 hours).

FIELD WORK EXPERIENCES

2021- August - Bird Ringing Camp, Station de baguage du Massereau, France.

2020- August - Bird Ringing Camp, Pôle Nature du Port de Vitrezay, France.

2019- January-June - Laboratoire Ethologie Cognition Développement (LECD), Université Paris Nanterre, France.

- Research project: Age-related changes in the song of the black redstart (*Phoenicurus ochruros).*

2018- March-April - Tamar otter wildlife centre / Newquay Zoo, Great Britain.

- Research project: Call function in Asian small-clawed otters (*Aonyx cinereus*).

FIELD WORK EXPERIENCES

2018- January - Kenya Field Course, Kenya.

- Research project: Mutualism between acacia (*Acacia drepanolobium*) and ants (*Crematogaster* sp.).

2016- June–August - Ugalla Primate Project, Researcher in Issa valley, Tanzania.

- Research project: Call types and uses in Red-tailed monkey (*Cercopithecus ascanius*).

PUBLICATIONS

Volle, T., Derégnaucourt, S., Chambon, R., & Draganoiu, T.-I. (2024). Foreign–local microdialect discrimination in a songbird, the black redstart. *Animal Behaviour*, *210*, 113–125. https://doi.org/10.1016/j.anbehav.2024.01.020.

Volle, T., Derégnaucourt, S., & Draganoiu, T.-I. (2024). *Lifetime evolution of vocal repertoires in a songbird, the black redstart: A longitudinal field approach* [Unpublished manuscript].

ORAL PRESENTATIONS

Volle,T. (2024). Ontogenesis and functions of vocal sharing in a songbird, the black redstart, *Phoenicurus ochruros*. In *5th seminar meeting European Bird Song Network, online.*

Volle, T., Derégnaucourt, S., Chambon, R., & Draganoiu, T.-I. (2023). Male black redstarts, *Phoenicurus ochruros*, react more aggressively to songs of local versus foreign micro-dialects. In *Behaviour, Bielefeld (Germany).*

Volle, T., Derégnaucourt, S., & Draganoiu, T.-I. (2023). Song learning in the black redstart, *Phoenicurus ochruros*, a longitudinal field study. In *Emerging bioacousticians days. Listening to nature, Unieux (France)*.

Volle, T., Derégnaucourt, S., Chambon, R., & Draganoiu, T.-I. (2023). Discrimination entre les chants du micro-dialecte local et les chants étrangers chez un oiseau chanteur, le rougequeue noir, *Phoenicurus ochruros*. In *52ème Colloque de la Société Française pour l'Etude du Comportement Animal, Tours (France)*.

Volle, T., Derégnaucourt, S., & Draganoiu, T.-I. (2022). Learning to sing like your neighbours: a long-term field study in the black redstart *Phoenicurus ochruros*. In *European Conference on Behavioural Biology: All of life is social, Gronigen (Netherlands).*

ORAL PRESENTATIONS

Volle,T., Piel, A., & Stewart, F. (2017). Red-tail repertoires: Establishing call types and uses in a savanna-dwelling forest guenon (*Cercopithecus ascanius*) in the Issa valley, Tanzania. In *Primate Society of Great Britain (PSGB), Spring Meeting, Manchester (Great Britain).*

Volle, T., Piel, A., & Stewart, F. (2017). Red-tail repertoires: Establishing call types and uses in a savanna-dwelling forest guenon (*Cercopithecus ascanius*) in the Issa valley, Tanzania. In *Association for the Study of Animal Behaviour (ASAB), Easter Meeting, Liverpool (Great Britain).*

GRANTS

2023- 150€ SFECA, Société Française pour l'Etude du Comportement Animal: Conference attendance grant.

2016- 1613£ ASAB, the Association for the Study of Animal Behaviour: Undergraduate Project Scholarships.

1438£ LJMU (Liverpool John Moores University), The Go Global Fund.

AWARD

2023- Prix Castor for the best student oral presentation.

2019- Second place "Outstanding Poster Award" at the 27th International Bioacoustics Congress (IBAC) in Brighton, Great Britain.

CERTIFICATIONS

2021- Specialist bird capture permit (*Phoenicurus ochruros*), Centre de Recherches sur la Biologie des Populations d'Oiseaux (CRBPO), France.

2019- The Bioacoustics Winter School (BWS), certification in bioacoustics, University of Lyon/SaintEtienne, France.

2019- TOEIC 990- **English level C1 (advanced).**

2018- Advanced Open Water Diver, PADI (Professional Association of Diving Instructors), Great Britain.

2018- «Marine Mammal Medic», the British Divers Marine Life Rescue, Great Britain.

2017- Advanced First Aid, Great Britain.

SKILLS

Languages: French, native language.

English, fluent (writing, speaking, reading).

Softwares: SPSS, R (statistics), Avisoft SAS-LabPro, Raven Pro, Audacity, PRAAT (sound analysis), GIS (geographic information system), BORIS (video analysis), LATEX, Microsoft Office, Inkscape.

Methods: European bird ringing, trapping and identification, sound recording, playback experiment implementation, travel and budget planning.

Strengths: Perseverant, autonomous, team player, open-minded, can work in extreme field conditions.

STUDENT SUPERVISION

2021- 2 months internship - Nicolas Coron, master student.

Research project: Territorial responses to geographical variations of songs in a passerine bird, the black redstart.

2022- 2 months internship - Léa Brun, master student.

Research project: Territorial responses to geographical variations of songs in a passerine bird, the black redstart.

OTHERS/RESPONSABILITIES

2022- Volunteer in the organising committee of the 5th International Student Course in Behavioural Biology (Institut Francilien d'Ethologie (IFE) at Université Paris Nanterre.

2021-2022- Organisation of the weekly “journal club” within the laboratory.

2020-2022- Representative of PhD students.

2019- Volunteer on the organising committee for the 27th International Bioacoustics Congress (IBAC) in Brighton, Great Britain.

RESEARCH KEYWORDS

birdsong; black redstart; *Phoenicurus ochruros*; longitudinal field study; microdialect; selective attrition*;* song learning; song sharing, sound similarity; vocal repertoire; dialect discrimination; playback; relative threat hypothesis; territorial defence; vocal communication.

ABSTRACTS

Abstract

Apart from humans only a few animals share the skill of vocal production learning and also possess vocal dialects. Oscines' song has been a model of choice in both the study of proximal aspects (vocal learning abilities, due to the parallels drawn with humans' language acquisition's process) and ultimate aspects (sexual selection, cultural evolution) of behaviour. The purpose of this thesis was to identify the processes leading to the establishment of dialects and their functions during social interactions in a population of black restarts (*Phoenicurus ochruros*) characterised by the presence of microdialects (covering distances under 2 km). A longitudinal field survey of males from one population, studied for over 20 years, allowed us to infer that microdialects establishment is dependent on the dispersal patterns of the first-year breeders. They can learn until the year after dispersal and keep some vocal flexibility later in life. In addition, three types of vocal changes during ontogeny (selective attrition, addition and gradual modification) were described for the first time in this species. Microdialects could play a role during territorial interactions and provide socio-sexual advantages. In a previous experiment, it was observed that male black redstarts could discriminate between a neighbour's song and a foreigner's song. We measured the behavioural reaction of birds during the broadcast of two unfamiliar stimuli: the local dialect and a foreign dialect. Males showed a stronger aggressive response to the local dialect compared to the foreign dialect. They also followed an escalation chain of aggression as the distance to the speaker at the start of the experiment influenced the territorial response. This thesis provides important information on the process leading to the establishment of dialects in the black redstart using a longitudinal field approach. It also shed light on the functions of microdialects which are still poorly studied to date.

Keywords: microdialect discrimination; microdialect establishment; *Phoenicurus ochruros*; song learning; territorial defence; vocal communication

Résumé

L'apprentissage vocal, qui est une composante importante du langage humain, est relativement rare dans le règne animal. Chez certaines espèces, cette capacité peut favoriser l'émergence de variations géographiques appelées dialectes. Le chant des oscines est un modèle privilégié pour l'étude des aspects proximaux (mécanismes neurobiologiques d'apprentissage en raison des parallèles établis avec le processus d'acquisition du langage chez l'humain) et ultimes (sélection sexuelle, évolution culturelle) du comportement. L'objectif de cette thèse était d'identifier les processus menant à l'établissement de dialectes et leurs fonctions au cours des interactions sociales dans une population de rougequeues noirs (*Phoenicurus ochruros*) étudiée depuis plus de 20 ans. Cette population présente des microdialectes (couvrant une distance inférieure à 2 km). Une étude longitudinale nous a permis de mettre en exergue l'importance du schéma de dispersion des mâles pendant leur première saison de reproduction sur le maintien et la mise en place des microdialectes. Ils peuvent apprendre jusqu'à l'année qui suit la dispersion et conserver une certaine flexibilité vocale plus tard au cours de leur vie. Trois types de transformations vocales (la suppression sélective, l'ajout et la modification graduelle de syllabes de chant) sont décrites pour la première fois chez cette espèce. L'existence de microdialectes pourrait permettre de réguler les interactions socio-sexuelles au sein d'une population. Au cours d'une expérience précédente, il avait été montré que les mâles discriminent les chants produits par un voisin de ceux produits par un étranger. Nous avons mesuré la réponse comportementale de mâles lors de la diffusion de deux types de stimuli non-familiers : des chants du microdialecte local et des chants étrangers. Les mâles ont montré une réponse agressive plus intense au microdialecte local qu'au microdialecte étranger. Ils ont également montré une escalade de l'agression au cours de l'expérience : la distance par rapport au haut-parleur au début de l'expérience a influencé la réponse territoriale. Les résultats de cette thèse fournissent des informations importantes sur le processus menant à la mise en place des microdialectes chez le rougequeue noir. De plus, ils mettent en lumière les fonctions des microdialectes, encore peu étudiées à ce jour.

Mots-clés : discrimination des microdialectes ; établissement des microdialectes ; *Phoenicurus ochruros* ; apprentissage des chants ; défense territoriale ; communication vocale