

**Charles University, Faculty of Science, Department of Ecology**

**Study programme: Ecology**



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**How the Yellowhammer became a Kiwi: stories hatched at the field margins of bioacoustics and invasion ecology**

Jak se ze strnada obecného stal Kiwi: příběhy zrozené na  
pomezí bioakustiky a ekologie invazí

**Ph.D. Thesis**

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**Prague, 2017**

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

In Prague, 24 April 2017

Pavel Pipek

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## Preface

## Preface

The story of how this thesis came to light is also a story about how our lives or professional careers can be shaped by luck. If it were not for several lucky coincidences, I would have been doing something completely different, if science at all. I have always been interested in too many things, thus deciding one subject for entire life seemed like a nightmare to me. Strangely enough, somehow most of my interests have met in the end.

When applying for university I hoped that I would pass only some application exams and thus everything would sort out without me having to make the decision. However, all my applications were successful, thus I had to decide anyway. And I chose biology, as the chances that I will pass the exams again were the least probable. Furthermore, my interest in nature, which had been put at bay by a burnt-out high school teacher, was reignited by a charismatic guide, a botanist, whom we had in our family trip to Mongolia a year back.

I graduated at the Department of Zoology, where I studied antipredatory behaviour of true bugs with blue and great tits and humans as model predators (well, the human participants were not hunting true bugs in a true sense – I designed a simple computer game in which I tested their detection capabilities). The topic was interesting and my supervisor, Alice Exnerová, was great to work with, however I did not feel that my contribution to the society was big enough, thus I have not continued on PhD straight away. Instead I took a year off and got involved in environmental education and web design. Next spring, I got a toughest fever of my life, during which I had more than enough time to think about my life. There was no escape, I had to face the thoughts. And I saw clearly that what I am doing is short-sighted. I missed the intellectual enriching atmosphere of university, I did not feel that I had reached the point when I could spread the knowledge, I wanted to know more, to grow yet.

I have started my PhD study without clear idea about my future research pathway – I had only three certainties: I wanted to do something that even general public could appreciate, I wanted to do it at the department of ecology, and I did not want to affect lives of any animals, least to kill them. Thanks to Adam Petrusk, Vojtěch Jarošík and Petr Pyšek, I have chosen invasion biology and I do not regret, although the original project has changed since then.

It is often the case that only being naïve allows thinking out of the box. Before I became swallowed completely by paradigm of biological invasions, I was pulled back to surface by another research field, bioacoustics, and was cheeky enough to endeavour to combine these two research fields together. I am well aware that by chasing too many rabbits you risk not catching one. I do hope though that the presented study is a good prey and that I have managed to get deep enough in both fields.

The bioacoustics originally served only as a methodological approach to explore the second field of interest, invasion biology. However, I became involved in the bioacoustics research on its own and this became integral part of this thesis too. Even the importance of yellowhammer historical study was unexpected beforehand. However, by integrating different primary sources, our yellowhammer paper become a pivotal study showing that history of avian invasions can be reconstructed in much greater detail. And it also cast me on new research pathway.

I always wanted to do history, to do biology and to be able to take advantage of programming (in my case especially web design, using PHP and SQL programming). And I am doing all. Why? Because I am more than lucky. Principally, I have met the right sort of people.

## Acknowledgements

This work would never come to light without a range of people.

Obviously, without my parents, I would never come to light either. I am not only grateful to them (though I express it less than I should) for their everlasting support, but also for letting me to find my own way, even though it is sometimes painful.

Adam Petrusk, however occupied he mostly is, did not hesitate to spend some of his time to help me to discuss my future when I was at a loss. During our conversation, he came up with an idea that I should switch my attention to invasion biology and contact Vojtěch Jarošík and Petr Pyšek. And that was a turning point in my career.

I am especially grateful to Vojta Jarošík (sadly, deceased in 2013), who first said “No”, when I came to his office yet undecided, but took me under his wings later on, when I made up my mind. He also let me to find my way and later even allowed me to switch the subject of my research completely, when new fascinating topic emerged.

Petr Pyšek, who was first my consultant and later “inherited” me from Vojta, supported me fully, in whatever idea I had. Although he is one of the most influential scientists, he always treated me with respect and trust.

Hanka infected me with her contagious enthusiasm when the doubts about my life pathway had come back and I was on the brink of quitting my PhD. Thanks to her I overcame this little crisis and continued.

Had Lucka Diblíková (Lu) not invited me to join the team working on Dialects of Czech Yellowhammers project and to help them with setting up the website, I would follow a different research path. It was in this creative spirit we had in the early days of the Czech project, when everything seemed possible, that I was bold enough to propose a childish idea of comparing two foreign

(and in the case of New Zealand very remote) countries.

Tereza Petrusková was always helpful whenever I needed advice, which was very important given that I started my PhD with only limited knowledge about birdsongs.

I thank Lenka Krejčíříková, the secretary of our department, who was my guardian angel during whole study and greatly compensated for my perpetual distractedness.

Without friends, I would have much less wrinkles around eyes and much more on the forehead. Moreover, I would have gone mad by now probably. I hope that the rest of my friends will not feel offended, but I would like to thank preferentially Tomáš and Anička at whose flat I felt like at home and was always welcome when I had dark thoughts (but do not be afraid, I do not plan to move in).

I thank Bára for her eternal patience with my moodiness. As the deadline approached, I was more and more nervous, but she stayed calm and supportive.

## **Abstract**

The presented thesis exploits the introduction of the yellowhammer (*Emberiza citrinella*) to New Zealand to study the cultural evolution of birdsong dialects in exotic populations after 140 years of complete isolation from the original source populations in Great Britain. The data are interpreted with detailed knowledge of yellowhammer past in New Zealand and of the global (Europe) and regional (Czech Republic) distribution of yellowhammer dialects.

Yellowhammer song is simple and males have very limited repertoire. Since the 19th century it is known that despite its simplicity the song exhibits fascinating geographical variation; the males share the terminal notes to create mosaic-like distribution of dialects. Although this phenomenon has been known for decades and thoroughly studied, many questions remain. One of them is a suspected border between “western” and “eastern” groups of dialects. By combining information about the dialect distributions obtained from works of previous researchers with recordings from online repositories and archives we demonstrate that these groups do not create macrogeographical patterns (Chapter 6).

The citizen-science project “Dialects of the Czech Yellowhammers” involved Czech citizens in mapping the distribution of yellowhammer dialects in the Czech territory. The resulting dataset of more than 4000 recordings, unique both in terms of geographical extent and fine level of detail, made it possible to test various hypotheses about dialect origin and maintenance. This dataset also allowed us to test the relevance of several dialects which were suspected to be part of the continuum. In total, we have identified six previously reported dialects distributed in typical mosaic-like distribution, few males alternating between two dialect types and few singing rare dialects (Chapter 7).

Good knowledge of dialect distribution in Europe and Czech Republic, and gained experience from Czech citizen-science project motivated us to extend the research abroad and explore the evolution of yellowhammer dialects after introduction to a distant island country. The recordings provided by British and New Zealand citizens were combined with recordings from online repositories, archives and our own field recordings (Chapter 9).

To interpret the observed dialect patterns correctly, a detailed historical information about the invasion of yellowhammer to New Zealand was needed. For that we analysed the original documents of New Zealand acclimatisation societies and archives of old newspaper articles. Between 1864 and 1879, 25 ships with yellowhammer on board departed from London to several New Zealand harbours. The species quickly established and spread all over the country. (Chapter 8)

Although we expected lower dialect diversity in the invaded range due to

initial bottleneck effect associated with low numbers of transported individuals, the opposite was true; New Zealand harboured almost twice as many dialects as Great Britain. The “additional” dialects likely did not originate in New Zealand, as these can be found in various localities in continental Europe, including Czech Republic. Instead they probably only persisted since the 19th century, whereas the same dialects disappeared from Great Britain due to recent rapid population decline (Chapter 9).

## Abstrakt (in Czech)

Strnad obecný (*Emberiza citrinella*) byl v minulosti vysazen na Nový Zéland, což nám umožnilo prozkoumat kulturní evoluci jeho dialektů v exotické populaci, která byla posledních 140 let zcela odříznuta od původní domoviny, Velké Británie. K interpretaci získaných dat jsme využili podrobné znalosti jak o historii strnadvánu na Zélandu, tak a o globálním i regionálním rozšíření strnadích dialektů, v Evropě a České republice.

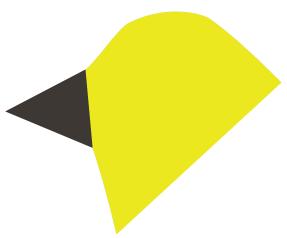
Strnadí zpěv je velmi jednoduchý, samci mají navíc velmi omezený repertoár. Již od 19. století je však známo, že ač zpěv není složitý, vykazuje značnou geografickou variabilitu. Samci spolu sdílejí koncové slabiky, a vytvářejí tak mozaikovité rozšíření dialektů. Přestože se o tomto jevu ví již desítky let a byl intenzivně zkoumán, mnoho otázek zůstalo nezodpovězeno. Jednou z nich byla poloha makrogeografické hranice mezi předpokládanou „západní“ a „východní“ skupinou dialektů. Když jsme propojili informace o rozšíření strnadích dialektů z předchozích studií s nahrávkami nalezenými v online úložištích a archivech, výsledná mapa odhalila, že tyto skupiny makrogeografické rozšíření nemají (Kapitola 6).

Projekt občanské vědy „Nářečí českých strnadvánu“ zapojil veřejnost do mapování strnadích nářečí na českém území. Výsledný soubor téměř 4000 nahrávek, který je jedinečný jak plochou, kterou pokrývá, tak podrobností, umožňuje testovat hypotézy o vzniku i udržování dialektů. Díky tomuto souboru jsme rovněž mohli ověřit, zda má smysl rozlišovat některé dialekty, u kterých bylo podezření, že by mohly tvořit kontinuum. Celkem jsme zaznamenali šest již dříve popsaných dialektů, které měly typické mozaikovité rozšíření, několik samců kombinujících více dialektů a několik zpívajících vzácným dialektem (Kapitola 7).

Vyzbrojeni znalostmi o rozšíření strnadích nářečí v Evropě, a detailněji v České republice, a zkušenostmi z úspěšného projektu občanské vědy, rozhodli jsme se rozšířit náš výzkum do zahraničí a prozkoumat evoluci strnadích dialektů po vysazení na vzdálený ostrov. Nahrávky zaslány dobrovolníky z Velké Británie a Nového Zélandu doplnily opět nahrávky z online úložišť a archivů a nahrávky, které jsme sami pořídili v terénu (Kapitola 9).

Abychom mohli správně interpretovat data o rozšíření strnadích dialektů v původním i exotickém areálu, potřebovali jsme podrobné informace o průběhu strnadí invaze na Novém Zélandu. Ty jsme získali z původních dokumentů novozélandských aklimatizačních společností a novinového archivu. Mezi lety 1864 a 1879 se z Londýna vypravilo 25 lodí se strnady na palubě, aby zakotvilo v některém z novozélandských přístavů. Strnadi rychle zdomácněli a rozšířili se po celém území (Kapitola 8).

Jelikož byl na Zéland převezen jen zlomek britské populace strnadů, očekávali jsme, že v exotickém areálu nalezneme méně dialektů. Opak byl ale pravdou. Na Zélandu je ke slyšení téměř dvojnásobné množství nářečí, co v Británii. Nářečí, která má Zéland „k dobru“, ovšem nejspíše nevznikla na jeho území, protože se s nimi můžeme setkat po celé Evropě, včetně České republiky. Spiše tam byla již od 19. století a zachovala se, zatímco v původní domovině vymizela při prudkém populačním poklesu (Kapitola 9).



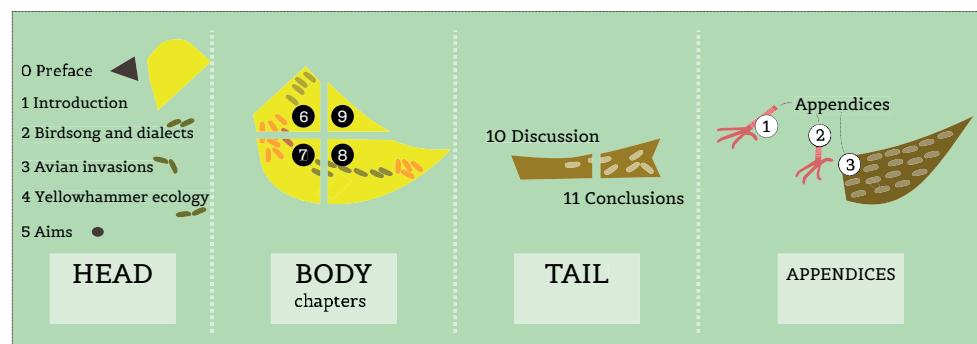
## **1 Introduction**

# 1 Introduction

As the title suggests, this work combines two scientific fields, invasion biology and bioacoustics, using a typical avian inhabitant of field margins, the yellowhammer (*Emberiza citrinella*), as a model species. The thesis exploits the introduction of the yellowhammer to New Zealand, to study the cultural evolution of birdsong dialects in exotic populations after 140 years of complete isolation from the original source populations in Great Britain (Chapter 9). The results can be interpreted in the light of knowledge about distribution of yellowhammer dialects in Europe (Chapter 6), and in even more detail, in the Czech Republic (Chapter 7), and of the invasion history of yellowhammers to New Zealand (Chapter 8).

The structure of this thesis is as follows (Figure 1): The thesis has 3 main parts). HEAD contains Preface and this Introduction, which is followed by three chapters, which give theoretical background to articles and manuscripts which are included as chapters. Chapter 2, Birdsong and dialects, traces the roots of dialects and summarises what is known about the processes responsible for their maintenance. Chapter 3, Avian invasions, briefly introduces the field of avian invasions with special emphasis on the role of propagule pressure in establishment success and acclimatisation in New Zealand. Finally, Chapter 4, Yellowhammer ecology, gives more information about biology and ecology of yellowhammer, which were not covered in research articles, but might be relevant in dialects research. The head is finished by Aims.

The BODY of this thesis is composed of four chapters (Chapter 6, Chapter 7, Chapter 8, Chapter 9), which are TAILED by Discussion and the thesis concludes with Conclusions and future research pathways. At the very end of this thesis, I APPEND articles which stem from the research presented in this work, however are not part of the main story (Appendix 1 and Appendix 2) and Table



**Figure 1:** The thesis has three main parts: HEAD (1) including Introduction, three chapters that give theoretical background to four chapters that create the main BODY (2) of the thesis. TAIL (3) includes Discussion and Conclusions and future research pathways. The thesis has also several APPENDICES.

1 in Appendix 3 which contain references to studies on dialects that I collected during writing this thesis (but not all of them were available to me).

Yellowhammer song would not be much interesting, it is simple and males have very small repertoire of one to four song types (Hansen 1999). The song can be heard from early spring to later summer (Hiett and Catchpole 1982), all day long. Since 19th century (Oppel 1869, Röse 1869) it is known that albeit simple the song exhibits fascinating geographical variation; the males share the terminal notes to create mosaic-like distribution of dialects (Hansen 1985).

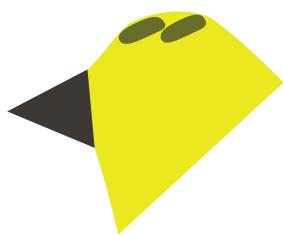
Dialects have been studied on many species (see Table 1 in Appendix 3). Although in the case of yellowhammer this phenomenon has been known for decades (Huxley 1947, Kaiser 1965, Hansen 1985) and thoroughly studied (Baker et al. 1987a, Frauendorf 2005, Caro et al. 2009, Wonke and Wallschläger 2009), many questions remain. One of them is an existence of suspected border between “western” and “eastern” groups of dialects (Cramp and Perrins 1994). By collating information about dialect distribution from works of previous researchers with recordings from online repositories and archives we demonstrate that yellowhammer dialects do not create such macrogeographical patterns (Chapter 6).

The citizen-science project “Dialects of the Czech Yellowhammers” involved Czech citizens in mapping the distribution of yellowhammer dialects in the Czech territory. The resulting dataset of more than 4000 recordings, unique both in terms of geographical extent and fine level of detail, made it possible to test various hypotheses about dialect origin and maintenance (reviewed in Slabekoorn and Smith 2002, Podos and Warren 2007, Catchpole and Slater 2008). This dataset also allowed us to test the relevance of several dialects which were suspected (Frauendorf 2005) to be part of the continuum. We have identified six previously reported dialects, that were distributed in mosaic-like fashion, several mixed singers and few birds singing rare dialects (Chapter 7).

Having good knowledge about both global and local distribution of yellowhammer dialects, and valuable experience from citizen-science project, we extended the research abroad to explore the evolution of yellowhammer dialects after introduction to distant island country. For that, new website was created (<http://yellowhammers.net>). The recordings provided by British and New Zealand citizens were collated with recordings from online repositories, archives and recordings made by us in the field. Contrary to our expectations we found greater dialect diversity in exotic than in native source range (Chapter 9). The website of the international project was later adapted to be able to host sister projects from other countries, i. e. Poland and Switzerland. The data from Swiss project were already published in journal of Swiss Ornithological Society, *Ornithologische Beobachter* (Appendix 2).

To interpret the dialect patterns in native and exotic range correctly, detailed

historical information about past invasion of yellowhammer to New Zealand, including the localities of capture and release, was needed. As the works of previous researches (e.g. Thomson 1922, Williams 1969, Duncan 1997) differed in reported numbers of liberated yellowhammers, we went back to roots and analysed the original documents of New Zealand acclimatisation societies and archive of old newspaper articles. Between 1864 and 1879, 25 ships with yellowhammer on board departed from London to several New Zealand harbours. The species quickly established and spread all over the country (Chapter 8). The methods developed for yellowhammer case study allowed as to critically review two articles published in *Notornis* (Santos 2012, Moulton et al. 2014). The authors claimed to discover previously unknown releases of passerines in Otago region, the data were wrongly interpreted, though (Appendix 1).



## **2 Birdsong and dialects**

## **2 Birdsong and dialects**

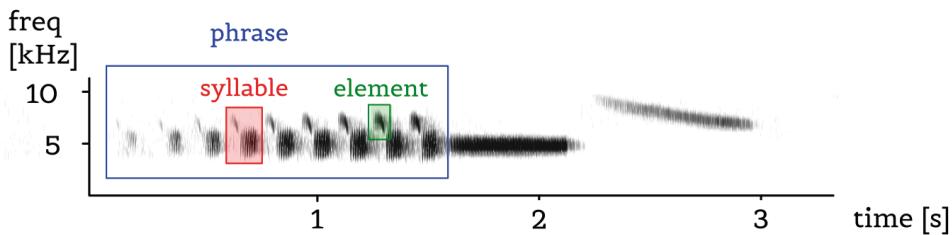
Birdsong is one of the most apparent behaviour of songbirds, the largest group of all birds, containing 50% of all known species. Indeed, most of the passerine taxa can be recognised just by listening to their typical song. However, already Aristotle (350 BC) mentions that characteristic song of a species can vary geographically. In fact, it would be more surprising if it did not, given the extent of some species' ranges. What is fascinating though, is the situation when the song characteristics are not changing gradually, but rather abruptly over short distances, even when there is no geographical barrier. This extreme cases, demonstrating mosaic-like patterns, are sometimes referred to as "dialect with sharp borders" (Catchpole and Slater 2008), but in classical definition these are the "true dialects" (Mundinger 1982). In the 2000s, the topic was very comprehensively summarised in two books (Kroodsma 2004, Catchpole and Slater 2008) and several papers (Slabbekoorn and Smith 2002a, Podos and Warren 2007, Planqué et al. 2014), however since then new discoveries were made. Furthermore, many studies (on dialects with or without sharp borders) were not included in these reviews (see Table 1 in Appendix 3).

Although many species were subject to studies on dialects (some of them non-passerines, see Table 1 in Appendix 3), the majority of research used only a few of them, e.g. American sparrows from genus *Zonotrichia*, especially white-crowned sparrows *Z. leucophrys* (Marler and Tamura 1962), incidentally, the focal species of this thesis, the yellowhammer (Hansen 1985) and other buntings (McGregor 1980, McGregor and Thompson 1988, Osiejuk et al. 2007, Skierczyński and Osiejuk 2010), which are distant relatives of *Zonotrichias*. This makes the generalization about processes behind origin and the maintenance of dialects difficult, if not impossible. Nevertheless, as the development of dialects is clearly associated with song learning (Catchpole and Slater 2008) and might be affected by various ultimate functions of the birdsong, in this chapter I will briefly answer three principal questions – why are birds singing in the first place, how do they learn their song and how the song varies in time and space.

### **2.1 What is a birdsong**

Although it is always not easy, in bird vocalization, we distinguish between calls and songs. Call is a short sound, which is usually produced in specific context, such as danger or aggressive interaction, throughout the year, and is often innate (Catchpole and Slater 2008). In contrast the song, more complex and "longer" sound is learned and produced especially but not exclusively during breeding period (Catchpole and Slater 2008). In parallel to human speech, the song can be split into phrases, syllables and elements (see Figure 1). This separation is however only structural; it does not tell anything about meaning.

The smallest unit of a song is element (sometimes also referred as note), which could not be separated any further and thus creates a continuous trace on the sonogram. Even though it is an elementary unit, it can be quite complex, as some birds, e.g. canaries *Serinus canaria*, can modulate the pitch with tremendous speed (Suthers et al. 2012). If we keep the analogy with human speech, element is like a letter. Syllable is higher unit than element, it consists of one or several elements, similarly like human syllables can consist of one, but typically more letters. Several syllables, which generally occur together or are otherwise easily distinguished from the rest of the song, add up into phrase. This can be a simple repetition of the same syllables as is the case of initial phrase of yellowhammer (Figure 2) or combination of different syllables. The same syllable might appear in several different phrases, just like different words are composed of limited set of syllables. Finally, several phrases constitute a strophe or song type. Often males have more song types in their repertoire, for example, yellowhammer males have 1 – 4 of them (Hansen 1999). In this respect, there is extreme inter-specifics variability; repertoire sizes range from one to several hundreds of different song types.



**Figure 2:** An example of song structure. Yellowhammer song is composed of initial and terminal phrase. The initial phrase is a simple repetition of same syllables which could be further split into elements. The terminal phrase, combination of two or three syllables, is shared by males in one region and constitute dialect.

## 2.2 Why do birds sing

When thinking about the functions of a song, it is important to consider who is singing and who is listening. Unfortunately, it is no longer as straightforward as Darwin proposed in his model of sexual selection (Darwin 1871). For long, it was assumed that males are the singers and females the listeners and that the song has evolved via male-male competition and female choice. This stems from large geographical bias in ornithological research towards the northern temperate zone, where the singers are mostly males (Riebel, 2003, but see Gar-

amszegi et al. 2006). In tropics and in southern temperate zone, female singing is a widespread phenomenon (Morton 1996, Slater and Mann 2004). Indeed, recent meta-analysis revealed singing females in more than 70% of the studied species (Odom et al. 2014). It is more and more suspected that female song is an ancestral state (Garamszegi et al. 2006, Price et al. 2009, Odom et al. 2014). In the rest of the work, though, I will refer to male songs unless I specify otherwise, as with only one exception of New Zealand bellbirds *Anthornis melanura* (Brunton et al. 2008) the dialect studies avoided analysing female songs.

The birdsong has three principal functions – to attract the opposite sex, deter the same sex and avoid interspecific hybridization (Catchpole and Slater 2008). Obviously, different song structures might be performing different functions; some parts might play role in individual recognition, e.g. initial phrases of yellowhammers (Hansen 1999) or note complexes in white-crowned sparrows (Nelson and Poesel 2007), while others can keep information about the dialect, such as terminal notes in the former (Hansen 1985) and trills in the latter case (Nelson and Poesel 2007, 2009). It is also suggested that different parts of the song (Petrusková et al. 2014, Linossier et al. 2015) or different way of performance of the song might be directed to different sexes, e.g. soft songs in song sparrows *Melospiza melodia* only to males (Anderson et al. 2007).

### *Territorial defence*

Species from different taxa (e.g. beetles, deer, frogs, fish) developed rituals or conventional signals which allow to assess quality of a rival without fighting him to death, thus saving both time, energy, and sometimes even lives. Birdsong, sometimes accompanied with flights and displays, belongs to such phenomena. By singing (and willing to fight if necessary), birds defend valuable resources, such as nesting sites, food resources or mates. Males listening to a singing male receive valuable information about quality of the “landlord” or his current aggressive state.

The risk of injury or unnecessary waste of energy can be further alleviated when the enemies are “long partners in the game”. The birds (both males and females) are capable to recognise their neighbours by song (Catchpole and Slater 2008). “Dear enemy hypothesis” suggests that once borders between competing males are settled they are less aggressive towards each other (Fisher 1954), provided they respect the borders when singing. This hypothesis is well supported by many studies (reviewed in Temeles 1994, Moser-Purdy and Menill 2016). Indeed, sometimes the neighbours can go further than just declaring “cease-fire”. After all, the rivals still have common interests, e.g. preventing establishment of new competitors (Getty 1987, Goodwin and Podos 2014, 2015, but see Akçay and Beecher 2015) or defence against predators (e.g. Krams et al. 2008).

These relations might be long-lasting even in temperate zones, where the territories are, in contrast to the Tropics, mostly defended only during breeding season. Great tits *Parus major* stay close to their neighbours also in winter flocks (Firth and Sheldon 2016), while migratory species, e.g. black red-starts *Phoenicurus ochruros* (Draganoiu et al. 2014) or hooded warblers *Setophaga citrina* (Godard 1991), remember the songs of their neighbour until next season. On the other hand, other tested species develop the “partnership” every spring de novo; in skylark *Alauda arvensis* the dear-enemy effect is the strongest in the mid-season, when the territories are already set (Briefer et al. 2008), similarly Eurasian wrens *Troglodytes troglodytes* reacted more strongly to neighbours at the beginning of the season (Courvoisier et al. 2014).

What might influence the relations among neighbours is song sharing (Catchpole and Slater 2008). It was suggested that singing a song type that is shared with the neighbour specify, to whom the song is addressed (Armstrong 1973) and that matched counter-singing is as “flinging the insult back at the opponent” (Bertram 1970). However, the results of numerous studies, including the thoroughly explored systems of western-larks *Sturnella neglecta* (Falls 1985) and song sparrows (Beecher et al. 2000, Beecher and Campbell 2005) or cardinals *Cardinalis cardinalis* (Lemon 1974), do not provide a clear picture (Catchpole and Slater 2008). Apparently, having songs of the neighbour in repertoire gives more possibilities of fine-tuning the conversation (expressing various levels of aggressiveness), which is not possible with complete strangers or when the repertoires are too small. However, that is where the dialects might come to play. The complete songs, including parts which are shared by all males in the population might be the strongest signal, as in the case of yellowhammer (Gruber and Nagle 2010).

In two species with documented dialects, sharing of the songs proved to be advantageous for males, giving white-crowned sparrows higher social mating success (Poesel et al. 2012) or song sparrows higher survival and longer territory tenure (Wilson et al. 2000).

### **Mate attraction**

As already suggested the song can carry different meaning to different sex. While males are trying to keep all potential male rivals out of their territory, they want to lure in potential mates, females, by broadcasting their qualities. In fact, the song does not have to lure a mate into a territory. In lekking species, it is only the mating opportunity which is at stake (Avery 1984). Males can also visit other territories and take advantage of extra-pair copulations (Birkhead and Biggins 1987). Females want males that are rich (i.e. have good territories), provide good parental care and have good genes. The song performance of a male might give them a clue.

There are many ways that may serve to attract female: e.g. incorporating sexy syllables or other specific structures (Bartsch et al. 2015, 2016), extending repertoire size (Catchpole et al. 1986) or increasing singing rate (Houtman 1992, Nolan and Hill 2004).

The singing rate (i.e. the amount of songs produced) is a good indicator of territory quality, as males face a simple trade-off, to sing or to eat, easily obtainable food thus give them more time to sing (Radesater and Jakobsson 1989, Alatalo et al. 1990, Berg et al. 2005, Yamada and Soma 2016). The amount of songs produced can be also negatively affected by parasite load (Møller 1991).

Although the repertoire size and other correlates of song quality might be affected by stress or other factors experienced during early development (Nowicki et al. 1998), songs of high quality (e.g. those approaching performance limits) may be also directly correlated with good genes and the ability to produce them, hereditary (Houtman 1992). It was demonstrated in several species, e.g. swamp sparrow *Melospiza georgiana* (Ballentine 2004) as well as canary (Draganoiu et al. 2002) that males producing highly challenging songs were preferred by females. It was also suggested that males might share songs to make the comparison of performance of different males more convenient for eavesdroppers, including females (Logue and Forstmeier 2008). Females thus might force males to sing specific song structures and to share them.

The female choice can also act as a selection pressure for acquiring large repertoires in some species, e.g. sedge warblers *Acrocephalus schoenobaenus* (Catchpole et al. 1984) or song sparrows (Searcy 1984). As dialects with sharp borders have been documented in species with small repertoires, redwings (Bjerke 1974), yellowhammers (Hansen 1985) or white-crowned sparrows (Marler and Tamura 1962), the female preference for extensive male song arsenal might be what is hampering the sharp dialect border formation in others.

What can, on the other hand, promote the dialect formation, is the conformism of females. The study on cowbirds *Molothrus ater* has shown that even female preferences might be dictated by fashion; it was possible to artificially change the female preferences using playbacks containing male song and positive acoustic feedback from other females (Freed-Brown and White 2009). If this were a general phenomenon, it would have direct implications for dialect maintenance; even females born in region with different dialect would prefer the dominant local one.

### *Reproductive barrier*

Female choice is also very important in preventing interspecific hybridization (Grant and Grant 1997). As the female have more to lose, they should be more selective (Trivers 1972). This trivial assumption was, however, rarely tested. In experiment with red-winged blackbird *Agelaius phoeniceus* males did not distin-

guish between songs of conspecific model and its mimic, mockingbird *Mimus polyglottos* (Brenowitz 1982), while females did (Searcy and Brenowitz 1988). In song sparrows, they also expressed much finer differentiating between local and distant dialects than males (Searcy et al. 2002). In fact, strong female preferences for local songs can eventually lead to speciation; populations that were separated naturally (e.g. due to climatic changes) and came into secondary contact can no longer recognise each other as conspecifics (Grant and Grant 1997). Similarly, recent translocations of endangered species done with good aim of conserving the species may also lead to failure simply because the individuals from different populations would not mate with each other (Parker et al. 2012, Valderrama et al. 2013, Bradley et al. 2014).

How do the birds recognise conspecific songs then? As it turned out (see review in Becker 1982), there is no universal answer. While some birds used rather syntactical rules, e.g. robins *Erythacus rubecula* (Brémond 1968), others with less complex songs, such as Bonelli's warbler *Phylloscopus bonelli* pay attention to shape of individual elements (Brémond 1976).

In fact, among some species it would be advantageous for females even to distinguish a male from the same subpopulation, because different subpopulations have alternate migratory routes along hostile geographic barriers, such as high mountains, and the inter-population hybrids might end up flying straight into a barrier. That hybrids might have intermediate migratory trajectories was shown e.g. in Swainson thrushes *Catharus ustulatus* (Delmore and Irwin 2014, Delmore et al. 2016) and blackcaps *Sylvia atricapilla* (Helbig 1991).

One would expect that when two closely related species meet in contact zone, their songs would diverge to avoid interspecific hybridization. However, it is often not the case. In contact zone of two closely related species with similar ecological niche, the song can become more similar as males display interspecific territorialism, e.g. common nightingale *Luscinia megarhynchos* and thrush nightingale *Luscinia luscinia* in Central Europe (Vokurková et al. 2013, Reif et al. 2015) or two warblers from genus Hippolais (Secondi et al. 2003, 2011). Therefore, apparently, the bird discrimination abilities range from population- to genus level.

## 2.3 Song learning

Song learning is expected to be a prerequisite for the formation of dialects, although in principle, they could emerge even if the vocalization was encoded in genes (Catchpole and Slater 2008) – in isolated localities, due to genetic drift, only some songs could remain out of the original richer pool. Indeed, the study on a suboscine species, three-wattled bellbirds (*Procnias tricarunculatus*), suggested existence of dialects (Kroodsma 2004). However, the axiom that suboscines do not learn their song was shaken by recent discoveries (Saranathan et al. 2007,

Kroodsma et al. 2013). At any rate, song learning (nicely reviewed in Brainard and Doupe 2002), or more precisely learning of vocalisation has surely evolved in three groups of birds – parrots, hummingbirds and true songbirds, oscines (Catchpole and Slater 2008).

To be precise, it is noteworthy that birdsong is probably learned only partially (Brainard and Doupe 2002); males of various species, e.g. zebra finches (Konishi and Akutagawa 1985), chaffinches *Fringilla coelebs* (Slater 1989), song and swamp sparrows (Searcy et al. 1985) that were raised in isolation, or were even deafened (Searcy and Marler 1987) developed songs similar to the songs of their conspecifics. Indeed, zebra finches (*Taeniopygia guttata*) isolated from wild populations for multiple generations, developed normal wild song types (Fehér et al. 2009). Some birds, e.g. white-crowned sparrows show even innate preference for conspecific songs (Nelson and Marler 1993).

Learning as such thus seems to be rather a fine tuning to some “Plato idea”, or crude template of species song. Marler and Nelson (1992) even suggested that each species can have the basic elements (universals) pre-coded in the brain, as albeit the syntax exhibit huge variability, the phonology seem to be constrained to few basic types across whole species range, similarly as millions of words are composed of only limited set of phonemes in human languages. Study of (Lachlan et al. 2010) supported the idea of some species-universal element categories in swamp sparrows, chaffinches and zebra finches. Previously (Soha and Marler 2000) revealed that white-crowned sparrows have innate preference for specific phrase in the song, the initial whistle. The global comparison of captive zebra finches also supported constraints in song, as despite rapid cultural evolution, the songs still consisted of limited set of elements (Lachlan et al. 2016).

Some birds, i.e. open-ended learners, can learn new sounds and incorporate them into their repertoire throughout their lives (e.g. starlings, Van Hout et al. 2012), while others, close-ended learners, learn their songs only during specific sensitive periods in first year after hatching (e.g. yellowhammer, Schön 1989). It was also suggested that most of the supposed open-ended learners could be in fact only remembering sounds they learned in their sensitive period and not truly learning them (Catchpole & Slater, 2008; Geberzahn, Hultsch, & Todt, 2002; Hough, Nelson, & Volman, 2000).

The song learning in closed-ended learners often goes through several stages – silent subsong, more audible yet not stereotyped plastic song and finally, highly stereotyped crystallised song (Brainard and Doupe 2002, Catchpole and Slater 2008). Birds first create an inner representation of the song by listening to adult tutors (sensoric phase) especially in the first few weeks after hatching (Brainard and Doupe 2002), which serves later as a template in sensomotoric phase, when birds are practising and comparing their performance with what

they learned previously. In this phase, adult tutoring is likely no longer needed (Thorpe 1958, Phan et al. 2006) and the birds rely on their ears as a feedback. In fact, some passerines, brown-headed cow birds, do not need adult male tutors at all and are guided by reaction of females instead (West and King 1988, Miller et al. 2008). Although the sensitive period for song learning is limited in close-ended learners, it seems that rather than time the crystallization of the song is triggered by experience; birds raised among heterospecifics or in complete isolation altered their song to the song of adult conspecific tutor well after the time when normally the song is crystallised (Brainard and Doupe 2002). The social context is indeed important. It prolongs the sensitive phase (in contrast to tape recordings) for white-crowned sparrows (Baptista and Petrinovich 1986) and wrens (Kroodsma and Pickert 1984) and allows canaries to learn more (Waser and Marler 1977). Apparently, until the brain gets the appropriate signal, it can remain flexible (Brainard and Doupe 2002).

## 2.4 Variability in time and space

As already mentioned, characteristics of a species' specific song exhibit geographical variability. The term dialect, which is often used to describe such variability, might be confusing. For some researchers this is a synonym for dialects with sharp borders, when the regions with different dialects are separated by very narrow transition zone (Mundinger 1982), while for others (e.g. Chilton et al. 2002, Warren 2002, Shizuka et al. 2016) it simply refers to any interregional differences even on much broader scale, spanning hundreds of kilometres. (Catchpole and Slater 2008) suggest that it might be better to avoid using this term for many different patterns. For this work, though, I will use the term in most cases broadly, i.e. dialect is a regional variant of a song, because similar processes might lead to both - dialects with as well as without sharp borders. What constitutes the dialect depends on the species. Patterns shared among individuals from the same locality can be found in final elements, e.g. trills (rufous-collared sparrows *Zonotrichia capensis*, Nottebohm 1969) or longer notes (yellowhammer, Hansen 1985). Rarely, dialects are defined by overall song structure (brown-headed cowbird, Rothstein and Fleischer 1987) or a combination of song types (corn buntings *Emberiza calandra*, McGregor 1980). Even in the last case, we can find sharp borders between dialect regions – each corn-bunting male has 2 or 3 song types, but whole repertoire is shared by males from one region (McGregor 1980). In swamp sparrows the dialects seem to be hidden in syntax, i.e. populations share the same elements, these are however in each population used in different numbers and in different orders (Marler and Pickert 1984). Slightly more complicated patterns are observable in whistle songs of starlings. Males share several whistles from their repertoire with other males, each one with different group of males, but each whistle type is limited

to well defined region (Adret-Hausberger 1986).

The dialect with sharp borders have been found (which does not mean that these cannot be in other tested species too) in songs of yellowhammers (Hansen 1985), corn buntings (McGregor 1980), white-crowned (Marler and Tamura 1962) and rufous-collared sparrows (Nottetbohm 1969), redwings (Bjerke 1974), orange-tufted sunbirds (Leader et al. 2000), in rain-calls of chaffinches (Sick 1939) and whistles of starlings (Adret-Hausberger 1983). Before introducing hypotheses about dialect origin and maintenance, I will trace roots, general patterns, which are more or less associated with dialect formation.

### ***Factor 1: Migratory patterns***

Males in rather sedentary species tend to have smaller repertoires in contrast to migratory species (Read and Weary 1992) as well as shorter natal dispersal distances (Paradis et al. 1998, Sutherland et al. 2000). This is an ideal situation for development of dialects – and indeed, the best studied are sedentary species with small repertoire, such as white-crowned sparrows and yellowhammers.

Even when within species different populations or subspecies adopt different migration strategies, the migratory behaviour can influence negatively the intensity of song sharing among neighbours, as in song sparrows (Peters et al. 2000) and white-crowned sparrows (Nelson et al. 2001) and positively the size of regions with one dialect, as in golden-crowned sparrows *Zonotrichia atricapilla* (Chilton et al. 2002, Shizuka et al. 2016). Among white-crowned sparrows, sharp dialect boundaries can be found in rather resident *nutalli* subspecies, while dialect structure is completely broken in migratory *gambelli* subspecies (DeWolfe et al. 1974, Austen and Handford 1991).

### ***Factor 2: Population density and structure***

Another factor that can influence the dialect patterns is the population density. For example, corn buntings exhibited dialect structure only in densely populated areas in the UK and Poland (McGregor 1981, Osiejuk and Ratyńska 2003). Similarly, while southern population of redwings in Norway show clear dialect structure (Bjerke and Bjerke 1981, Bjerke 1982), these patterns disappear when you move 500 km northwards (Espmark 1982), where there is likely lower population density and individuals tend to migrate further. It was also suggested that greater distance between individuals may disfavour high frequency notes (even when corrected for habitat properties), which generally deteriorate quicker (Lijtmaer and Tubaro 2007).

When the population density is not low, but population is fragmented, opposite patterns may arise. Clustering of the population, e.g. due to landscape fragmentation, can lead to intensified sharing among neighbours which may resem-

ble true dialect structure (Laiolo and Tella 2005, Briefer et al. 2010, Petrusková et al. 2010). Indeed, it was suggested that fragmentation might be behind origin of some dialects; cultural drift in isolated patches might have led to dominance of only some phrases out of original richer pool (McGregor 1980). Alternatively, patches that faced local extinction might be recolonised (Baker 1975), and if by only small group, there might be strong founder effects.

Several hypotheses were proposed as a driver of birdsong dialects development and their subsequent maintenance. These are not necessarily mutually exclusive, as different processes might have been behind origin of the dialects (e.g. isolation, geographic barriers, acoustic properties of habitat) and behind their maintenance (e.g. preference for local dialects). In contrast to some previous researchers (Podos and Warren 2007, Catchpole and Slater 2008), I have divided these according the factors that are shaping them (habitat filtering, female choice, male-male interaction).

### *Hypothesis 1: Habitat filtering*

Different habitats differ by their acoustics properties and thus act as a selective filter for different sounds. In general, close habitats, such as forests, causes the sounds of lower frequencies to deteriorate sooner than those with higher ones. In contrast, in open habitats it is advantageous to use lower frequencies, which, having now no obstacles, travel further. This can indirectly shape the songs of birds, as songs with appropriate frequencies would reach wider audience and thus can be a) more effective in territorial defence or mate attraction or b) be preferentially learned by young birds (Hansen 1979, Peters et al. 2012). Bird also adjust the song/syllable rate so that the echoes from the previous ones do not hinder the next (Catchpole and Slater 2008).

That habitat can influence dialect patterns was shown by studies on rufous collared sparrow (Handford 1981, Tubaro et al. 1993). The mere definition of dialects of rufous-collared sparrow makes the habitat association unavoidable. These are defined by thrill frequency (Nottebohm 1969, Handford 1988, Handford and Lougheed 1991), which clearly have to be associated with acoustic properties of the habitat. In studies on white-crowned sparrows (Derryberry 2009) and little green bulbul (Slabbekoorn and Smith 2002b) habitats affected only some song characteristics, maximum frequency and song rate, but the dialect distribution was unaffected. Habitat did not explain geographical variation in songs of other tested species, orange-tufted sunbirds (Leader et al. 2005), splendid sunbird (Payne 1978) or yellow-naped amazon (Wright et al. 2005). Overall, this hypothesis has a very weak support. One reason might be that birds likely do not rely on absolute pitch but rather on relative frequencies when recognizing song patterns (Bregman et al. 2016).

However, it is not only the physical properties of the environment that can put a pressure on the song characteristics. Background noise, no matter whether of natural abiotic (e.g. wind, surf or waterfalls), biotic or artificial (e.g. traffic, industry) origin, can act as another filter (Lenske and La 2014, Roca et al. 2016, Derryberry et al. 2016). In case of white-crowned sparrows the background noise might have been directly affecting the distribution of dialects; in just 30 years, the dialect with highest minimal frequency has been replacing two others, while the overall minimal frequency has risen up (Luther and Baptista 2010, Luther and Derryberry 2012).

### *Hypothesis 2: Female preferences*

In short, cherchez la femme. Female preferences to local dialect points, though, to two different hypotheses. By singing a song type or combination of song types, typical for a region, a male can demonstrate to females...

a) that he has spent some time here and thus is familiar with the place. For a female, this is a guarantee that he will be able to find enough food or nesting sites. By choosing local male the female thus gets direct benefits in terms of enough resources for her chicks,

and/or

b) that he was hatched here, and as such, should have the genes adapted to local conditions (local adaptation hypothesis, Podos and Warren 2007, Catchpole and Slater 2008).

Both hypotheses are valid; to distinguish between them, the experiments must be designed appropriately. To explore the influence of female choice, researchers undertook either genetic analysis or playback experiments. I would argue that both tests are necessary, as genetic divergence might arise even without active female choice, e.g. due to low dispersal, which might be the case of yellowhammer (Baker et al. 1987a). Contrastingly, female may actively select their mates which does not have to translate into genetic divergence of populations, as is the case of brown-headed cowbirds (O'Loghlen 1995). A third possible approach is to determine whether males learn (or finalise) their songs before or after dispersal.

I am not aware of any study that would test both the female preferences (expressed by number of soliciting displays) and correlation between genetic and song variability at the same locality. Nevertheless, for several species both type of studies (playback experiments, genetic analyses) were performed at different times and together their results lead to some conclusions (see list of the studies

in Table 1 in Appendix 3).

Still the results are highly variable even within species. Although both for white-crowned sparrows, in *nutalli* (Milligan and Verner 1971, Tomback et al. 1983) or *oriantha* subspecies (Baker et al. 1981c, 1982a), and rufous-collared sparrows (Danner et al. 2011) the female preference for native dialect (Baker et al. 1981c) was confirmed, the genetics studies yielded contradictory results both for former (Lougeed and Handford 1992, Lougeed et al. 1993, MacDougall-Shackleton and MacDougall-Shackleton 2001, Derryberry et al. 2016) and latter species (Baker 1974, 1975, 1982).

In other subspecies of white-crowned sparrows, *gambelli* and *pugetensis*, females were not able to distinguish even song of different subspecies (Chilton et al. 1990, Chilton and Lein 1996). What seems consistent for all subspecies of white-crowned sparrows; the males learn the song before arriving to the breeding locality (Baker et al. 1982b, Cunningham and Baker 1983, Ho et al. 2014), initially overproduce only to discard part of their repertoire when settling down to match the songs of their neighbours (Nelson et al. 2001, Nelson and Poesel 2009).

In song sparrows (Searcy et al. 1997, 2002, Stewart and MacDougall-Shackleton 2008) and for some populations of swamp sparrows (Balaban 1988a, b) the genetic and song variability was correlated. This does not go well with the fact that song sparrows learn their songs after dispersal though (Beecher 2017).

Also brown headed cowbirds learn their songs after dispersal (O’Loghlen 1995, O’Loghlen and Rothstein 2010) and the banding data suggest extensive gene flow among dialect regions (Anderson et al. 2005), still females do prefer the local songs; the proper local song is a honest signal of age, because males reach the final proper local variant when two or more years old (Rothstein and Fleischer 1987, O’Loghlen and Rothstein 2003). In this case, therefore, females seem to be responsible for maintaining the local variants but the female choice is unrelated to genes.

Despite decades of intensive research, we still lack a consistent picture about the role of females in dialect formation in New World. In Old World, it is even worse, the reactions of females were not much tested. Yellowhammer females have shown preference for local dialect, but no association between genetic and song variability was found (Neye et al. 2006). Corn bunting females do not use native dialect as a cue in pairing (McGregor et al. 1988), however males singing non-local songs within particular dialect region were avoided (Hegelbach 1986). Female preferences for local dialect were not found in orange-tufted sunbird (Leader et al. 2008).

Unfortunately, the playback experiments (Baker et al. 1987a, Searcy et al. 2002) often suffer from one significant methodological flaw – instead of abstracting the concept of dialect they compare the local song (which is also geo-

graphically close) and non-local (distant) songs. Therefore, we can easily overlook some hidden variation or clues that birds use to distinguish the songs. For example, song sparrow females preferred song of their mates to other local males (O'Loghlen and Beecher 1997). The studies should be therefore corrected for geographical distances (Soha et al. 2004) or made using non-local songs with the same dialect. Unfortunately, the same holds for playback experiments on males, which are being used to explore another hypothesis.

### *Hypothesis 3: Male-male interaction*

The residency can be broadcasted not only to females, but also to males. One of the principal function of birdsong is to repel rivals from the territory. To be effective the signal must be properly understood by the audience and that is where the local-specific parts may come to play. It was suggested that dialects can act as honest signal of long-time residency and high status (Rothstein and Fleischer 1987), which happened to be the case for brown-headed cowbirds who finalise their songs after two years (O'Loghlen and Rothstein 2003).

Many studies using playback experiments (Table 1 in Appendix 3), e.g. on white-crowned sparrows (Milligan and Verner 1971, Petrinovich and Patterson 1981), corn buntings (Mcgregor 1983, Pellerin 1983), orange-tufted sunbird (Leader et al. 2002), swamp sparrows (Balaban 1988a) and song sparrows (Searcy et al. 1997), have shown that males distinguish local to nonlocal dialects – in most cases the local dialect elicited stronger response. It is thus possible that males with foreign dialects are not able to establish territory (Slabbekoorn and Smith 2002a) as their signal is not strong enough.

Unfortunately, male-male interactions offer also other perspective. It was suggested (Baker and Mewaldt 1978) that if males react more aggressively towards local dialect, it might allow birds from distant population to sneak in. (Baker et al. 1981a) then found opposite pattern than previously mentioned works (Milligan and Verner 1971, Petrinovich and Patterson 1981), the local songs elicited milder response than non-local. The authors (Baker et al. 1981a) put forth that this situation might be just extension of neighbour-stranger discrimination. Dialects would be then just extreme example of song sharing among neighbours – when the song is so simple than it is not difficult to copy it without significant errors, which surely is the case of yellowhammer song. However it was demonstrated in white-crowned sparrows that they are capable to distinguish among neighbours and strangers singing the same dialect (Baker et al. 1981b), while ortolan buntings did not distinguish between dialects (Osiejuk et al. 2007, 2012) but were able to tell neighbours from strangers (Skierczynski et al. 2007).

Also in this case, it might be important how and when the males learn their song. In previous example cowbirds learn after dispersal (O'Loghlen 1995, An-

derson et al. 2005), which is also case of redwings (Espmark et al. 1989) and might be the case of corn buntings and yellow-naped amazon. White-crowned sparrows (Nelson et al. 1996, Nelson 2000) and song sparrows (Nordby et al. 2007) learn before dispersal; however they initially overproduce and later discard the songs to match their neighbours. Anyhow, the males do conform to the locality customs in which they settle.

Finally, social membership can be broadcasted without territorial intentions. For example starlings of the same whistle dialects stay close together also in communal roosts (Hausberger et al. 2008).

#### *Hypothesis 4: By-product*

Finally, it also possible that some dialect patterns emerged simply as a by-product of errors in learning without any functional significance (Catchpole and Slater 2008). This can surely be a sufficient explanation for cases when the songs vary with distance. When the birdsong exhibits mosaic-like patterns, this would not work unless there is a physical barrier (Andrew 1962). Due to inaccurate copying small changes in songs can accumulate (Lemon 1975) or the songs can be recombined in separated areas. The geographical barrier is likely responsible for dialect maintenance of white-throated sparrows, as duplet final notes seem to be dominant over triplet ones – they elicit stronger responses both in duplet and triplet populations and therefore without any barrier one would simply disappear. (Ramsay and Otter 2015).

Alternatively, the dialect structure might arise due to local extinctions followed by recolonization with a strong founder effects, which was suggested for South Island saddlebacks (Jenkins 1978), corn buntings (Holland et al. 1996) and white-crowned sparrows (Baker and Thompson 1985). Finally, when there is a significant pressure on some other traits in bird body-plan, e.g. overall size, size of beak, vital capacity of lungs, the song can alter simply because of that. Even in white-crowned sparrows the songs are correlated with beak morphology (Derryberry 2009, Derryberry et al. 2012)

It seems that there is no universal answer. Each hypothesis got some support, though only for few species, and sometimes the studies are even yielding contradictory results. In fact, all the suggested processes could easily work hand in hand. After all, the song has multiple purposes, therefore can have more drivers as wells.

## **2.5 Stability of dialect borders in time**

In previous subchapters, I offered some explanations, why the dialect borders are maintained, without giving a proof that borders are stable and therefore maintained. What if the borders are only transient state after two populations

formerly separated by geographical barrier have met as was suggested in last point? To address these doubts, in the final subchapter I will present examples of temporal stability of the songs. Few studies unfortunately span longer than 40 years, in fact, most of them even much shorter periods, in most cases, not on fine scale either.

Although the dialect borders in white-crowned sparrows over large continuous areas seem to be more or less stable over decades (Trainer 1983), when the population is fragmented (Harbison et al. 1999), or there is a strong selection pressure against some of the dialects (Luther and Baptista 2010), the evolution is apparently faster and the borders do move. However, the evolution is going on even within dialect regions. Old recordings of white-crowned sparrows were less efficient in eliciting responses (Derryberry 2007, 2011), both from males and females, and were on par with current neighbouring dialect songs (Derryberry 2011). The changes in the songs – rate of trills, absolute frequency of a whistle, bandwidth (Derryberry 2007) - were likely associated with habitat changes (Derryberry 2009). In rufous-coloured sparrows, the dialect borders remained stable during 24 years (Garcia et al. 2015). Already in 1988, (Handford 1988) noted that at least some dialect patterns remained stable over 20 years (Nottetbohm 1969). In fact, the author (Handford 1988) suggested that the dialect might be reflecting distribution of habitats 200 years aback – before the onset of modern agricultural praxis. However, in different part of species range, (Tubaro et al. 1993) noticed that one dialect disappeared due to destruction of forest just 50 years aback. The song elements within dialect regions were not stable, however there were no trends – some of the changes that appeared after 13 years (Kopuchian et al. 2004), have disappeared in next 11 years (Garcia et al. 2015).

Even the dialects of yellowhammer seem to be stable, though long term study on finer scale is missing. In related corn buntings, the dialect distribution has changed quickly due to drastic land-use changes (Holland et al. 1996)

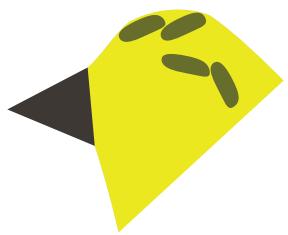
After 11 years, yellow-naped Amazon retained border between two dialect regions while in other locality, the border started to melt (Wright et al. 2008). In brown-headed Cowbirds, the results are also mixed – some song elements changed others remained stable, but the overall structure of the song remained constant (O’Loghlen et al. 2011, 2013).

Some of the previous examples have shown apparent long-term stability of dialect system. However, in some cases the evolution of dialects can be so rapid that it can constitute a conservatory issue. Following translocations, just in 20 years, population of North Island saddlebacks, that were of the same origin, but were translocated to different Island, started distinguish to each other songs as foreign (Parker et al. 2010). This have not happened in kokakos (Valderrama et al. 2013), however even they show tendency to assortative pairing (Bradley et

al. 2014).

Contrastingly, in recent expansion of light-vented bulbul, the dialect structure disappeared, the authors suggest lack of geographical barriers as a primary cause (Xing et al. 2013). Extremely valuable would be therefore studies comparing two populations, which were separated but share the same history. Although there are several studies (Lynch et al. 1989, Lang and Barlow 1997, Hamao 2015) comparing the overall song variability (syllable diversity, repertoire sizes) of exotic and native populations, only one compared the dialect patterns (Adret-Hausberger 1988). The presented thesis is the second.

To sum it up, dialect borders can apparently persist long time when the environment or population size do not change dramatically. When the population gets fragmented or there are significant land-use changes, the cultural evolution can be very fast, and the system of dialects may even collapse. Indeed, it was suggested that geographical song patterns may serve as an indicator of population fragmentation (Laiolo and Tella 2005, Petrusková et al. 2010) or of population decline (Holland et al. 1996).



### **3 Avian invasions**

## **3 Avian invasions**

Similarly to chapter on Birdsong, also this one will be based on reviews, most importantly by Blackburn et al. from 2009, updated with information from more recent works, e.g. on impacts of invaders (Kumschick and Nentwig 2010, Kumschick et al. 2011, Nentwig et al. 2016). Some topics, directly related to my research, has been also widely discussed in the literature, e.g. propagule pressure as a principal determinant of establishment success (Blackburn et al. 2015b) and the reliability of historical data (Moulton et al. 2011, 2012, Andrew and Griffith 2016).

In their review (Blackburn et al. 2009a) call for more intense research on avian invasions, which seemed a bit overlooked at the time. In that they succeeded; impacts of some introduced birds are now considered on par with those of the worst mammalian invaders (Kumschick and Nentwig 2010, Evans et al. 2014), and collective effort resulted in a large database on avian introductions, GAVIA (Dyer et al. 2017b), with extent comparable to GloNAF, the global database for naturalised alien plants (van Kleunen et al. 2015). The emerging patterns are alarming. According to the authors (Blackburn et al. 2015b), the process of avian introductions has been accelerating rather than slowing down, as is the case for the majority of other taxa, with the exception of mammals and fish (Seebens et al. 2017). In contrast to the 19th century, when most avian introductions were organised and planned, recent introductory events are driven by pet trade (Dyer et al. 2016), which is not only difficult to regulate (Smith et al. 2009) but to monitor as well; quite paradoxically, although recent events are more proximate in time, the quality of recent data is worse than those from 19th century (Blackburn et al. 2009a). Avian invasions definitely warrant further intensive research, as despite the progress made, some gaps still remain (Blackburn et al. 2015b).

In this chapter I will explore some general concepts of invasion ecology that are either essential or directly related to part of my work (Chapter 8, Appendix 1). Whenever possible, I will give examples from bird studies. At the end of this chapter I will introduce the specifics of acclimatisation of birds in New Zealand.

### **3.1 Which birds are invaders: Invasion stages**

Before becoming invasive, an alien species has to go through several stages – it needs to be transported, establish a viable population in the new range, and finally start to spread (Williamson and Fitter 1996, Blackburn et al. 2009a). In 2011, Blackburn et al. proposed a unified framework for invasion process that would allow for easier integration of findings from studies on different taxa and regions as well as clarifying the terminology. This framework (Blackburn et al.

2011b) combines concepts from previous frameworks, developed specifically for plants (Richardson et al. 2000) and animals (Williamson and Fitter 1996), and is based on series of barriers (geography, captivity/cultivation, survival, reproduction, dispersal and environmental) that an alien species has to overcome in order to pass on to next population stage (transport, introduction, establishment and spread).

I agree that it is useful to analyse all these different stages of invasions separately, as otherwise the analyses, exploring the factors affecting the establishment success, e.g. species traits or location, or other issues, might be largely biased (Williamson 2006). For example, some traits might be a reason for selection of the species (e.g. body size or colourfulness), while others (e.g. competitive ability or fecundity) may play role in subsequent outcome of the introduction (Blackburn et al. 2009a, 2011b). A simple comparison of established species with world pool of bird species could hinder any signal, as the selected species might not be good colonizers by nature – they were transported with human assistance. Each stage therefore sets a source pool, from which the species are filtered to enter the next stage (Cassey et al. 2004b, Blackburn et al. 2009a).

I suggest, though, that in studies on bird invasion we should split also the first stage, transport, into two, as the variation in mortality among different transport events is huge (Pipek et al. 2015, Pipek et al. unpublished data), possibly affected by parasite load (Blackburn and Ewen 2017). The transport as regarded by Blackburn et al. (2011) is in fact a double filter, only some species are selected for the transport, and of these only some survive the trip. A species might appear not to have been selected for introduction, but it could only fail to survive the transport. Furthermore, it is likely that the chances of survival of a bird species during transport affected the likelihood of its inclusion in further transports, although it is difficult to determine in which way. Unsuccessful shipment could stimulate further efforts (to compensate for the loss) or result in their discontinuation (if the “lesson” was taken); see below the discussion about causality of propagule pressure.

The data about survival on ships can be obtained, at least for New Zealand and Australia (Andrew & Griffith, 2016; Pipek et al., 2015; Pipek et al. in prep.), and our preliminary results suggest that it will be possible to analyse the factors that were affecting the survival of individuals during transport, such as the date of departure or duration of the trip (Pipek et al. in prep.).

Unfortunately, given the current state of knowledge, it is still practically impossible to split the transport stage into two, as in the vast majority of cases (as an exception see Cassey et al., 2004), the data on the survival during shipments are not available (Blackburn et al. 2009a). For the time being, we have indeed to treat selection and transport as one combined stage as e.g. in (Jeschke and Strayer 2006). In the following text, I will introduce the stages of invasion pro-

cess. To illustrate the filtering process, the numbers in brackets after the title of each stage represent the proportion of birds that entered the previous stage and successfully passed into the one that is being dealt with in that section. The data come from the study of (Jeschke and Strayer 2005) and refer to birds transported to America from Europe and vice versa. Because the authors did not distinguish between transport and introduction, the figures for the first stage are not available.

### *Selection and Transport (NA)*

Unlike some other taxa, especially invertebrates and many plants, the transport of birds was deliberate (Blackburn et al. 2009a) with only few exceptions, e.g. house crows hitchhiking ships to Africa, Asia and recently to Netherlands (Otten and Ryall 2003, Ryall 2013). The choice of introduced species was therefore non-random and driven by the reason for their relocation, be it a biological control (as was the case of most small birds introduced to New Zealand, but see Cassey et al. 2015), attractive companion (cage birds) or future food source (game birds). And these motivations have changed over time (Blackburn et al. 2010). Recent studies (Cassey et al. 2015, Dyer et al. 2017), supported by robust dataset of GAVIA database, revealed a shift from organised introductions in the colonization era before 1900 to rather accidental releases of pets in recent decades.

As already mentioned, before 1900 the transports were organised, especially by acclimatisation societies, bodies specifically founded with the aim to introduce foreign animals and plants (e.g. McDowall, 1994). Most introduced species at the time were game birds, and thus the families typically associated with hunting dominated in the beginning, i.e. Phasianidae (pheasants, partridges or quails), Anatidae (ducks, geese and swans) and Columbidae (pigeons and doves), later followed by Psittacidae (parrots) and Passeridae (Cassey et al. 2015). Most species that were transported in this period originated in Europe, while the most invaded countries were the former British colonies, such as South Africa, Hawaii, Australia or New Zealand, or USA (which were not a British colony anymore at the time, but the ties remained) (Dyer et al. 2017a). Two thirds of all introductions occurred on islands (Cassey et al. 2015).

Given the fact that avian introductions were especially in their beginnings deliberate it is not surprising that the rate of accumulation of new introductions slowed down in the first half of the 20th century (Seebens et al. 2017) when it was already known (e.g. Thomson, 1922) that introduced species can do more harm than good. In fact, after the Second World War some New Zealand acclimatisation societies switched their actions to prevention of further introductions (Simberloff and Rejmánek 2011). In the second half of the 20th century, the rate of bird introductions increased again, mainly because of the growth of

trade with cage birds (Dyer et al. 2017a), associated with economic development in countries where having birds as pets is a symbol of a higher social status (Cassey et al. 2015). As most introductions after 1983 were associated with this trade, the prevalent families are those that contain attractive species, Psittacidae, Estrildidae and Sturnidae. The birds originated mainly from sub-Saharan Africa, India or Indochina. The historical colonial ties with Britain are no longer a good predictor of invasibility; instead it is the GDP. The rich countries or countries with fast growing economy have higher numbers of new introductions (Dyer et al. 2017a), with hotspots in East Asia, Taiwan, Hong Kong or Singapore, Arabian Peninsula, Spain and Florida. The ultimate reason for transport of cage birds is usually not their liberation, although in Taiwan and some other countries of South-East Asia animals are being released into nature for religious purposes (Agoramoorthy and Hsu 2007).

Besides the biogeography of transported birds, one question that remains is which traits do these birds possess? Species either could possess traits that were desirable for humans, e.g. big body in case of game birds, assumed insectivory (passerines) or colourful plumage in case of cage birds, or were easy to obtain due to ubiquity (large range, high abundances). Obviously, some of these traits are correlated with the geographic origin – the colourful birds that make good cage birds are more often found in the Tropics. The birds in temperate zones, on the other hand, generally have larger ranges, reach higher population densities and tend to be bigger. Introduced birds are also bigger (Jeschke and Strayer 2006, Blackburn and Cassey 2007, but see Su et al. 2014), have larger native ranges and are also more abundant in their native range (Blackburn and Duncan 2001). (Dyer et al. 2016) speculate that one of the reasons why there are disproportionately low numbers of introduced species originating from Neotropics is that their small geographic ranges (smaller than in Africa or Asia) make them difficult to obtain.

Unfortunately, all the cited studies merged transport and introduction stage into one. To my knowledge, only two studies analysed the species traits for these two stages separately, one on the parrots (Cassey et al. 2004c), the second on cage birds traded in Taiwan (Su et al. 2014). The parrots that had larger geographic range size and spent more time as fledgling in the nest were more often transported (Cassey et al. 2004c). The importance of native range size was confirmed also for cage birds available at Taiwanese market (Su et al. 2014).

### *Liberation (11.1% / 5.4%)*

Some transported birds were liberated immediately or shortly after arrival to the new location, whereas others were kept in captivity for some time.

In 19th century New Zealand, the acclimatisation societies such as in Canterbury (Canterbury acclimatisation society 1866) had their own hatcheries, where

birds (especially game birds, and pigeons) were being hatched and both living birds and eggs were sold to other societies (e.g. Lyttelton Times, 29 Jan 1870, Page 2). It is likely that the incoming game birds were kept to increase the size of the population for liberation. The game birds are still being hatched and liberated nowadays, at least since 2003 (<http://www.nzgamebirds.co.nz/game-birds.html>). The Auckland acclimatisation society (North Island, New Zealand) kept also some passerines in captivity, especially the larger ones, such as rooks, whose wing feathers were trimmed to make the voyage safer for them (Auckland acclimatisation society 1871).

Whereas in the 19th century the liberation was part of the plan, recent years are dominated by more haphazard releases, e.g. cage birds whose owners freed them when the collapse of their price on the market made their further breeding infeasible (Robinson 2001), or releases that are motivated by other, e.g. religious reasons, such as prayer-animal releases organised by temples in east Asia (Severinghaus and Chi 1999, Liu et al. 2012). The latter should not be underestimated (Liu et al. 2012) – in Taiwan alone, 30% of the population engage in these liberations (Severinghaus and Chi 1999) and release as many as 200 million animals per year including birds (Agoramoothy and Hsu 2007), even though this number is mainly composed of native, i.e. cheaper species (Su et al. 2015). Data from Hong Kong suggest that there is a huge mortality among birds released in this way (Shiu and Stokes 2008), which is bad news for Buddhists but good for biodiversity.

Due to the great amount of bird trade worldwide, which peaked in the 1970's at 7.5 million individuals per year, decreased to 3 million individuals in the 1990's and even more so recently (Romagosa 2015), it is also inevitable, that many birds escape from captivity accidentally.

### *Establishment (30.0%/25.0%, for New Zealand roughly 28%)*

Once released into nature introduced species faces several challenges, such as novel environment, new biotic interactions (novel predators, lack of mutualistic relationships) and often the low population size. What will be the outcome of an introduction event depends thus both on parameters of that event (e.g. number of released individual or geographic distance among native and exotic localities), and on intrinsic characteristics of the species, e.g. behavioural flexibility or population growth rate (Blackburn et al. 2009b).

When the conditions at the exotic locality are not within the species' fundamental niche, those species are favoured that are behaviourally flexible, e.g. have larger brains, as they can adjust their behaviour and innovate and thus cope with new abiotic or biotic conditions better (Sol et al. 2005). Even though species can miss some mutualistic relationships or favourite food items in new region, leaving other species behind can in fact bring more benefits than costs, e.g. when

transported species escapes from its predators or parasites (so-called Enemy Release Hypothesis, ERH; Elton 1958).

While the effect of predators was not properly tested yet as it is very difficult to measure (Blackburn et al. 2009a), the studies on effect of “abandoned” parasites do not give a definite answer (Colautti et al. 2004) (Su et al. 2017). The analysis of (MacLeod et al. 2010) revealed that instead of being left behind in the home range, the ectoparasitic chewing lice followed the fate of their hosts; if the host failed to establish so did the lice.

Maybe more important than parasite load is immunity (Blackburn et al. 2009b) which allows to cope also with the novel parasites in exotic range; the stronger immunocompetency of nestlings enhanced establishment success in a tested set of terrestrial birds, but only if more than 100 individuals were introduced (Moller and Cassey 2004). The authors suggest that either a higher number of birds transported increase the risk that their parasites will be transported along with them, or simply that small populations face more significant issues than parasitism. The propagule pressure and parasites can in fact mask the effect of each other (Blackburn and Ewen 2017); when the propagule pressure is low (which decreases the chance of establishment), the number of transported parasites is also low (which enhances the chance of establishment), and vice versa, potentially resulting in low detected signal of both.

Alternatively, the parasites transported along with an alien species can facilitate the invasion (Strauss 2012), when the native species are more susceptible than the aliens, and thus the parasites can act as a novel weapon (Novel Weapon Hypothesis, NWH; Callaway and Ridenour 2004). Examples of this phenomenon, though not from avian world, are the invasion of North American crayfish species in Europe which is facilitated by massive mortality of native species due to crayfish plague brought along (reviewed in Svoboda et al. 2017) or replacement of red squirrel (*Sciurus vulgaris*) by grey squirrel (*Sciurus carolinensis*) due to parapoxvirus (Tompkins et al. 2003). In a study of (Lymbery et al. 2014) 14 out of 16 helminths that were transported along with alien hosts (mainly fish) and later infected also native host species were more virulent in native than in alien hosts. However, the authors (Lymbery et al. 2014) suggest that it does not prove that parasites are driving the invasion success, instead it is a simple by-product – only those parasites that are not virulent in alien species can get established along with it. In general, neither ERH nor NWH seem to explain establishment success well, even though case studies do exist (Blackburn and Ewen 2017).

Most species were initially introduced in low numbers therefore were in direct risk of local extinction (Blackburn et al. 2009a). It was thus proposed and later widely accepted (e.g. Lockwood et al. 2005, Colautti et al. 2006, Simberloff 2009) that it is the number of liberated animals (as a proxy for propagule pressure) that primarily affects the establishment success. Although the prominent

role of propagule pressure is consistently supported by analyses (Blackburn et al. 2011a, 2013, 2015a), some variation associated with population growth and the species susceptibility to Allee effect remains to be explained (Lockwood et al. 2005). The population growth could be deduced from some life-history parameters, although none of them appear to increase the establishment success consistently (Blackburn et al. 2009b). Some researchers (e.g. Cassey 2001) proposed, that species with rapid population growth should be able to escape the risks associated with small population size sooner than those with slow-growing populations, and thereby establish more easily. Others (e.g. Sæther et al. 2004) argued that species with rapidly growing populations display greater variation in population size, and are therefore at a high risk of extinction. The results supports both previously mentioned assumptions, but it seems that more successful in establishment are species with slower life history strategies; one of the possible explanation is that such species do not have to breed immediately and therefore have more time to acclimatise or modify its behaviour (Blackburn et al. 2009a).

The establishment success is also generally lower in migratory and dichromatic species (Blackburn et al. 2009b), as both intensive sexual selection in species with sexual dimorphism and longer natal dispersal in migratory species makes them especially susceptible to Allee effect (Taylor and Hastings 2005). In migratory species, the low establishment success can be also associated with difficulties in finding new wintering grounds (Blackburn et al. 2009b), even more than in species with innate migratory routes.

When analysing the factors that might be responsible for establishment success, it is especially important to keep in mind the framework suggested by Blackburn et al. (2011). For example, as already mentioned the species with large geographic ranges or high abundances were transported more often. This is also true for parrots, however, out of the parrots selected for transport, those with smaller native populations had on average higher establishment success (Cassey et al. 2004b). Parrots are in fact very good at establishment – more than 16% of all extant parrot species have established exotic population (Menchetti and Mori 2014).

### *Spread (66.7%/28.6%)*

Finally, some birds with established populations start to spread and thus become invasive. Populations of the same species exhibit great variation in this respect – of self-sustainable populations established in several exotic localities only some turned into troublesome invader (Zenni and Nuñez 2013, though the authors analysed only 6 bird species).

Given the dispersal capabilities of most birds, it might be surprising at first sight, that with few exceptions (e.g. European starling or house sparrow), the

exotic ranges are usually smaller than native ones with median of exotic range sizes reaching only 0.3% of that of native range sizes (Dyer et al. 2016). However, when geometry, i.e. to what degree is the exotic range limited by overall size of the exotic region, is considered, we may see more sense in the results. The birds introduced from continental Europe certainly cannot reach the same range size on an island, even as large as New Zealand. And most of the older introduction events were from a continent to islands (Cassey et al. 2015), where reduction of the potential range the species can occupy is bound to occur. Nevertheless, the species with larger native ranges had also larger exotic ranges in Australia (Duncan et al. 2001) and globally, even when the colonial pressure was taken into account (Dyer et al. 2016)

The spread is usually associated with fast exponential growth – much faster than in non-invasive populations in their native ranges (Blackburn et al. 2009a) – and the population growth is one of the drivers of the exotic range size. The rate of range expansion is highly variable, even within species, and spans from few kilometres to dozens of kilometres per year (Blackburn et al. 2009a), with the highest estimated figure exceeding 90 km per year for European starling spread in North America (van der Bosch et al. 1992).

Some species start to spread after certain time, i.e. lag phase, which can reach up to decades (Sakai et al. 2001). For plants it has been firmly established that the exotic range size correlates with the time since introduction (Pyšek and Jarošík 2005, Williamson et al. 2009)(Williamson et al. 2009), but a robust evidence for birds is lacking. The studies on birds introduced to New Zealand after 1850 (Duncan et al. 1999) or globally (Dyer et al. 2016) in fact showed the opposite – the species with longer residence times had smaller ranges. The authors of the latter study (Dyer et al. 2016) suggested that the observed opposite relationship might be a result of switch from well-planned transport of birds to specific regions to unintentional multiple releases on larger areas that happened in 20th century. Therefore, instead of reflecting the dynamics of exotic population, exotic range sizes might reflect the dynamics of transport. Another possible explanation is that after some time, species reaches its maximum and then slowly retreats. Some species display a “boom and bust” dynamics, which means that they initially spread and reach high densities, and later decline or even disappear (Williamson 1996, Simberloff and Gibbons 2004). Some passerine species introduced from United Kingdom to New Zealand apparently experienced boom and bust dynamics as few decades after their introduction in the 1860’s their populations were so numerous that they became a target of organised culling, which is no longer happening nowadays (Pipek et al. 2015, Pipek et al. in prep., Chapter 8). The causes of boom and bust dynamics are still largely unexplored, among likely candidates are introduction of competitors (Blackburn et al. 2009a), enemies or diseases (Colautti et al. 2004) or even

accumulation of deleterious mutations at expanding front (Peischl et al. 2013) or evolution of viruses (Faillace et al. 2017).

Whereas species can be harmful even when restricted to small areas (Kumschick and Nentwig 2010) their impacts are especially apparent when it is happening on large scale. What are these impacts, will be a subject of the next subchapter.

### **3.2 What are the impacts of alien birds?**

Until recently most assessments of impacts, that served as a basis for management, were based on expert opinions (e.g. Lowe et al. 2004). In 2009, Nentwig et al. (2010) developed generic impact scoring system (GISS), based on categories of environmental and economic impacts of mammals, that allowed for objective, evidence-based comparison of impacts among different species. Later on the scheme was used for other taxonomic groups such as birds (Kumschick and Nentwig 2010), plants (Kumschick et al. 2015, Rumlerová et al. 2016) or amphibians (Kumschick et al. 2017) (see Nentwig et al. 2016 for review). This GISS system served as a base for EICAT (Blackburn et al. 2014, Hawkins et al. 2015), which was adopted by IUCN as an official tool for scoring impacts of alien species by vote of its general assembly (<https://portals.iucn.org/congress/motion/014>).

The scoring using above systems revealed that birds on average have smaller negative impacts than mammals (Kumschick et al. 2011), but there are few species whose impacts are comparable (Kumschick and Nentwig 2010), e.g. Canada goose (*Branta canadensis*), sacred ibis (*Threskiornis aethiopicus*), ruddy duck (*Oxyura jamaicensis*) and ringed-necked parakeets (*Psittacula krameri*). The authors, however, originally analysed only species that were introduced to Europe (Kumschick and Nentwig 2010). The same impact scoring system was used later for alien birds in Australia (Evans et al. 2014) and on limited set of species also globally (Martin-Albarracín et al. 2015). Among worst invaders identified in these latter analyses were mallard (*Anas platyrhinchos*), common myna (*Acridotheres tristis*) and red-whiskered bulbul (*Pycnonotus jocosus*). This corresponds well with IUCN list of 100 worst invaders of the world, which mentions once again common myna, and then starling and relative of red-whiskered bulbul, red-vented bulbul (*Pycnonotus cafer*) (Global Invasive Species Database 2017). On these three worst invaders the scoring was later applied too (Nentwig et al. 2016).

And what are the impacts? While the birds do not affect significantly the whole ecosystems (Evans et al. 2016), they can have a direct impact on individual species through hybridization, such as ruddy duck on white-headed ducks (*Oxyura leucocephala*), or on whole bird communities, e.g. ring-necked parakeets (Yosef et al. 2016, Mori et al. 2017) and other species (Charter et al. 2016) on the community of cavity-nesters. Among other important impact belongs trans-

mission of diseases (Martin-Albarracín et al. 2015) or predation (Evans et al. 2016). See more in (Baker et al. 2013).

Finally, are there any traits that predispose a species to become a successful invader? It was demonstrated that the invaders exert similar impact in exotic as in native range (Kumschick et al. 2011), from which it follows that a species successful in its native range (large range area, high abundancies) should be also successful in its exotic range. The trait that was consistently correlated with impact both in Europe and Australia (Evans et al. 2014) and in previous study also globally (Shirley and Kark 2009) is habitat generalism, in Europe alone also body size and native range size (Kumschick et al. 2013).

### **3.3 What is the role of propagule pressure?**

What is directly related to some of the studies included as chapters or appendices (Chapter 8, Appendix 1) in this thesis is the role of propagule pressure. Given the fact that the outcome of introduction events is to certain degree driven by stochasticity, it is widely accepted (Colautti et al. 2006, Simberloff 2009, Blackburn et al. 2015a) that it is especially important how many individuals were transported to new regions (propagule size) and in how many events (propagule number), which combines into propagule pressure. A large number of released individuals allows for minimizing the risk associated with population fluctuations or Allee effects, while multiple introduction events help to cope with seasonal variation or genetic variability impairment, as individuals from different events could have also different origin, and by that genetical background.

This hypothesis is based on solid theoretical grounds and has gained empirical support (e.g. Cassey et al. 2004a, Blackburn et al. 2009a, 2015a), however, some researchers still question its validity (Moulton et al. 2010, 2012, Moulton and Cropper 2014, 2015, 2016). There are several levels on which these authors attempt to discredit this hypothesis.

#### *Causality*

In theory, it is true that as some species were introduced multiple times in the region, the direction of the causality could be twisted: because the initial introduction was successful, people continued with its transport and liberation. This hypothesis was suggested, but not supported by Colautti (2006), and later adopted by Moulton et al. (2011). Although hypothetically the problem with causality of propagule pressure can exist (Blackburn et al. 2013) were able to demonstrate on New Zealand data, by testing six logical predictions, that in reality it does not. That it is the number of introduced individuals that affects the success and not vice versa was also supported by analyses of unintentional introductions, and experimentally (Colautti et al. 2006). The arguments present-

ed by Blackburn et al. (2013) were not accepted by Moulton & Cropper (2014b). While their criticism based on statistical grounds is justified (e.g. arbitrary limit of 2 years of persistence to separate apparent successes from apparent failures seems too short also to me) and they are partly right that the data underlying Blackburn et al. (2013) analysis, which was the study of Duncan (1997), contain some gaps or errors, some of their arguments are not justified.

### *Gaps in data*

Although the data presented in a book by Thomson (1922), which is often used as a source in analyses related to propagule pressure and was also partly used by Duncan (1997), indeed contain gaps and thus warrant criticism, the recent studies are introducing new errors instead of correcting for the old ones. The “additional releases” of dunnocks (Santos 2012) and other passerine species (Moulton et al. 2014) in 1870s were proven to be mere translocations (Pipek et al. 2015b, Appendix 1). Unfortunately this erroneous data were already perpetuated in subsequent works of the authors (Moulton and Cropper 2015, 2016). Nevertheless, the authors rightly criticise the test of the fifth prediction of Blackburn et al. (2013), which is that “there is no relationship between propagule size and establishment success in those cases where there is just a single release event”, as the numbers for sparrows (Moulton et al. 2011) are not correct. However, they are not right in that redpolls were introduced multiple times in Auckland region (Pipek et al., unpublished data). Instead of including the corrected number for sparrows (which is still unreliable, Pipek et al., unpublished data) and dropping out the redpolls, as suggested by Moulton and Cropper (2014b), it would be more appropriate to drop the sparrows from the analysis (Blackburn et al. 2013) while keeping redpolls, for which the number of released individuals can be corrected. Redpolls indeed went to Auckland only once, although in less numbers than indicated by (Duncan 1997a), whereas sparrows went to Wanganui/Wellington region several times (Pipek et al., unpublished data).

### *Multiple localities of release*

Moulton et al. (2014b) further claim, that birds were often released in isolated localities and thus the total number of liberated birds per year and region is not a good proxy for propagule pressure. Although it is true that some societies (Auckland, Canterbury) sometimes distributed imported birds among several localities or sold them to their members for liberation, that should not be a problem. If the total number of individuals released in the given year was split among several localities, it could still enhance their chances of survival – the more localities, the higher the chance of finding a suitable habitat. Nevertheless,

if the total number split into smaller pieces did not contribute to establishment success, it would not turn out to be a good predictor.

### Determinism

Finally, Moulton and his colleagues argue with instances of birds that succeeded in establishment, even though they were introduced in very small numbers (Moulton et al. 2011), citing (Simberloff 2009). Indeed, there are examples of populations establishing from few individuals or even one pair (phenomenon called Noah fallacy by James Carlton; Simberloff 2009) or one female. However, successes of small introduced populations are not that frequent (Corbett King and Reed 2016) and even if they were, it simply does not invalidate the prediction. I am not aware of anybody believing in the prominent role of propagule pressure that would expect small populations to fail and large ones to succeed at any circumstances and with no exceptions. Larger numbers increase the probability of success but not guarantee it. In fact, even if the population was already established (and thus small numbers might seem sufficient and not affecting the results), subsequent individuals (propagules) could bring some benefit, e.g. new alleles, that would improve their chance of establishment or invasion (Sakai et al. 2001, Simberloff 2009).

I agree with Colautti et al. (2006) and other researchers, e.g. Blackburn et al. (2009a) that propagule pressure should be taken as a null model in invasion ecology and all the analyses exploring other factors should account for that. I might be mistaken, however, in my eyes the debate is not about whether propagule pressure is the most important determinant of invasion success (as put into mouth of others by (Moulton and Cropper 2015), the thing is that it is the only one factor that is obviously and consistently (Lockwood et al. 2005, Blackburn et al. 2015a) affecting the outcome. It is obvious that in some situations other factors might be more important – e.g. if the locality is outside tolerance limits of the species, the numbers are irrelevant.

Interestingly, most of the studies on propagule pressure were done on system of birds introduced to New Zealand. The rest of this chapter will be thus dedicated to acclimatisation of birds to this country.

## 3.4 Acclimatisation in New Zealand

Overall there were around 120 bird species introduced to New Zealand, mostly from Europe or Australia, of which 34 established (Duncan et al. 2006), representing roughly 27%. Some alien bird taxa are distributed only in a limited area (e.g. cirl bunting, *Emberiza cirlus*), while others (e.g. blackbird *Turdus merula* or chaffinch) can be found on most of the territory (Robertson et al. 2007).

Some were detested by farmers in the past, and some of these (e.g. house

sparrows *Passer domesticus*, rooks *Corvus frugilegus*, or common mynahs) are still considered as significant crop pests ([www.birdproof.kiwi.nz/pest-bird-species.php](http://www.birdproof.kiwi.nz/pest-bird-species.php)). Ironically, as a worst threat for nature is currently considered species which was introduced just two decades ago, rainbow lorikeet (*Trichoglossus haematodus*), which is competing with native species for food and nesting sites ([www.doc.govt.nz/nature/pests-and-threats/animal-pests/animal-pests-a-z/rainbow-lorikeet](http://www.doc.govt.nz/nature/pests-and-threats/animal-pests/animal-pests-a-z/rainbow-lorikeet)). Unlike with mammalian predators, it is impossible to protect this species from entering wildlife sanctuaries or offshore islands.

The reason why avian invasions in New Zealand are so popular subject of invasion studies is simple; the introductions were in most cases organized and documented. The transport and subsequent releases were planned by acclimatisation societies, that were established around principal cities of New Zealand – most active were those in Auckland, Canterbury, Otago, Nelson, Wellington and Hawke's Bay regions (McDowall 1994). As these societies made some erroneous assumptions when selecting the species for introduction, often people think that the members were mere amateurs (Bathgate 1897). It is difficult to judge now, though. The societies had direct ties with the county leadership through prominent members of the government and furthermore, and some members were respectable scientists.

The societies imported birds mainly for two reasons – as a biological control against crop pests (Fereday 1872), which swarmed the country (so called “English insectivorous birds”) and as a food source (game birds). It is especially the first reason which later led to members of the society being mocked by newspapers (Auckland Star 5 March 1880, Page 2) and the acclimatisation opposed by the public. (Drummond 1906) also later quotes some very harsh opinion on what should be done to people responsible for introducing sparrows into the country. The Canterbury society has already years before that hastened to wash their hands by cover-up story (e.g. Press, 17 December 1879, Page 3), which was an obvious lie as clearly identified (Otago Witness, 18 February 1892, Page 19). At about the same time, also the Otago acclimatisation society denied the responsibility (Evening Star, 11 Mar 1880, Page 1; Minutes of the Otago acclimatisation society), although it organised import of this species in 1868 on ship Warrior Queen (Otago Witness, 1 Feb 1868, Page 11).

The societies kept records of their activities in minute books and annual reports, along with letters copied and stored in letter books. Several researches attempted to compile the data about introductions in one book, either for their region (Andersen 1916, Ashby 1967, Wellwood 1968, Sowman 1981, Sullivan 1998), or for all together (e.g. (Thomson 1922, Lamb 1964, Druett 1983, McDowall 1994). These books are often used as a source of quantitative data for rigorous analysis of factors determining the outcome of introductions - recently the hottest debate is about role of propagule pressure (Blackburn et al. 2011a,

2013, Moulton et al. 2011, 2012, Moulton and Cropper 2015). Moulton et al. (citation) rightly pointed out that the authors (Veltman et al. 1996, Duncan 1997a) are not consistent in reported numbers of introduced birds. Main reason, of course, is that the authors differ in selection of compilations used.

Most influential is already mentioned work of G. M. Thomson (Thomson 1922), for some time a member of the Otago acclimatisation society. (Moulton et al. 2012) quote Thomson introducing chapter, in which he criticises early members of the acclimatisation society for “being careless in the matter”, as many information is missing (Thomson 1922). However, this Thomson’s statement is fair. Nelson reports were lost in the fire (Sowman 1981), the reports of Hawke’s Bay in earthquake (Wellwood 1968) and the reported lack of some reports of other societies is rather due to carelessness of Thomson’s contemporaries – many of these reports, inaccessible in the past (Bathgate 1897), are currently available (Pipek et al. 2015a, Chapter 8), especially from the beginnings, when the societies were most active. However, with one but important exception, the annual report of Canterbury acclimatisation society from 1875 was never published in proper form (Canterbury acclimatisation society 1877) due to some issues in financial audit and it was in the very same year when largest shipment on Tintern Abbey came to Canterbury. Luckily enough, the report was published in newspapers (Press 21 January 1876, Page 2) and the shipment covered in large detail (e.g. Star 5 May 1875, Page 2).

Lamb (1964) presented some data that was missing from the Thomson’s book, which he extracted similarly to our study (Pipek et al. 2015a, Chapter 8) from newspapers, most importantly, the data about shipment of Tintern Abbey in 1875. However, for obvious reasons – the newspapers were not searchable at the time – sometimes he did not interpret the data correctly and thus introduced new errors, similarly to (Moulton et al. 2014). More on the quality of these compilations can be read in Chapter 8 and Appendix 1.

The issue of quality of historical data was lately addressed by (Andrew and Griffith 2016) on sparrows introduced to Australia, but they explored only part of available resources and thus missed some data.

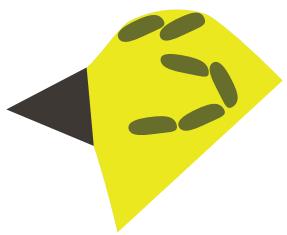
Unfortunately, it is easy to misinterpret data without having appropriate context. Recently, Corbett King and Reed (2016), who were trying to reduce the number of single-event introductions, nicely demonstrated the importance of going to real primary sources and reading whole texts. Duncan (1997) refers to Drummond (1906) saying that there are instances of species establishing only from one pair. The authors (Corbett King and Reed 2016) quote direct Drummond words, pointing out that Drummond does not say explicitly that these two birds were liberated. However, there are two problems – first, Drummond is not a primary source, second, what Duncan (1997) most likely had in mind were greenfinches and not Australian magpie, about which the quote in (Cor-

bett King and Reed 2016) is. When talking about the Greenfinches, it is directly stated by Drummond (1997), as well as 30 years earlier by Potts (1872) in his speech, that one pair was liberated in Canterbury in 1863 and started to multiply rapidly. I do not include it here to defend one-pair idea (more ships with greenfinches went to Canterbury after this single-event; Pipek et al. unpublished data), but to warn from hasty conclusions.

Along with the data on the numbers of introduced birds, there are several shorter works related to acclimatisation, sometimes from direct witnesses (e.g. (Fereday 1872, Potts 1872, Bathgate 1897, Drummond 1906, Chrisholm 1907). Besides the facts about shipments we can extract valuable information about public opinion, distribution of the introduced species, status of native ones (e.g. Kirk 1895 expected that Kakapo is doomed to extinction – he would be very pleased to see current population recovery) and plans for future, i.e. which species should be introduced next.

I especially welcome the ideas about utility of introductions, defended by Thomson (quoted in Drummond, 1906) and, e.g. Bathgate (1897); it is true that introduced birds were pests but without them the situation could be much worse. The anecdotes about trains, whose wheels were spinning due to thousands of crushed bodies of caterpillars, were still alive at the time (Bathgate 1897) and from hindsight we may see only the wrong side of the coin. Even G. M. Thomson believed that sparrows are helping to keep insects in check (Drummond 1906). The birds were also not accused of displacing the native species (Kirk 1895).

Indeed, although many introduced species became pests, only few people doubted the benefits of further introductions (Bathgate 1897, Drummond 1906) at the onset of 20th century. The question was rather what species should be selected (Bathgate 1897). On top of the list of most out of hundreds of correspondents was a robin (Drummond 1906). Despite the effort was made, robins never established in New Zealand.



## 4 Yellowhammer ecology

## 4 Ecology of Yellowhammer

In this chapter I will provide more detailed information about yellowhammer biology, which did not fit into limited space of scientific articles, but is relevant for the interpretation of dialect patterns. I will also include some new discoveries.



Figure 3: Singing yellowhammer male (foto Steve Attwood)

### 4.1 Phylogenesis

Yellowhammer (*Emberiza citrinella*, Figure 3) is a small passerine (Passeriformes) belonging to large family Emberizidae, which includes also New World sparrows that appear throughout this work, e.g. white-crowned or rufous collared sparrows. Old world genus *Emberiza*, contain also several other species with documented dialects, corn bunting (McGregor 1980), ortolan bunting (Osiejuk et al. 2007).

Closely related buntings (Alström et al. 2008), cirl (*Emberiza cirlus*), Cretzschmar's (*Emberiza caesia*), grey-necked (*Emberiza buchanani*), ortolan, pine and white-capped (*Emberiza stewarti*) buntings, have all similar songs (Rubtsov and Opaev 2012) which suggest that the song, especially the thrill part, is rather phylogenetically conservative trait, unlike, e.g. the colouration (Rubtsov 2007).

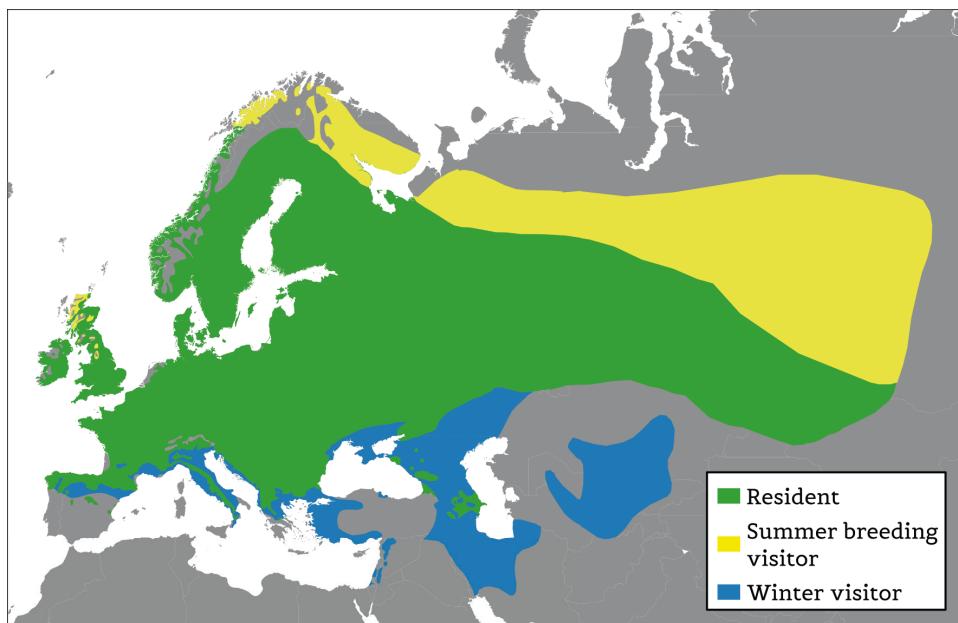
The closest relative is a pine bunting *Emberiza leucocephalos* (Alström et al. 2008), which hybridize with yellowhammer in contact zone in Asia. Although the two species split as early as four millions ago (Rubtsov and Opaev 2012), their song is almost indistinguishable; both elicited aggressive response in play-

back experiments on distant German yellowhammer males (Tietze et al. 2012).

Interesting is the difference in dialect distribution – whereas yellowhammer dialects have mosaic-like distribution, in case of pine buntings there is no clear pattern. Authors attribute this to differences in the extent of ice-cover during glacial periods, in Europe this created mosaic of hostile areas and refugia, whereas the range in East Asia was continuous. However, this might be simply a sampling bias, as yellowhammer dialects were a target of scientific scrutiny for quite a long time (Petrusková et al. 2015b).

## 4.2 Distribution and population trends

Yellowhammer is widely distributed in Europe and its native range covers also part of Asia (del Hoyo et al. 2011), see Figure 4. It was introduced to United States, Australia, New Zealand and Fiji, however, only in New Zealand it has established (Lever 2005). From there it spread to distant Kermadec islands (Williams. 2008)



**Figure 4:** Yellowhammer distribution (excluding New Zealand), data source: BirdLife International and Handbook of the Birds of the World (2016)

If the population sizes are taken into account, it is clearly visible, that the species is most abundant in central and eastern Europe – Czech Republic, Poland, Germany and Ukraine. Yellowhammer population sizes are more or less stable in Central Europe and are declining in Western Europe and Scandinavia (BirdLifeInternational, 2004,2017), mainly due to land-use changes (Bradbury et al. 2000, Morris et al. 2005, Whittingham et al. 2005).

Yellowhammers prefer transition zones between open and close habitats, such as farmland with hedges, forest clearings, or natural grasslands (BirdLife International 2017). They are mostly sedentary, only the northern populations vacate in winter (del Hoyo et al. 2011, Figure 4)

## 4.3 Behaviour

### *Diet*

Like other buntings, yellowhammer diet consists mainly of seeds, though they pick invertebrates in breeding season too (del Hoyo et al. 2011). Mainly because of that they are negatively affected by insecticide use (Morris et al. 2005).

### *Breeding*

Yellowhammers are monogamous – nest is built by females, which also incubate eggs, whilst males provide the food; they have typically two broods of about 4 eggs per year (del Hoyo et al. 2011) Average life-expectancy is around 3 years, between-years mortality rate is around 46 % (Robinson 2017).

It was demonstrated that the colouration of males might be an important signal for females. Old, colourful males provide better parental care (Sundberg and Larsson 1994) and also benefit from extra-pair copulations (Sundberg and Dixon 1996).

Females preferred also males with local songs and larger repertoire (Baker et al. 1987a)

## 4.4 Updates on yellowhammer song

Although the history of yellowhammer song research and current state of knowledge is well described in following chapter (Chapter 8), since its publication we made several new discoveries and some facts, known already at the time, did not fit in.

### *The research started much sooner*

Firstly, the research started much sooner than we claim. Already in 1869, there are first notions about different yellowhammer songs in German journal *Der Zoologische Garten* (Oppel 1869, Röse 1869), and song variants are even depicted using notes (the sonograms were not yet available at the time).

### *Advances in research*

Secondly, since the publication of our review (Chapter 6, the research has great-

ly accelerated. We have initiated creation of citizen-science projects focused on yellowhammer dialects in other countries than Czech Republic and UK / New Zealand - in Latvia, Poland and Switzerland. The latter two are taking advantage of the same website as original “Yellowhammer Dialects” project, which was for their sake translated into respective official languages (Polish, German, French and Italian). Thanks to my recent adaption, the web allows creating any subproject with any set of languages.



## 5 Aims

## **5 Aims**

The principal aim was to explore how the invasion history was reflected in current birdsong dialect distribution in native source range (Great Britain) and invaded range (New Zealand), with the use to of historical data about yellowhammer invasion in New Zealand and additional knowledge about the current distribution of yellowhammer dialects in native range, but outside the source population (Europe, Czech Republic). We expected that in exotic range there would be reduced dialect diversity in comparison to mother country, due to bottleneck effects associated with low numbers of bird transported, even though some new dialects could evolve. We also presumed, that the localities of capture and release would have the similar dialect composition due to shared history.

The partial aims are given separately for each chapter:

1. to collate available information about the distribution of yellowhammer dialects in Europe and unify the dialect nomenclature.
2. to map the distribution of yellowhammer dialects in the Czech Republic using citizen-science approach and assess the relevance of dialects that are suspected to be part of a continuum
3. to reconstruct the history of yellowhammer colonization of New Zealand using newspapers and original document of acclimatisation societies
4. to map the distribution of yellowhammer dialects in Great Britain and New Zealand using citizen-science approach and other sources of data and interpret the results in the light of known invasion history



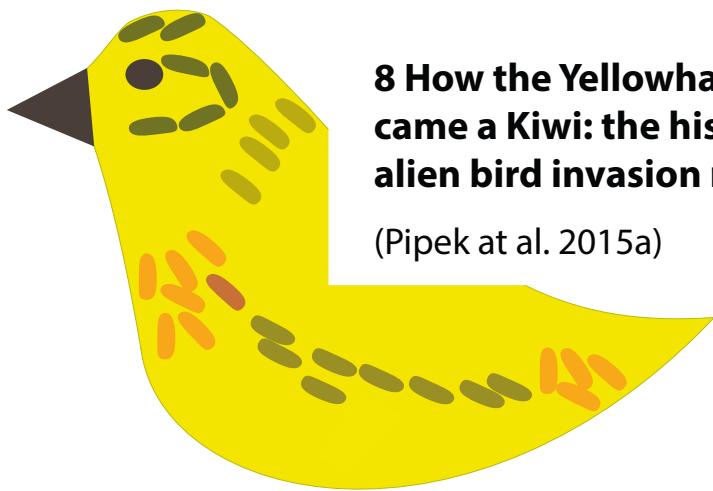
**6 A review of the distribution of  
Yellowhammer (*Emberiza citr-  
inella*) dialects in Europe reveals  
the lack of a clear macrogeo-  
graphic pattern**

(Petrusková et al. 2015)



**7 Dialects of Czech Yellowhammers: detailed large-scale mapping of birdsong geographic variation thanks to a citizen-science project**

(Diblíková et al., unpublished manuscript)

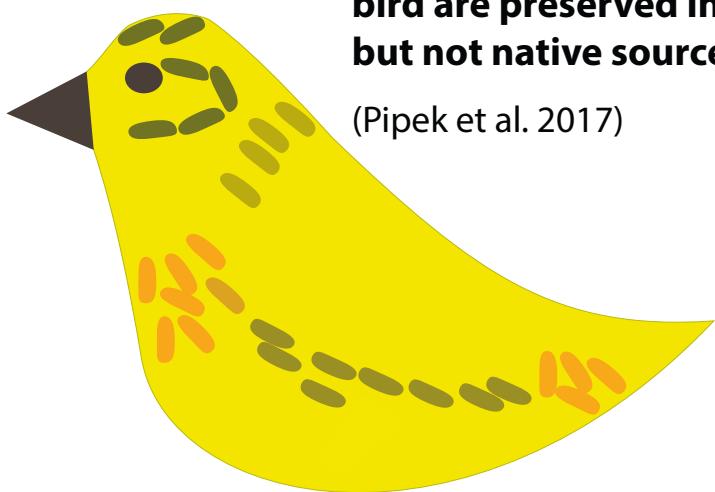


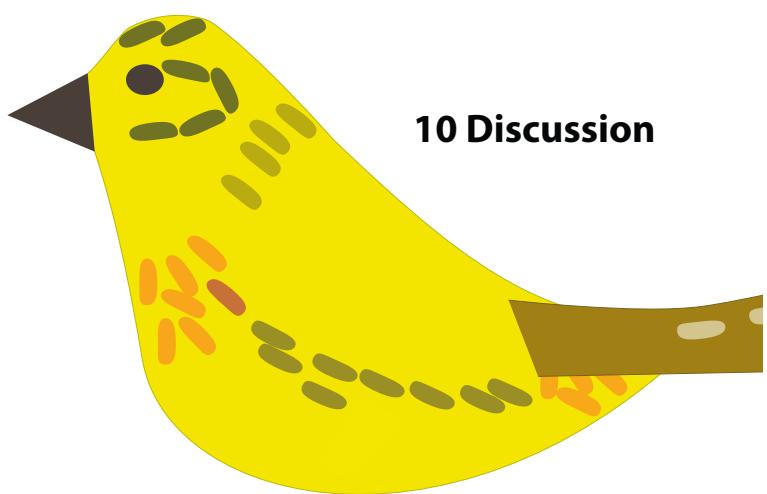
## **8 How the Yellowhammer became a Kiwi: the history of an alien bird invasion revealed**

(Pipek et al. 2015a)

**9 Dialects of an invasive song-bird are preserved in its invaded but not native source range**

(Pipek et al. 2017)





## 10 Discussion

## 10 Discussion

The thesis is composed of four articles (one of them is a manuscript under review as chapters and two articles as appendices. These studies contributed to the general knowledge of yellowhammer dialect distribution, both on global (Chapter 6) and regional level (Chapter 7, Chapter 9 and Appendix 2), and of the history of New Zealand avian invasions (Chapter 8, Appendix 1). All chapters include discussion of the specific topics they address, here I will summarize the results and place them into a broader perspective.

In our European review (Chapter 6) we combined data about dialect distribution included in previous studies and derived from recordings available in online repositories and archives, mostly from Central and Western Europe. The dialects are distributed in mosaic-like fashion even on fine scale in the well-mapped localities (Germany, Denmark). Most dialects were found to occur discontinuously, in multiple countries, which was especially prominent for the two most common dialects BC and XIB. Similar patterns were found when dialects were merged into two groups according to the first terminal syllable. We could therefore rule out the possibility that yellowhammer dialects form macrogeographical groups defined by the first terminal syllable, which was suggested in the past (Salomonsen 1935, Cramp and Perrins 1994). We managed to link old nomenclature used some previous researchers (Salomonsen 1935, Kaiser 1965), Moller 1982 to a new one proposed by Hansen (1985, though in some cases it was not possible, because some authors (Salomonsen 1935, Kaiser 1965) did not distinguish the frequencies in combinations of two B syllables and thus considered the BlBh, BhBl and BBe dialects as the same type. The importance of this unification is highlighted by the fact that the old nomenclature was still used as late as in 2012 (Rubtsov and Opaev 2012). These authors suggested their own modification of the old nomenclature, apparently ignoring Hansen's work (Hansen 1985). Our unification of the nomenclature allows to compare the results of different studies, which might be especially useful for future studies on the long-term stability of dialect types.

The large dataset of almost 4000 recordings, that were collected within the Czech citizen-science project (Chapter 7), confirmed the mosaic-like distribution of yellowhammer dialects in the Czech Republic which was previously reported from other regions (e.g. Hansen 1985, Glaubrecht 1989, 1991). Overall, we identified six previously described dialects. Like in the European review, the most common dialects in the Czech Republic were BC and XIB, followed by BE. Similarly to (Frauendorf 1994) we found that several dialects described by Hansen (1985) seem to overlap in their spectrotemporal characteristics. A thorough analysis of these characteristics led us to dissolve the BD dialect into BlBh or BE categories. Several mixed singers, i.e., birds alternating between two dia-

lect types, on dialect borders and birds singing rare dialects were recorded too.

Interestingly, while the numbers of studies dealing with dialects of white-crowned sparrows and yellowhammers are similar (see Table 1 in Appendix 3), there are many studies testing the reactions of both male and female white-crowned sparrows to playback of local or foreign dialect, but only one such study of yellowhammer (Baker et al. 1987b). In several regions of the Czech Republic, the dialects were mapped in such a detail that they allow for testing hypotheses about the origin or maintenance of dialects and about the existence of observed sharp borders. One of the key advantages of our dataset is recordings of the same dialect from distant localities. This makes it possible to overcome problems associated with spatial autocorrelation, which might have biased the results of some previous studies, e.g. on white-crowned sparrows (Baker et al. 1987a, Searcy et al. 2002 but also on our focal species (Baker et al. 1987b).

It is interesting that despite a very long border between BC and XB dialects in the Czech Republic we did not detect the XBC dialect, which is typically found on such borders in other parts of Europe (Petrusková et al. 2015a,) including Great Britain (Pipek et al. 2017). Instead, we identified the mixed singers. I can only speculate that the same situation of two neighbouring dialects can produce two different outcomes – mixed singers, or a new dialect containing notes from both previously separated dialects of the neighbours. The role of mixed singers is also underexplored. In a study on ortolan buntings the mixed singers were suspected for bringing in the other dialect and thereby being responsible for shifting the borders (Conrads 1976).

Our historical excursion into yellowhammer past in New Zealand (Chapter 8), revealed 25 ships with yellowhammers on board that departed from London between 1864 and 1879 to six different ports in New Zealand. For some of the ships, the information about mortality during the shipments were also available. The birds that were liberated around Dunedin (Otago) were originally caught near Brighton (south England). The total number of transported birds is not certain; however, it was surely more than 600 birds. The yellowhammers quickly established and spread so rapidly that by the 1880s' they were regarded as pests. The shipments were discontinued and the birds became a target of organized culling that continued until the beginning of the 20th century. We have identified the source of discrepancy in numbers of individuals liberated as reported by previous researchers – some of the data were omitted, some erroneously interpreted, some birds that were liberated in fact hatched in New Zealand and finally some birds that were transported to New Zealand were never liberated. Although we cannot provide final numbers, we identified the gaps and did not introduce new errors.

This is not the case of two articles published in *Notornis* (Santos 2012,

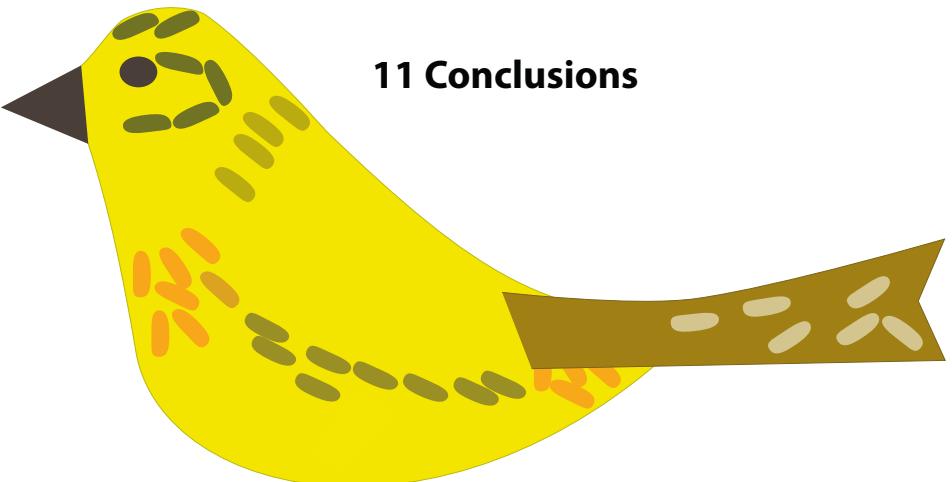
Moulton et al. 2014). The authors claimed to discover previously unpublished information about introduction events of several passerines to Otago region between 1876 and 1882. Their conclusions are based only on one table published in Annual reports, however each report contains also information about localities of release and sometimes also about origin of these birds. By combining information from other documents of acclimatisation societies and newspaper articles we demonstrate that most of these events were only translocations within New Zealand and that significant part of these birds was not liberated in Otago region (Appendix 1). When done for other species, the updated database of avian introductions in New Zealand, including information about mortality of birds during transport, might lead to more robust analyses regarding the role of propagule pressure and other factors in establishment success. As indicated by Andrew (Andrew and Griffith 2016) and also partly by our study (Pipek et al. 2015,) data of similar quality can be obtained even from Australian newspapers and reports of acclimatisation societies.

In the final chapter (Chapter 9), a study connecting bioacoustics with invasion ecology, we obtained 300 recordings of yellowhammers songs from Great Britain and 200 from New Zealand, with decent geographical coverage of both countries. Contrary to our expectation, the dialect diversity was higher in New Zealand and we proved by rarefaction analysis that the difference could not be attributed to different sampling effort. The only identified localities of capture (Brighton, Sussex, Great Britain) and release (Dunedin, Otago, New Zealand) did not have similar dialect composition, in fact, they did not have any dialect in common. We identified seven different dialects in New Zealand and five in Great Britain. Two of these dialects were shared by these countries. The New Zealand dialects that were not recorded in Great Britain, were however reported by several previous studies (e.g. Hansen 1985, Glaubrecht 1991) from continental Europe, including our study in the Czech Republic (Chapter 7), and thus most probably did not evolve in New Zealand. We suggest that New Zealand yellowhammers still sing the dialects of 19th century Britain, which have disappeared from the mother country due to decline of yellowhammer population in last decades (Robinson et al. 2016). The parallel evolution of these dialects in New Zealand is also possible, but we regard it as less plausible.

These results are in contrast to the only one other study exploring evolution of dialects after introduction to new territory, on starling whistles, which revealed reduced dialect diversity in exotic range (Adret-Hausberger 1988). The dialect systems of starling whistles and yellowhammer songs are very different and might be maintained by different processes. Whereas I suspect that in case of yellowhammer, the female choice is the most important factor as suggested by the study of Baker et al. (1987b), the starling dialect seems to serve as a signal of social membership, as birds singing the same dialects stay close also

in roosts (Hausberger et al. 2008). It is also noteworthy, that although New Zealand probably retained the original dialects of Great Britain, there is one important difference between this archipelago and the rest of the world, the relative rarity of BC dialect. This dialect was recorded only in a small locality in the North Island, and is probably missing altogether in the South.

As may be seen it Table 1 in Appendix 3, a few species are over-represented in studies on dialects, mainly yellowhammer and white-crowned sparrows. This thesis does little with this phylogenetical bias, however I would say that chapters included in thesis and the ever-increasing coverage in Europe (<http://yellowhammers.net/recording/full>), represents a good starting point for intensified research on yellowhammer and other species dialects, leading to increased knowledge about their role in bird ecology.



## 11 Conclusions

## 11 Conclusions and future research pathways

Before the start of my PhD study, the knowledge about yellowhammer dialects was fragmented. We pulled the information scattered across many papers into one review and later one map ([www.yellowhammers.net/recording/full](http://www.yellowhammers.net/recording/full), which was substantially enriched by data from our three citizen-science projects (Chapter 7 and Chapter 9 and Appendix 2) and by recordings collected elsewhere. Where it was possible, we linked the old nomenclature to the currently used one. The website that I established for Great Britain/New Zealand project is already serving other two sister projects, in Switzerland and Poland, and the map includes also recordings from available online sources. To my knowledge, the scale and detail of knowledge about yellowhammer distribution exceed that of other model species in dialect research.

Still many research gaps remain. Although yellowhammer dialects have longer research history than other species studied (see Table 1 in Appendix 3), little is known about the processes that maintain the typical mosaic-like patterns. Genetic differences between populations have not been satisfactory explored as yet (but see Neye et al. 2006). Previous experiments on females (Baker et al. 1987a) compared reactions to local versus distant dialects (not only foreign, thus the results must be interpreted with care, in fact it would be better to repeat the experiments, however this time using recordings that would for both dialects come from non-local area. The large Czech dataset (Chapter 7) already allowed our team to test the reactions of males to local / non-local dialects (Bílková et al. in prep. and assess whether or not the dialect distribution is associated with the distribution of different habitats (Kauzál et al. in prep.. These results are not included in this work.

The study on dialects in UK / New Zealand (Chapter 9) adds to other studies that addressed behavioural changes following the introduction to an exotic range (Suarez et al. 2016. It is one of a few studies (Lynch et al. 1989, Lang and Barlow 1997, Hamao 2015) exploring the cultural evolution of birdsong after introduction to exotic range. In terms of dialect part of such an evolution, our study is preceded only by the pioneering paper on starling whistles (Adret-Hausberger 1988). Whereas the songs of starlings following invasion to Australia lost some diversity (Adret-Hausberger 1988) we found a greater dialect diversity in the exotic range of New Zealand than at home in Great Britain (Chapter 9), which we assign to different population trends in the two countries (Robinson et al. 2016).

The historical study in New Zealand (Chapter 8), followed by our short comment on two articles in *Notornis* (Appendix 1 demonstrate the potential hidden in primary historical sources. We already extended our analysis of old documents of acclimatisation societies and newspaper articles to other passerines

introduced to New Zealand (Pipek et al., in prep.). Analysis of such a dataset will make it possible to assess the generality of results on the patterns of historical introduction we obtained for yellowhammer, and provide insights into the variation among species.

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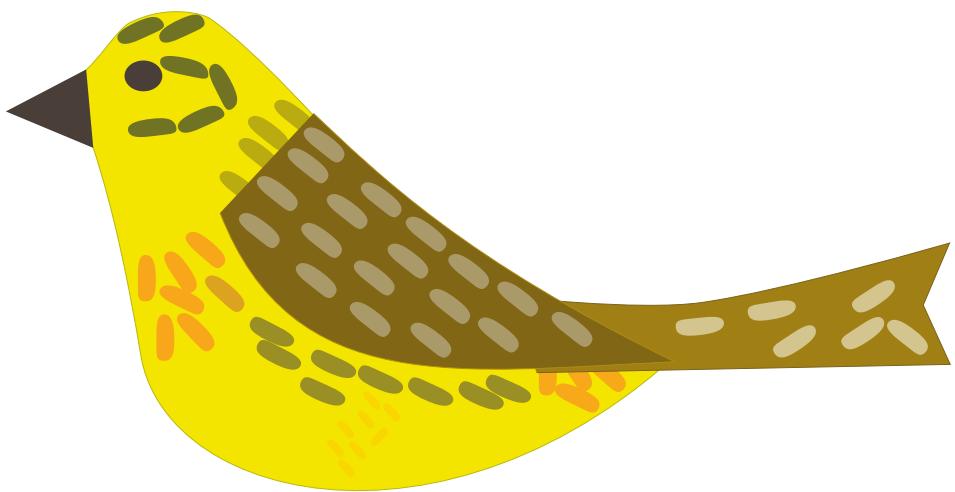
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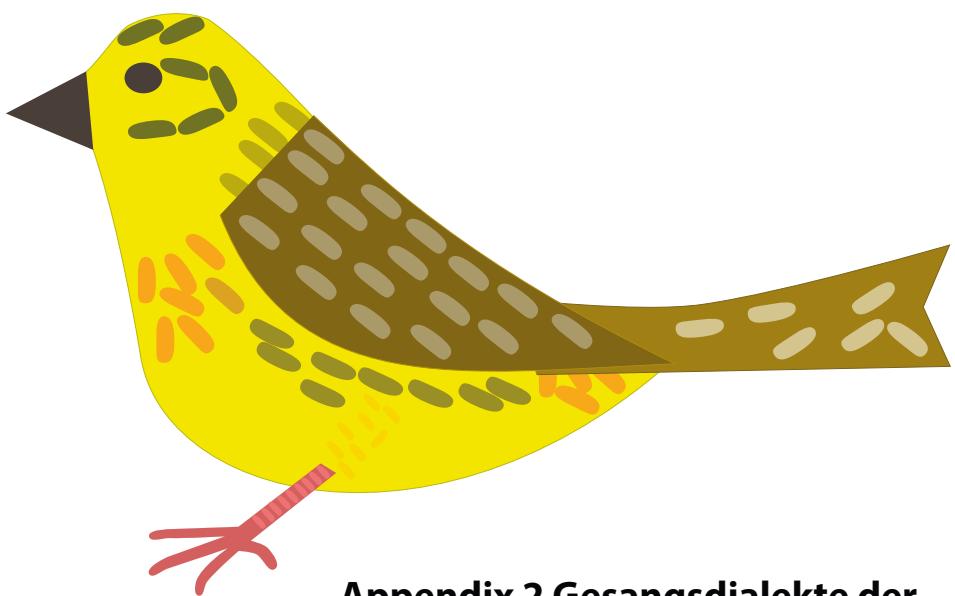
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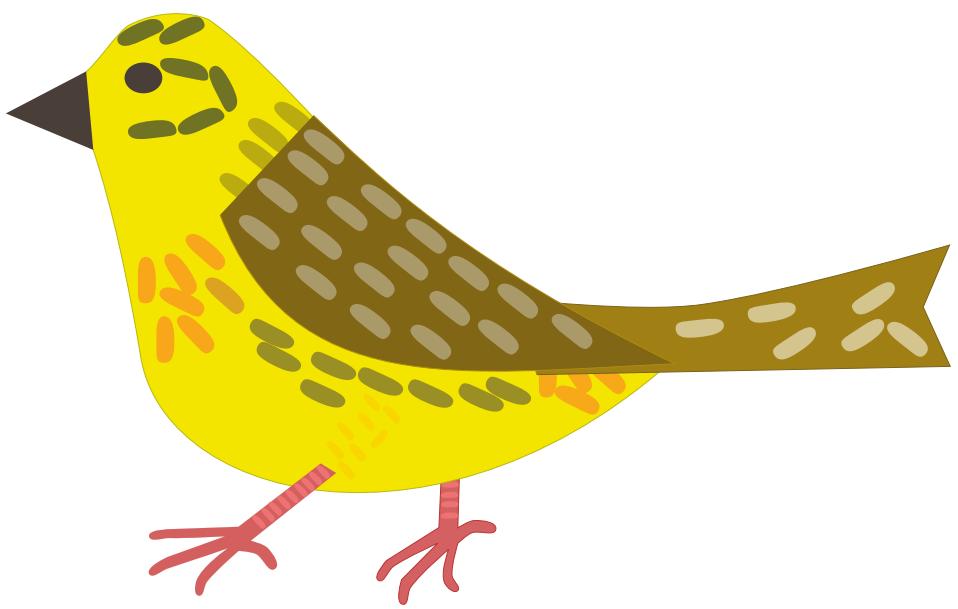
**Appendix 1 A clarification of the  
origins of the birds released by the  
Otago Acclimatisation Society  
from 1876 to 1882**

(Pipek et al. 2015b)



**Appendix 2 Gesangsdialekte der  
Goldammer *Emberiza citrinella*  
in der Schweiz**

(Ambühl et al. 2017)



### **Appendix 3 Table 1**