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

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# Patterns of song variation in migratory and sedentary birds: A comparison of two sister pipit species

## Variabilita zpěvu u migrujících a sedentárních pěvců: porovnání dvou sesterských druhů lindušek

Doctoral dissertation

Supervisor: Tereza Petrusková

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# DECLARATION OF ORIGINALITY

I declare that this dissertation has not been submitted for the purpose of obtaining the same or another academic degree earlier or at another institution. My involvement in the research presented in this dissertation is expressed through the authorship of the included publications and manuscripts. and my personal contribution to the conception, data collection, curation, analysis and manuscript writing for each of the following chapters is truthfully described in the "chapters and author's contributions" section. All literature sources I used when writing this dissertation have been properly cited.

Prague, 06.08.2024

Javier Oñate Casado M.Sc.

As a supervisor of this dissertation and a co-author of all involved studies and manuscripts, I declare that the contribution of the PhD-student, Javier Oñate Casado, to the published, submitted and finished manuscripts can be considered more than sufficient to justify the inclusion of these papers in this PhD dissertation.

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Berthelot's Pipit at Charco de la Araña with the Teide volcano in the background, Tenerife (Canary Islands, Spain)

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# CHAPTERS AND AUTHOR'S CONTRIBUTIONS

## Chapter 1

**Oñate-Casado, J**., Porteš, M., Beran, V., Petrusek, A., Petrusková, T. (2023). Guess who? Evaluating individual acoustic monitoring for males and females of the Tawny Pipit, a migratory passerine bird with a simple song. *Journal of Ornithology*, 164: 845–858.

> JO-C: conceptualization, data curation, formal analysis, funding acquisition, visualization, writing – original draft, writing – review & editing.

## Chapter 2

**Oñate-Casado, J**., Porteš, M., Beran, V., Petrusek, A., Petrusková, T. (2021). An experience to remember: lifelong effects of playback-based trapping on behaviour of a migratory passerine bird. *Animal Behaviour,* 182: 19–29.

> JO-C: data curation, formal analysis, visualization, writing – original draft, writing – review & editing.

## Chapter 3

**Oñate-Casado, J**., Porteš, M., Beran, V., Pérez-Granados, C., Traba, J., Barrero, A., Sakhalkar, S, P., Petrusek, A., Petrusková, T. (manuscript submitted). When individuality obscures geographic song variation: a comparison of two passerine sister species with different migratory strategies

> JO-C: conceptualization, data collection, data curation, formal analysis, funding acquisition, visualization, writing – original draft, writing – review & editing.

# PREFACE

It has been a long journey to get to this point, and it feels appropriate to reflect on where and when my adventure into scientific research began. Back in 2016, as an undergraduate with practically no research experience and limited confidence in expressing myself in a foreign language, I found myself on the Big Island of Hawaiʻi. At that time, a PhD was not even on my radar; I could not even imagine that I would one day have the chance to pursue this path. However, my determination to achieve whatever I set my mind to never wavered.

The LOHE Bioacoustics Lab gave me my first opportunity to work in bird behaviour and bioacoustics, but above all, introduced me to the essence of research by encouraging me to conduct my own project from scratch, to freely explore ideas and to develop my thoughts without limitations. This experience ignited my passion for research, a lesson for which I will be always grateful.

The image below symbolizes this key moment in my life. Working on the Hawaiʻi ʻElepaio on the north-eastern slope of Mauna Loa Volcano, I discovered my calling. Many experiences since then have shaped my journey to this point. And with many more to come, this is just the beginning. I can't wait to see what comes next.

Illustration of male (lower) and female Hawai´i ´Elepaio (*Chasiempis sandwichensis*)
by Sailee Pradeep Sakhalkar.

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I am deeply grateful for my time in the LOHE lab and the TROPIMUNDO program, and for every person I had the fortune to meet through these experiences. They were two of the most memorable moments of my life, and although they did not directly contribute to my thesis, they certainly prepared me for the challenges I faced later in my PhD journey. I owe them a part of my success.

Thanks to all the great people I met in Prague over the last 4 years. Loui, thank you for being such a pure soul full of contagious joy; I hope Texas is treating you well. Vojta, thank you for the scientific discussions, for the unforgettable experience of the Fledglings Meeting, and for fico d'Italia. Jeff, what a nice surprise to meet you, and what a nice connection in just a few weeks, we have pended a field trip to the Galapagos. Constantinos, thanks for the nice and engaging conversations about whatever, the discussions on how to kidnap Pascal, and for introducing melomakarona into my life. Guillermo, from our roots in Arganzuela to fighting hand in hand to get a PhD in Prague; thanks for being a great partner of joys and sorrows on this journey—nosotros siempre elegimos aventura. Riccardo, mio fratello, pure calm and always with the right words to say to me in stressful moments. Thanks for dealing with my constant attempts to monopolize the acoustic space in the office and for sometimes even joining me, and of course for all the great Italian meals you have fed me over the last 4 years. I also want to acknowledge everyone from the Cibulkach crew who crossed my path; thank you for any given advice, those marathons of complaining and the evening chats over tea, beer or whisky.

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# ABSTRACT

Individuality in acoustic signals is crucial for animal communication, facilitating individual recognition across diverse taxa and social contexts. This PhD thesis examines the role of individual vocal signatures in the behaviour, ecology, and conservation of bird species, focusing on the Tawny Pipit (*Anthus campestris*) and the Berthelot's Pipit (*A. berthelotii*). A series of interlinked studies in this thesis assesses the potential of individual acoustic monitoring (IAM) as a non-invasive method for studying and conserving these species.

Chapter 1 investigates IAM's suitability for both male and female Tawny Pipits, a migratory species critically endangered in Central Europe. The findings confirm that Tawny Pipits possess simple, individually distinct songs that are temporally stable within and between seasons. This supports IAM as a reliable approach for monitoring this species, providing a proof of concept for its application in passerines with small repertoires and simple songs.

Building on these insights, Chapter 2 evaluates the long-term behavioural effects of playback-associated mist netting on male Tawny Pipits. The study reveals that males remember negative experiences associated with mist-netting for several years, modifying their responses to similar stimuli in future encounters. This underscores the potential of IAM to replace invasive monitoring practices, which can negatively impact individuals' behaviour and health, thus reinforcing the conclusions from Chapter 1 regarding the advantages of non-invasive monitoring.

Chapter 3 extends the methodology validated in Chapter 1 to Berthelot's Pipits, confirming song individuality in this sedentary island species endemic to Macaronesia. By comparing song variation across geographic scales between Tawny and Berthelot's Pipits, this chapter explores the similarities and differences between the species, evaluating the potential influence of migratory behaviour and population isolation on song divergence. Contrary to our expectations, we found no region-specific song characteristics in either species, possibly due to rapid cultural evolution in birds with simple but individually unique songs, which can override founder effects. Both species exhibited high intrapopulation song variation and increased mean song differentiation at broader scales. In Berthelot's Pipits, however, the gradient of song differentiation was more pronounced, showing higher mean song similarity at the smallest spatial scale, presumably due to their sedentary nature, and the highest mean song dissimilarity between two subspecies of Berthelot's Pipits, which inhabit the Madeira and Canary archipelagos, respectively. This comparative study provides hints into how different ecological and life history traits may influence acoustic communication and cultural evolution in closely related species.

Overall, the thesis demonstrates the efficacy and potential of individual acoustic monitoring for studying bird behaviour and ecology, advocating for its broader implementation in species conservation and management. The findings emphasize the need for such non-invasive monitoring methods in both research and conservation, particularly for species in challenging environments. Finally, this thesis highlights the complexities of acoustic signal evolution and the significance of geographic and ecological factors in shaping vocal behaviour, contributing to a broader understanding of song variation and cultural evolution in migratory and sedentary birds.

## ABSTRAKT

Individualita v hlasových projevech je zásadní pro komunikaci zvířat a usnadňuje rozpoznávání jedinců v rámci různých taxonů i sociálních kontextů. Tato disertační práce se zaměřuje na dva sesterské druhy pěvců, lindušku úhorní (*Anthus campestris*) a lindušku kanárskou (*A. berthelotii*), a na jejich příkladě se zabývá rolí hlasové individuality v chování, ekologii a ochraně ptačích druhů. Vzájemně propojené studie v této práci hodnotí potenciál individuálního akustického monitoringu (IAM) jako neinvazivní metody pro výzkum a ochranu těchto druhů.

První kapitola zkoumá vhodnost IAM pro samce i samice lindušky úhorní, stěhovavého druhu, kriticky ohroženého ve střední Evropě. Studie potvrzuje, že lindušky úhorní mají jednoduché, individuálně odlišné zpěvy, které jsou stabilní v rámci sezóny i meziročně. Výsledky podporují předpoklad, že IAM může být spolehlivým přístupem k monitorování nejen tohoto druhu, ale i dalších pěvců s malým repertoárem a jednoduchými zpěvy.

V návaznosti na tyto poznatky druhá kapitola testuje, zda běžně používaná metoda odchytu pěvců do nárazové sítě za pomoci playbackové nahrávky dlouhodobě ovlivňuje následné chování odchycených samců lindušky úhorní. Výsledky ukazují, že si samci pamatují negativní zkušenosti spojené s odchytem až pět let a chovají se odlišně od těch, kteří nikdy odchyceni nebyli. Studie poukazuje na potenciál IAM, který umožňuje sledovat jedince bez potřeby odchytu. Může tak být vhodnou alternativou jak při ochranářských projektech vyžadujících dlouhodobé sledování jedinců, tak při výzkumu, kde je nutné jedince rozlišovat.

Třetí kapitola rozšiřuje metodologii ověřenou v první kapitole na lindušky kanárské a potvrzuje individualitu zpěvu i u tohoto nemigrujícího endemického druhu makaronéských ostrovů. Dále porovnává variabilitu zpěvů lindušek úhorních a kanárských napříč různými prostorovými škálami a vyhodnocuje rozdíly mezi oběma druhy, jež by mohly být výsledkem odlišného migračního chování obou druhů a míry izolace jejich populací. Oproti našemu očekávání jsme ani u jednoho druhu nenašli charakteristiky zpěvu specifické pro konkrétní region. To by mohlo být důsledkem velmi rychlé kulturní evoluce jednoduchého a

přitom individuálně specifického zpěvu, která vede k rychlé akumulaci odchylek a přemaže případné efekty zakladatele. Oba druhy vykazují nárůst odlišnosti zpěvu na větších geografických škálách, ale tento efekt je výraznější u lindušek kanárských. U nich byla největší podobnost zpěvu na nejmenší lokální škále, což může být důsledek jejich sedentarity, a naopak největší rozdíly byly mezi poddruhy z Madeiry a Kanárských ostrovů. Tato srovnávací studie naznačuje, jak mohou rozdíly v ekologii a životních strategiích ovlivňovat hlasovou komunikaci a kulturní evoluci zpěvu sesterských druhů.

Celkově tato disertační práce prokazuje účinnost a potenciál IAM pro studium chování a ekologie ptáků a poukazuje na vhodnost širšího využití takových neinvazivních monitorovacích metod ve výzkumu, ochraně přírody a managementu ohrožených druhů. V neposlední řadě poukazuje na složitost evoluce akustických signálů a vlivu geografických a ekologických faktorů na utváření hlasových projevů, čímž přispívá k širšímu pochopení variability a evoluce zpěvu stěhovavých i stálých ptáků.

# INTRODUCTION

## Individuality in acoustic signals

Individual recognition primarily relies on individuality – the existence of consistent differences in appearance, smell, sound, and behaviour between individuals, making them distinctive from one another. The presence of individually unique patterns in vocalizations can serve as an acoustic channel for individual recognition as observed in many animals using individual vocal identification to communicate during various social contexts, such as territorial conflicts, mating, parent-offspring interactions, and cooperative breeding (Godard 1991; Crowley et al. 1996; Insley 2000; Tibbetts & Dale 2007; Bradbury & Vehrencamp 2012).

While vocal signatures play an important role in social interactions, the degree of individuality in vocalization might vary across taxa and contexts. For instance, increased individuality in vocal cues has been largely reported in species living in large social groups, where the need to be distinct is more evident. For example, dolphins use unique signature whistles to identify and interact with specific individuals within their pods (Janik & Sayigh, 2013). Similarly, elephants produce distinctive vocalizations that function as "names", enabling them to address specific members of their social groups (Pardo et al. 2024). Bats primarily use the echoes of echolocation calls to navigate their environment, but species such as the Greater Mouse-eared bats (*Myotis myotis*) also exhibit individual-specific features in their echolocation calls to recognize conspecifics and maintain social bonds within their colonies (Yovel et al. 2009). In large colonies, such as those of penguins and pinnipeds, individual vocal recognition is crucial for parental care and social cohesion (Aubin et al. 2000; Aubin & Jouventin 2002). Among birds, corvid species exhibit individual and group recognition based on acoustic cues, highlighting the role of vocalizations in maintaining social cohesion and individual identity (Hopp et al. 2001; Kondo et al. 2010; Kondo et al. 2012; Boeckle et al. 2012; Sierro et al. 2020).

Even solitary animals or those living in pairs show high individuality in their vocal signatures, such as vocalizations used during territorial defence, mate attraction, and individual recognition among conspecifics. Vocal individuality has been documented across various vertebrate species, including frogs (Bee & Gerhardt 2001; 2002; Feng et al. 2009), manatees (Sousa-Lima et al. 2022; 2008; Merchan et al. 2019), tapirs (Walb et al. 2021), and birds (Osiejuk et al. 2007; Wilson & Mennill 2010; Petrusková et al. 2016, Chen et al. 2020). Remarkable variation among individuals has been revealed in bird species. For example, up to 1000 unique individual vocal signatures can potentially be encoded by a sample size of 104 male Corncrakes (*Crex crex*; Budka & Osiejuk 2013; Linhart et al. 2019), showing the high level of individuality within this species. These studies support that, like highly social animals, solitary animals also possess individually distinct acoustic signals. Besides, an analysis of over 200 studies on individual vocalizations across various bird and mammal species indicates that individuality is most pronounced in acoustic signals related to sexual selection (e.g., mate attraction and territorial defence) compared to those used for communication within social groups (P. Linhart, unpublished results). While this observation aligns with previous theoretical studies (Johnstone, 1997; Thom & Dytham 2012), it has also been suggested that the evolution of individual acoustic vocalizations may be shaped simultaneously by both sexual and social selection within the same bird species (Keen et al. 2016). Overall, these insights suggest that the primary evolutionary drivers of individuality in animal acoustic signals are still not fully understood.

While the processes affecting acoustic individuality vary among species, its practical role in wildlife conservation is promising. Vocal signatures have been effectively used for monitoring bird individuals to assess population density, survival rates in sedentary species, return rates in migratory species, and changes in territorial dynamics and replacements (Laiolo et al. 2007; Vögeli et al. 2008; Adi et al. 2010; Kirschel et al. 2011; Petrusková et al. 2016). Due to its non-invasive approach, individual acoustic monitoring (IAM), monitoring based on the analyses of individual vocal cues, can be used on wild species with fewer concerns about impacts on the behaviour of target individuals (reviewed in Terry et al. 2005) and might even provide more accurate information about behaviour or population dynamics than classical methods, or effectively complement them (e.g., Laiolo et al. 2007; Petrusková et al. 2016). However, IAM has not been used very frequently despite the advantages it offers. This could be because methods of acoustic individual identification were closely tailored to a single species with little attention paid to developing more general approaches that could be used across different species (Linhart et al. 2019).

Although individually distinctive vocalizations have been reported in several taxa (e.g. Bee & Gerhardt 2001; Janik & Sayigh 2013; Petrusková et al. 2016; Merchan et al. 2019; Pardo et al. 2024), most of the work using acoustic signatures to study behaviour and ecology has been traditionally focused on birds (Terry et al. 2005). Within birds, although a few studies have confirmed the efficiency of IAM in passerine species (Laiolo et al. 2007; Vögeli et al. 2008; Adi et al. 2010; Kirschel et al. 2011; Petrusková et al. 2016), research is mostly limited to non-passerine species with simple vocalizations such as Great Bitterns (*Botaurus stellaris*), ducks and owls (Gilbert et al. 2002; Volodin et al. 2005; Galeotti & Sacchi 2001; Tripp & Otter 2006; Grava et al. 2008; Choi et al. 2019). This could be because the implementation of IAM for passerines with higher song complexity is time-intensive, especially at the beginning, when the temporal stability and individual uniqueness of target species' song must be evaluated (Petrusková et al. 2016).

Besides, IAM on passerines has mostly focused, if not only, on male individuals. The phenomenon of females singing has been traditionally overlooked, especially in temperate zones where studies on female songs are much less prevalent than in the tropics (Langmore 1998; Odom et al. 2014; Hall & Langmore 2017). This could be because female birds in temperate areas are quiet and visually cryptic (Price 2019), might only sing for very short periods during the breeding season (e.g., McDonald & Greenberg 1991), and in many species, males and females cannot be visually distinguished (Langmore 1998; Hahn et al. 2013; Odom & Benedict 2018). Nevertheless, in some temperate songbird species, not only has it been shown that females sing, as recently documented in one of the most studied model species, the Blue Tit (*Cyanistes caeruleus*; Sierro et al. 2022), but also that songs can be used to discriminate between males and females (Yamaguchi 1998). In such cases, acoustic monitoring might also provide reliable information about the sex of the vocalizing individuals.

In **Chapter 1**, we evaluated the suitability of IAM for both male and female of the Tawny Pipit (*Anthus campestris*), a migratory Palearctic species critically endangered in Central Europe for which occasional female singing was documented (Neuschulz 1986). Our study, conducted in the only remaining population for this species in Czechia, situated in an active surface coal mine area, confirmed that Tawny Pipits have simple and individually distinct songs. Although no-sex specific differences between the songs of male and female individuals were found, Tawny Pipits songs are, at least for males, temporally stable within and between seasons. These findings thus support IAM as a reliable, non-invasive approach for studying the behaviour and ecology of passerine species with a small repertoire and simple songs. This study also serves as a proof of concept for applying IAM to Tawny Pipits. We validated our methodology for both ringed and non-ringed individuals by first testing assumptions on song individuality and temporal stability in a subset of ringed males and females, and then extending these findings to non-ringed individuals.

While the insights in **Chapter 1** leave the door open to considering less intrusive alternatives like IAM, why is there such a need to implement this approach in Tawny Pipits? In **Chapter 2**, we evaluated the long-term effects of playback-associated mist netting on the behaviour of male Tawny Pipits from the same population. Traditional mark-recapture methods involve physical manipulation that may negatively impact individuals' health (Marco et al. 2006; Mulcahy et al. 2011; Spotswood et al. 2012) and affect behaviour (Linhart et al. 2012; Camacho et al. 2017; Seress et al. 2017; Budka et al. 2019). Previous studies have also reported cumulative effects of the playback lure plus capturing and handling on the subsequent behaviour of birds (e.g. Linhart et al. 2012; Budka et al. 2019). Given this and based on incidental field experience that suggested the increased difficulty of recapturing once-caught males (e.g. to retrieve attached geolocators; V. Beran pers. comm.), we hypothesized in **Chapter 2** that mist netting after playback influences males' behaviour in comparable situations later in life. Through playback experiments simulating territorial intrusion of conspecifics, our study provided evidence that male Tawny Pipits remember conditions associated with one-time negative experience. They appear to retain the memory of having been lured into mist-nets by playback of a conspecific song (a common bird ringing technique) for several years and modify their subsequent behavioural response to a similar stimulus. Specifically, there were no differences in the responses of males captured and ringed one to two years before to the experiment compared to those captured up to five years before, and all differed from naïve males with no previous capture experience. To our knowledge, such long-term memory of a single event in passerines has only been demonstrated in corvids (Johnson 1994; Marzluff et al. 2010; Blum et al. 2020), not for much smaller migratory species.

Ringing in this population usually involves capturing and handling by using mist-net and playback luring, practices that **Chapter 2** demonstrates to have an influence on in future capturing events, and consequently, affect the estimates of mark-recapture methods. This has implications for a wide range of ornithologists, as well as for researchers focusing on territorial behaviour, memory and vocalization. These results also reinforce the conclusions of **Chapter 1**. Tawny Pipits are undergoing a severe population decline in Central and Western Europe (Briedis et al. 2016; Tyler & Christie 2020), with only one remaining breeding population in Czechia, situated in an active coal mine area. This population, comprising about 200 breeding pairs, has been intensively monitored since 2012 (Briedis et al. 2016; Beran et al. 2018). However, monitoring in the coal quarries is challenging due to habitat fragmentation, limited accessibility to the species' territories, and the high level of anthropogenic disturbance. Considering insights from **Chapters 1 and 2**, we stablish IAM as a valuable non-invasive method that can replace commonly used monitoring practices, even in harsh mining landscapes.

Building on the findings of **Chapter 1**, our study reveals that song learning in Tawny Pipits is age-limited, resulting in individually distinct and stable songs after the learning phase. This has been also proven by our research group in another pipit species, the Tree Pipit (*A. trivialis*; Petrusková et al. 2016). Furthermore, song-learning capabilities appear to be conserved among closely related songbird species (Catchpole & Slater 2008). Given this background, and based on our initial visual inspection of songs, we hypothesized that our conclusions regarding individuality and temporal stability in Tawny Pipits could potentially extend to their sister species, the Berthelot's Pipit (*A. berthelotii*). Building upon our reliable method established in **Chapter 1** for identifying Tawny Pipits by their songs, which was validated for non-ringed individuals, we applied the same approach to non-ringed Berthelot's Pipits. This enabled us to confirm song individuality in Berthelot's Pipits (**Chapter 3**), thereby enhancing our understanding of patterns of song variation at the individual level in both Tawny and Berthelot's Pipits.

Having established individually unique acoustic signatures for Tawny and Berthelot's Pipits, we scaled up our project to study and compare song variation at geographic scales in both species (**Chapter 3**). This endeavour involved recording bird songs across diverse landscapes in central and southern Europe, as well as in oceanic islands with warm, subtropical climates. This comparative study added depth to our research and allowed us to increase our understanding of song variation in migratory and sedentary pipit species from a broader point of view.

## Scaling up: Song variation across geographic scales

Oscine passerines use song for species recognition and intraspecific interactions, such as mate attraction and territorial defence. Song development in these birds is influenced by vocal learning and is culturally transmitted, resulting in significant song variation within and between species (Slater & Ince 1979; Podos et al. 2004; Lachlan et al. 2018). Through learning from parents and neighbours, cultural transmission can maintain specific song types within populations over generations (Marler & Tamura 1964; Baptista 1977; Baptista & Morton 1988). However, song learning strategies in oscine species vary in copying strategy and timing of learning (Beecher & Brenowitz 2005; Brenowitz & Beecher 2005), which may be directly related to geographic song variation.

Song learning between neighbouring groups of birds that might interact with each other can result in different patterns of song sharing between conspecifics in the same location, ranging from a complete overlap of song types to no sharing at all (Handley & Nelson 2005; Catchpole & Slater 2008). Song variation at this scale is referred to as microgeographic variation, as contrasted against macrogeographic variation (Mundinger, 1982) which refers to between populations separated by many kilometres, where individuals are unlikely to encounter each other (Catchpole & Slater 2008).

Geographic variation can manifest in several ways, including differences in song complexity, specific song phrases, and the functions of song features. For example, Singh and Price (2015) examined two Himalayan warbler species and found that song complexity increases with latitude, suggesting that environmental factors like habitat structure and ambient noise levels may drive these differences, leading to distinct regional dialects within species. Additionally, studies on White-crowned Sparrows (*Zonotrichia leucophrys*) and Savannah Sparrows (*Passerculus sandwichensis*) have shown that specific song elements play crucial roles in individual and local identity. Nelson (2017) found that the introductory whistle phrase, presumed to have an alerting function, does not vary geographically. In contrast, the note complex phrase and the trill phrase, which are used for individual recognition among territory neighbours and to indicate geographic origin, respectively, show geographic variation. Furthermore, Williams et al. (2019) demonstrated that the buzz segment of Savannah Sparrow songs acts as a population marker, highlighting the role of specific song elements in local population identification. These studies indicate that selective pressures acting on different aspects of bird acoustic communication can lead to diverse patterns of geographic variation. Therefore, studying geographic variation in birdsong might provide valuable insights into the relationship between geographic signal variation, reproductive isolation, and speciation.

Bird songs, being culturally transmitted, can diverge more rapidly than genetic traits and thus serve as early indicators of speciation (Irwin & Price 1999). This divergence can also contribute to speciation by promoting prezygotic reproductive isolation. Divergence in bird songs is often driven by strong selective pressures. According to the Acoustic Adaptation Hypothesis (Morton 1975), song traits that optimize sound transmission in specific habitats are favoured in song evolution. For instance, low-frequency sounds transmit further and are less absorbed by trunks and leaves in dense vegetation environments. However, it is important to note that a recent global analysis on song frequency including most passerine species (Mikula et al. 2021) contradicts the hypothesis. While the approach followed by this study lacks detailed information on bird behaviour, habitat density, and habitat characteristics at each recording site, it suggests that there may be other factors at work that cause shifts in body size affecting sound properties, such as sexual and natural selection.

Sexual selection may also play an important role in song evolution. For example, song complexity and repertoires in songbird species can be influenced either by female mate choice (MacDougall-Shackleton 1997; Catchpole et al. 1984; Catchpole 1986; Buchanan and Catchpole 1997; Reid et al. 2004) or by male-male competition (Slater 2003, Beecher & Brenowitz 2005). In addition, selection on parts of the vocal apparatus used for non-vocal functions may have secondary effects on song evolution. An example of this is the indirect evolution of song as a consequence of beak evolution in Darwin's finches of the Galápagos Islands (Podos & Warren 2007). Vocal parameters such as trill rate and frequency bandwidth have been observed to correlate with beak morphology (Podos 2001; Podos & Nowicki 2004; Huber & Podos 2006), which in Darwin's finches varies with food availability and interspecific competition (Grant & Grant 1995; 2002; 2006).

Cultural evolution of learned vocalizations is strongly influenced by the choice of tutors. In songbirds, juveniles can learn from a large number of singing males around them, making them more likely to adopt a common song variant—a phenomenon known as conformist bias (Morgan et al., 2012). This, combined with moderately precise learning, leads to stable traditions in bird populations (Lachlan et al., 2018). On the other hand, imprecise song learning can result in strong cultural drift, accelerating song divergence and potentially contributing to allopatric speciation when populations become geographically isolated by various barriers (Lachlan & Servedio, 2004).

Because oceanic islands are geographically discrete units, they provide suitable systems to understand evolutionary diversification processes. On archipelagos, populations are smaller and less connected; when coupled with other conditions, this leads to differences in the effects of evolutionary processes between island and mainland systems. This also applies to cultural evolution, with the isolation of islands enabling us to observe how populations within species evolve their cultures independently (e.g. Emerson 2002; Parker et al. 2012; Lachlan et al. 2013; Illera et al. 2014). Considering this, songbirds with recently founded and spatially isolated populations are suitable models for studying acoustic and genetic differentiation because each colonization event represents an independent evolutionary episode.

The evolution of acoustic signals in insular birds remains poorly understood, especially when compared to their mainland relatives. Robert et al. (2021) analysed the acoustic signals of 22 island endemic bird species endemic to the islands of São Tomé and Madeira and their closest mainland relatives in Mount Cameroon and southern France. They found some trends indicating a decrease in song complexity on islands compared to mainland areas. In contrast, Price (2008) reviewed 15 studies and found that only 8 showed a decrease in song complexity in island species. Similarly, Morinay et al. (2013) found no consistent pattern of reduced complexity or vocal performance in their comparison of 49 pairs of island-mainland relatives, and Robert et al. (2022) found no differences in syllable diversity, syllable rate, or song duration between 11 pairs of island and continental relatives. These inconsistent results suggest that previous studies comparing island and continental bird song are inconclusive, and that further research is needed to gain more insight into differences in acoustic signals between closely related species from island and mainland systems.

The Tawny Pipit and the Berthelot's Pipit, sister species in the genus *Anthus* (Motacillidae), present a suitable system to study and compare evolution of song. They are closely related genetically (Voelker 1999) and sing simple songs; however, they differ in history of population isolation and migration behaviour. Tawny Pipits are trans-Saharan migrants, widespread in the Palearctic (Briedis et al. 2016), while Berthelot's Pipits are strictly sedentary taxon endemic to Macaronesian islands (Martín & Lorenzo 2001; see section on "Study species" for details). Therefore, these two sister pipit species provided a suitable framework for exploring spatial patterns of song variation in sedentary and migratory species across different geographic scales (**Chapter 3**).

In **Chapter 3**, we expected to find clear geographically structured song variation in both studied pipit species, a phenomenon well-documented in many passerine species. For example, Barišić et al. (2018) reported that regional dialects are defined by the final part of the song in Black-headed Buntings (*Emberiza melanocephala*) across populations along the Adriatic Sea, a feature also observed to show distinct regional characteristics in other *Emberiza* species, such as the Yellowhammer (*Emberiza cintrinella*; Petrusková et al. 2015; Diblíková et al. 2023) and the Cinnamon-breasted Bunting (*Emberiza tahapisi*; Osiejuk 2011). Within the genus *Anthus*, Petrusková et al. (2010) studied geographic song variation in five different Czech populations of the Tree Pipit (*Anthus trivialis*), showing clear regional differences in their song. Contrary to our expectations, both Tawny and Berthelot's Pipits showed lack of clear, geographically structured song variation.

Previous genetic studies on Berthelot's Pipit populations have shown limited gene flow and clear phenotypic variation between archipelagos (Illera et al. 2007; Spurgin et al. 2014; Armstrong et al. 2018; Martin et al. 2021). Additionally, gene flow is also quite restricted between island populations within the same archipelago (Martin et al. 2021). Given these findings, we anticipated observing greater song divergence between populations from the Canaries and Madeira compared to populations from different islands within the same archipelago, reflecting the colonisation trajectory pattern. In contrast, Illera et al. (2014) conducted a study on sedentary populations of another passerine species, the Spectacled Warbler (*Sylvia conspicillata*), and found no clear genetic, morphological, or acoustic differentiation among populations across three Macaronesian archipelagos. Our study, however, found that the mean song dissimilarity between geographically distant individuals (from different archipelagos) was significantly higher than between birds within the same archipelago, thereby aligning our initial expectations. While our approach was based on the comparison of structural differences in song, the acoustic analysis of Illera et al. (2014) was based on measurements of spectro-temporal parameters, which may not sufficiently capture variation in the structural characteristics of songs. Additionally, the genetic structure of Berthelot's Pipit populations is clearly different from the one described for Spectacled Warblers. These differences may explain the discrepancy between the results of the two studies.

Both species exhibited high intrapopulation song variation and increased mean song differentiation over larger geographic scales. Although we did not observe differences in patterns of song similarity on medium spatial scales, these patterns varied between species at smaller scales, which might be due to their different migratory strategies. Berthelot's Pipit songs were generally more similar among neighbouring and nearby individuals (up to 3.5 km) than between those birds considered at any other larger scale. In contrast, Tawny

Pipit songs did not differ in similarity between nearby individuals and those further away from the same field site. This effect can likely be attributed to the sedentary nature of Berthelot's Pipits.

In oscine passerines, juveniles learn songs from adult tutors, such as parents and neighbours (Slater & Ince, 1979; Podos et al., 2004). The song learning process, however, can be influenced by the migratory behaviour of each species. In sedentary species, the distribution of potential tutors is more stable, reinforcing local song traditions among individuals in the same area. For example, Hansen (1999) found long-term stability in the song elements of Yellowhammers (*Emberiza citrinella*), indicating that stable territorial behaviour helps maintain local song traditions. Similarly, Goodale and Podos (2010) documented the persistence of song types in Darwin's finches (*Geospiza fortis*) over four decades, underscoring the role of stable populations in preserving song types. In contrast, migratory birds may learn songs from a broader range of individuals during breeding, wintering, and migration (Hultsch & Todt 2004; Beecher & Brenowitz 2005). Additionally, several studies have shown that song sharing among neighbours is higher in sedentary species than in migratory ones (Ewert & Kroodsma 1994; Kroodsma & James 1994; Kroodsma et al. 1999; Wilson et al. 2000; Nelson et al. 2001; Handley & Nelson 2005). For instance, in *Zonotrichia* sparrows, migratory subspecies do not form dialects (Nelson 1999), while sedentary subspecies exhibit geographic song variation (Baker 1982; Searcy et al. 2022). Thus, we can infer that the differences in song learning opportunities between sedentary and migratory species also apply to Berthelot's and Tawny Pipits, contributing to the distinct patterns of local-scale song variation observed in these species.

Despite our results, it is important to note that high levels of song similarity, specifically song sharing, can also be found at small geographical scales in bird species, regardless of their migratory behaviour. Briefer et al. (2008) found that resident male Skylarks (*Alauda arvensis*) show high syllable sharing with neighbouring individuals, but very little sharing with those just 2 km away. Similarly, Hensel et al. (2002) found that migratory Savannah Sparrows show greater acoustic similarity to neighbours within a few hundred metres than to distant individuals within the same island population, suggesting that this is primarily due to the high degree of natal site philopatry in this species. Additionally, in Black Redstarts (*Phoenicurus ochruros*), song sharing occurs among individuals within small areas but rarely between those separated by distances ranging from a few hundred metres to a maximum of 2.4 km, leading to stable songs forming local microdialects (Draganoiu et al. 2014). These findings demonstrate that small-scale patterns of acoustic similarity may be present in both migratory and non-migratory passerine species.

## OVERVIEW OF CHAPTERS AIMS AND HYPOTHESES

- **Chapter 1**: The main aim of this chapter was to validate the potential of using Tawny Pipits for individual acoustic monitoring by assessing the individuality and temporal stability of their songs. To achieve this, we used data from a long-term monitored population, the only remaining one in Czechia. Given that learning abilities might be conserved between genetically close congeners, we expected that our findings on the temporal stability of Tawny Pipit songs could potentially be extended to Berthelot's Pipits.

- **Chapter 2**: The aim of this chapter was to determine whether Tawny Pipits remember conditions associated with previous negative capture experiences. Our previous observations while monitoring this species in the field suggested increased difficulty in recapturing previously caught male individuals. We therefore hypothesized that capture methods using mist nets and playbacks would affect the behaviour of males in similar situations later in life. Specifically, we predicted that previously captured individuals would be more cautious and less aggressive than those who had never been captured. Findings from this chapter could potentially support the use of less intrusive alternatives, such as individual acoustic monitoring, to study and monitor this species.

- **Chapter 3**: The main aim of this chapter was to explore the intraspecific geographic variation of song in Tawny and Berthelot's Pipits, two sister species with simple song structure but different natural histories and population dynamics, across Europe and Macaronesia. We hypothesized that migration strategy and population isolation would affect song type sharing, increasing song variation in a gradient from sparse, highly isolated island populations (Berthelot's Pipits) to dense migratory populations (Tawny Pipits). We therefore expected differences in song similarity between geographically distant populations and regions for both species. Specifically for Berthelot's Pipits, we hypothesized strong song divergence between different islands, particularly between populations from different archipelagos. Consequently, we anticipated lower within-island variation compared to between-island variation, and lower variation between islands within the same archipelago compared to islands from different archipelagos.

## PIPITS AS MODEL SPECIES

The Tawny Pipit (*Anthus campestris*) and Berthelot's Pipit (*A. berthelotii*) are two sister species of the genus *Anthus* (Passeriformes: Motacillidae; Fig. 1), which comprises over 40 species distributed worldwide (Voelker 1999, Fitzpatrick et al. 2004). Berthelot's Pipit diverged from its sister species about 2.5 million years ago by colonizing the Canary Islands from mainland Africa (Voelker 1999). A more recent colonization (ca. 8.000 years ago) from the Canaries to Madeira and Selvagens took place in two independent, northward colonization waves (Illera et al. 2007; Spurgin et al. 2014; Armstrong et al. 2018; Martin et al. 2021) and has resulted in clear genetic and phenotypic variation among archipelagos. The initial colonization by a small number of individuals led to a reduction in genetic variation due to founder effects while subsequent population bottlenecks further diminished this genetic diversity (Spurgin et al. 2014; González-Quevedo et al. 2015; Amstrong et al. 2018). Currently, there are two subspecies recognized within Berthelot's Pipit based on morphological differences: *A. b. berthelotii* (the Canary and Selvagens islands) and *A. b. madeirensis* (Madeiran Archipelago; Martín & Lorenzo 2001).

**Figure 1**. Pictures of the study species, the Tawny Pipit (left) and the Berthelot's Pipit (right). Photographs credit: Adam Petrusek.

These two pipit species have very similar songs; however, they differ in history of population isolation and migratory behaviour. Tawny Pipits are trans-Saharan migrants widespread in the Palearctic (Briedis et al. 2016). Although their centre of distribution is the Mediterranean basin, they are currently undergoing a population decline in Western and Central Europe mainly because of habitat loss through conversion to forestry, intensification of agriculture and abandonment of farmland (Birdlife International 2020). On the other hand, Berthelot's Pipits are a strictly sedentary taxon endemic to three of the Macaronesian archipelagos: Madeira, Selvagens and the Canary Islands (Martín & Lorenzo 2001). Songs in both species are short (on average ca. 0.5 s for Tawny Pipits and ca. 0.3 s for Berthelot's Pipits) and have simple structures composed of several elements forming a simple song type; although birds singing two song types in populations of both species have been observed but always in low proportions (Fig. 2 **Chapter 1**; **Chapter 3**). Tawny Pipit songs are known to be individually unique (Neuschulz 1986; Osiejuk et al. 2007; **Chapter 1**) and temporally stable (**Chapter 1**). Although Berthelot's Pipit's songs have been less studied, they are also individually unique (**Chapter 3**) and potentially stable over time (JOC, AP, TP; unpublished data).

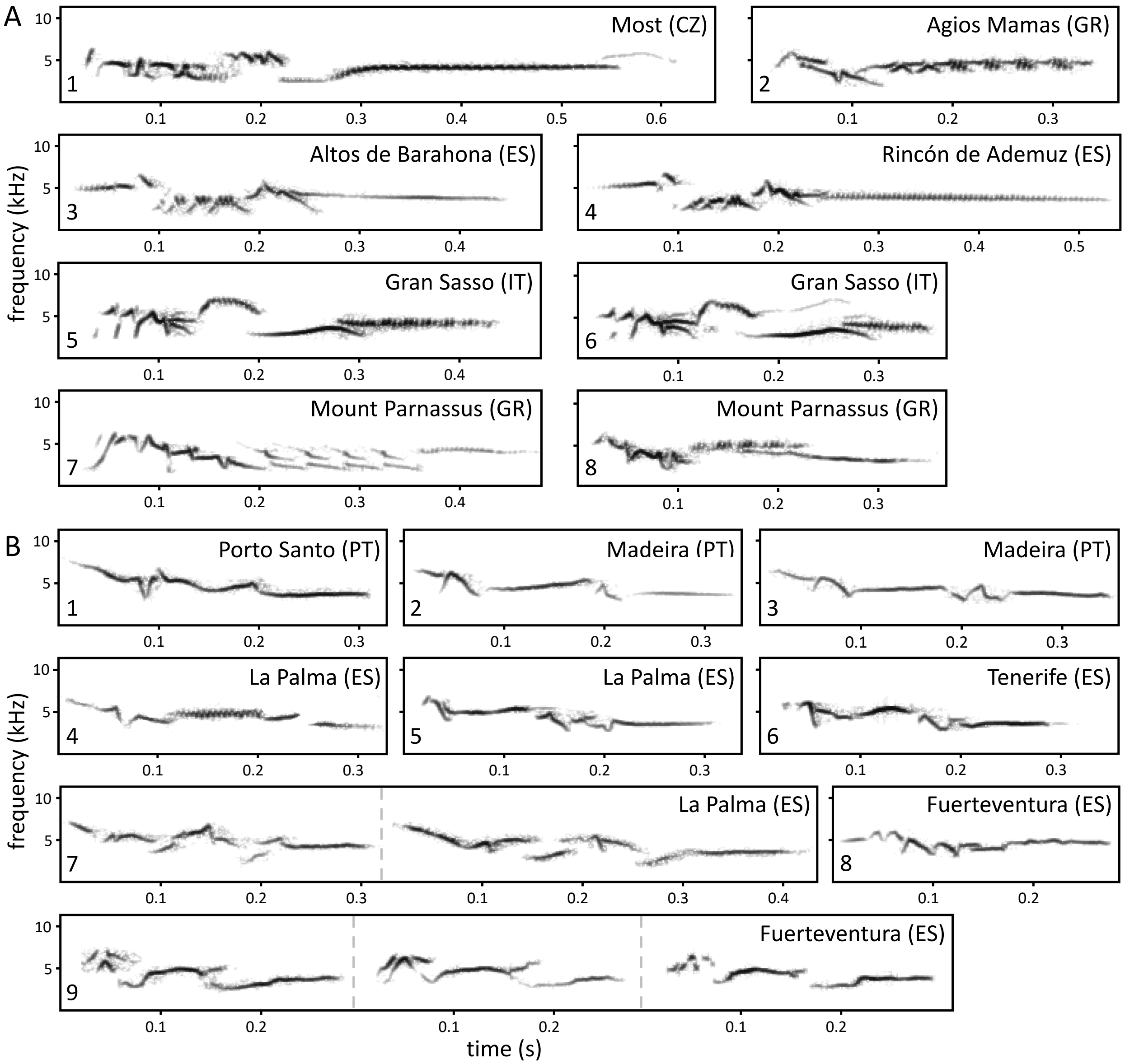

**Figure 2**. Spectrograms illustrating the variation of song types of Tawny Pipit (A) and Berthelot's Pipit (B), and individuals from the studied populations across Europe and Macaronesia, respectively. Origin of each bird with countries indicated by 2-letter ISO codes is shown. Spectrograms no. 3 & 4 and 5 & 6 in A show structurally similar song types sung by Tawny Pipits from the different and the same field sites, respectively. Spectrograms no. 5 & 6 and 2 & 3 in B illustrate corresponding patterns in Berthelot's Pipits males from the different and the same island, respectively. No. 7 in B shows two distinct song types sung by a Berthelot's Pipit male from La Palma, no. 9 unusually high variation among song renditions by a single male from Fuerteventura. (The latter bird was represented by the leftmost variant in all analyses, except of that of within-individual song stability) – Chapter 3.

Both species require for their breeding bare ground with sparse vegetation cover. During the breeding season, Tawny Pipits occur in dry open habitats with low vegetation, such as fallow agricultural land, dry steppe, sandy heaths, coastal sand-dunes, and dry mountain slopes (Alström & Mild 2003; Fig. 3). This species shows a wide altitudinal range, although in Europe they mostly breed at low altitudes between 500-1000 meters (Alström and Mild 2003; Calero-Riestra & García 2019). Berthelot's Pipits are found in several types of open habitat such as rocky areas in plains, hillsides with some vegetation, clearings in wooded areas and scrubby slopes from sea level up to alpine habitats at elevations of 2500 m above sea level (Illera 2007; Illera et al. 2007; Fig. 4). Both species are territorial and socially monogamous with no sexual dimorphism. The song, which is very similar between the two species (Alström & Mild 2003; **Chapter 3**), should therefore be critical for male success in territorial defence and mate attraction for the two species.

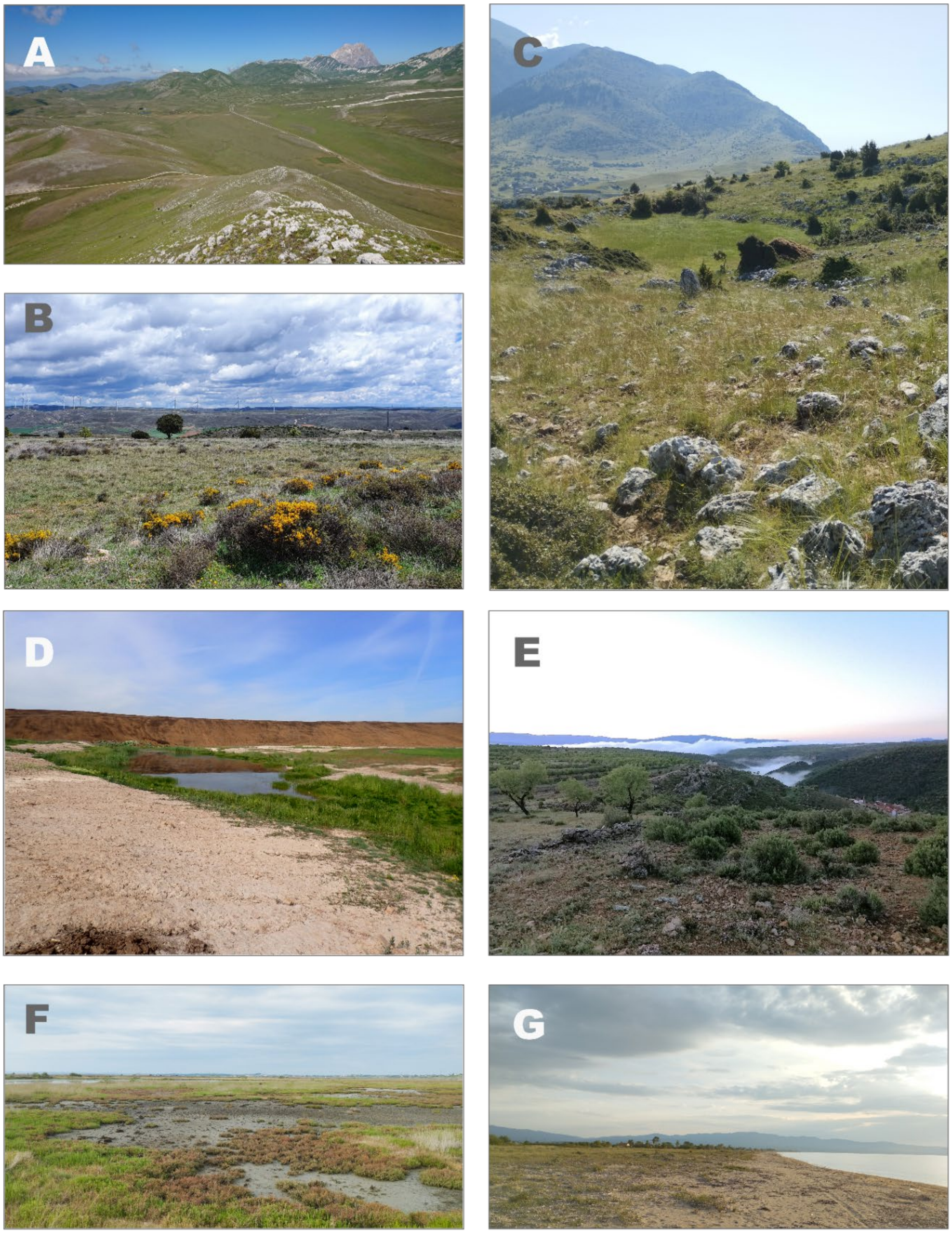

**Figure 3**. Pictures of the field sites where Tawny Pipits were recorded – Gran Sasso National Park, IT (A); Altos de Barahona, ES (B); Mount Parnassus, GR (C); Coal mines near Most, CZ (D); Rincón de Ademuz, ES (E); and Agios Mamas marsh, GR (F, G). Photographs credit: Javier Oñate Casado, Adam Petrusek, and Václav Beran.

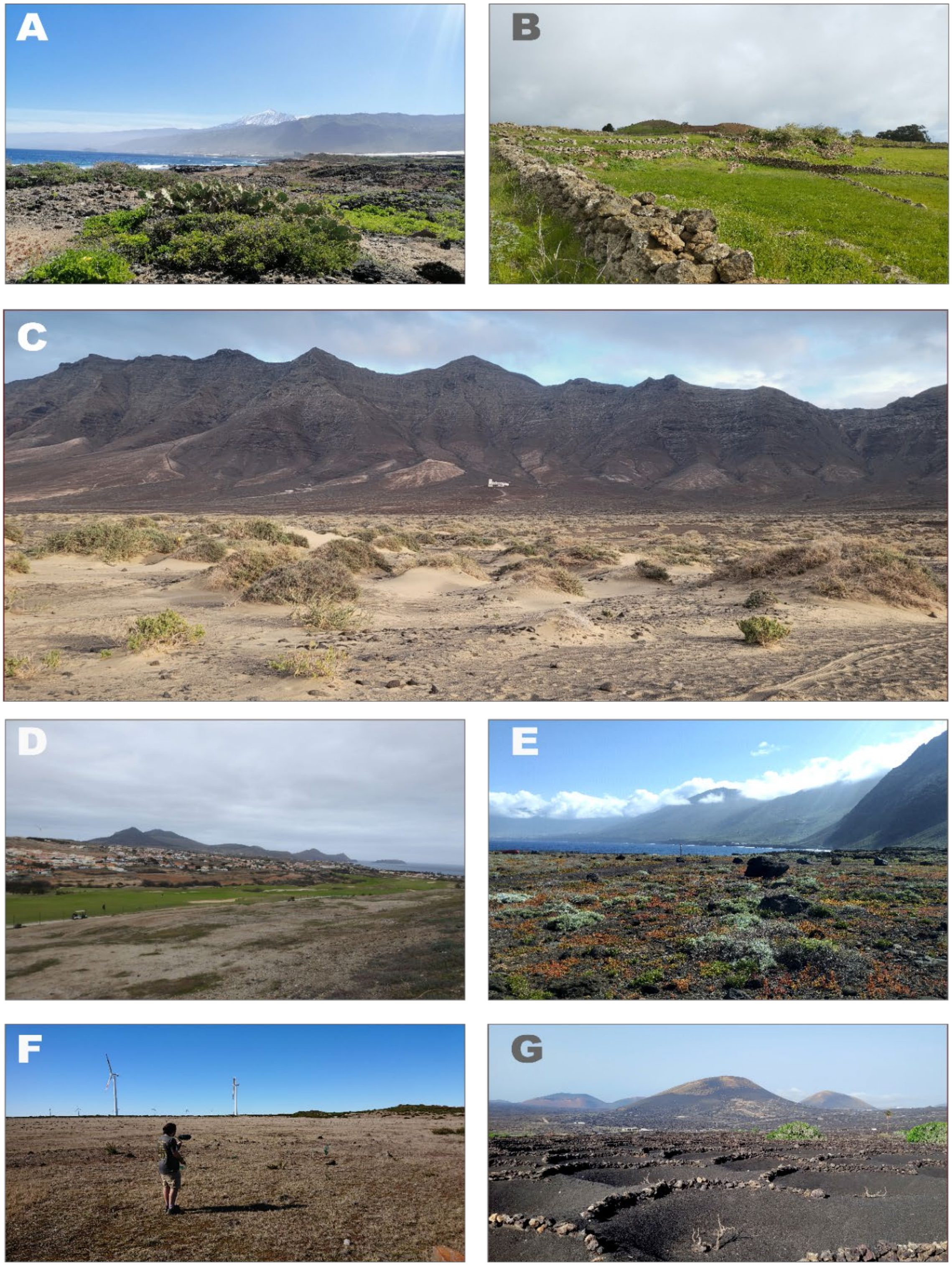

**Figure 4**. Pictures of habitats at some of the islands where Berthelot's Pipits were recorded – Tenerife, ES (A); El Hierro, ES (B, E); Fuerteventura, ES (C); Porto Santo, PT (D); Madeira, PT (F); and Lanzarote, ES (G). Photographs credit: Javier Oñate Casado, and Adam Petrusek.

## OUR STUDY SITES

We recorded singing male Tawny Pipits in six different field sites across Europe, specifically in Czechia, Italy, Spain, and Greece (Fig. 5). This allowed us to compile a comprehensive dataset representing Tawny Pipit populations across western, central, and eastern Europe.

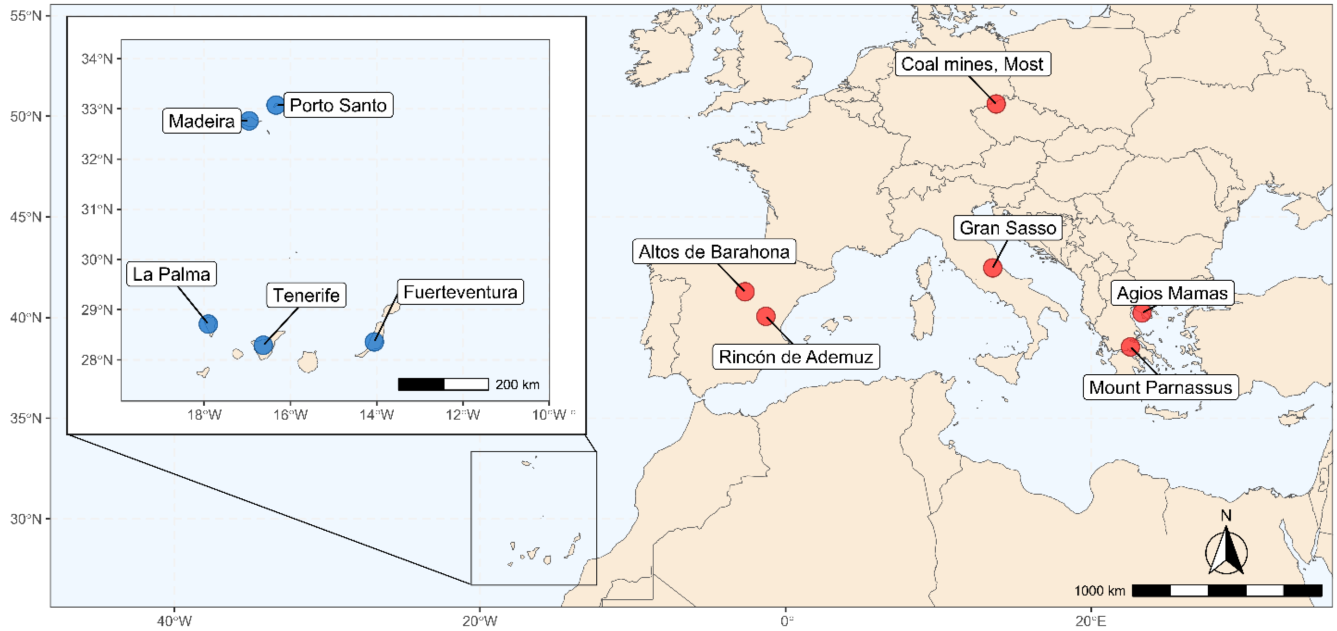

**Figure 5**. Maps showing the distribution of our study sites across mainland Europe for Tawny Pipits (red dots) and the Madeira and Canary archipelagos for Berthelot's Pipits (blue dots). The map on the left is at an enlarged scale to represent in greater detail our study sites in the Madeira islands (archipelago on the top: Madeira, Porto Santo) and in the Canary Islands (archipelago on the bottom: La Palma, Tenerife, Fuerteventura) – Chapter 3.

Song recording in Czechia was restricted to the only remaining Tawny pipit population located in an active brown coal mine area in the Most region (Fig. 3D). In Italy, we focused on a dense, high-elevation population within the Gran Sasso National Park, nestled in the Apennines in central Italy (Fig. 3A). In Greece, we recorded songs at two separate sites The first one was Mount Parnassos, a limestone mountain in central Greece situated in an alpine zone (Fig. 3C), and Agios Mamas, a small coastal wetland with standing water, sand-dunes, and reedbeds located on the Chalkidiki peninsula in northern Greece (Fig. 3F, 3G).

Tawny pipits were also recorded in two different sites in Spain. The first one was Altos de Barahona, a Special Protection Areas (SPAs) site in central Spain relevant for the conservation of steppe birds and characterized by a plateau landscape dominated by short shrubs (< 50 cm), with a high proportion of bare soil, and a smaller area of cultivated fields and scattered trees (Gómez-Catasús et al. 2019; Barrero et al.

2024; Fig. 3B). This site comprises two subpopulations, Altos de Barahona and Paramos de Layna, located about 15-20 km apart, both fostering high population densities (Calero-Riestra & García 2019). We referred to this entire field site as Altos de Barahona since most of the sampled area was within this subpopulation. The second Spanish site was in Rincón de Ademuz, a region in the eastern of the Iberian Peninsula characterized by fragmented habitat and hosting three different populations (Hontanar, Losar, and Pinar) with relatively low densities (Pérez-Granados et al. 2016; Fig. 3E). Each has a range of approximately 200 ha and the distance between them is about 2-4 km (Pérez-Granados 2014).

Additionally, we recorded male Berthelot's Pipits from different populations on three different Canary Islands (La Palma, Tenerife, and Fuerteventura; Fig. 4A, 4C) and two islands of the Madeira Archipelago (Porto Santo and Madeira; Fig. 4D, 4F). This way, we collected song recordings from islands in two different archipelagos, and covering the western, central, and eastern regions of the Canary archipelago. For details on the recording periods and years for each field site (Tawny Pipits) or island (Berthelot's Pipits), see Table 1.

**Table 1**. Characteristics of study areas (with countries indicated by two-letter ISO codes), recording periods, and the number of recorded males (those with two song types in the repertoires are enumerated in parentheses). Median and maximum distances between males in each area were calculated from birds recorded in the same season. For the field sites with Tawny Pipits, months of recording are provided; all recordings of Berthelot's Pipits were obtained in mid- to late February of the respective years – Chapter 3.

| **Sp.** | **Field site / Island** | **Location** | **Altitudinal range (m)** | **Median / max. distance (km)** | **Years recorded** | **No. males** |
|---|---|---|---|---|---|---|
| Tawny Pipit | Coal mines (CZ) | 50.3–50.55°N,<br>13.31–13.64°E | 150–370 | 3.8 / 29.4 | 2015–2017, 2021<br>(early May to mid-July) | 81 (3) |
| | Gran Sasso (IT) | 42.34–42.45°N<br>13.54–13.75°E | 1400–2210 | 3.9 / 15.7 | 2019, 2020<br>(early to mid-July) | 63 (1) |
| | Altos de Barahona (ES) | 41.09–41.35°N<br>2.33–2.82°W | 1030–1220 | 19.3 / 45.4 | 2021, 2022<br>(mid to late May) | 95 (3) |
| | Rincón de Ademuz (ES) | 39.95–40.17°N<br>1.32–1.4°W | 1000–1200 | 3.9 / 25.2 | 2021, 2022<br>(mid to late May) | 51 (6) |
| | Agios Mamas (GR) | 40.22–40.54°N<br>22.82–23.34°E | 0–580 | 22 / 52.7 | 2023<br>(mid-May to early June) | 18 (1) |
| | Mount Parnassos (GR) | 38.49–38.57°N<br>22.54–22.61°E | 1160–2120 | 3 / 9.3 | 2023<br>(mid-May to early June) | 32 (2) |
| Berthelot's Pipit[1] | Madeira (PT) | 32.71–32.82°N<br>16.7–17.26°W | 0–1660 | 16.8 / 53.5 | 2020 | 38 |
| | Porto Santo (PT) | 33.03–33.05°N<br>16.36–16.39°W | 50–140 | 1.1 / 2.7 | 2020 | 25 |
| | Fuerteventura (ES) | 28.05–28.66°N<br>13.83–14.39°W | 0–370 | 21.7 / 84.1 | 2022 | 75 |
| | Tenerife (ES) | 28.01–28.53°N<br>16.15–16.85°W | 0–2310 | 24.9 / 76.9 | 2021 | 139 |
| | La Palma (ES) | 28.46–28.85°N<br>17.77–17.99°W | 0–910 | 16.9 / 44.7 | 2021 | 99 (1) |

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[1] Although not detailed in any of the chapters, we also collected song recordings of Berthelot's Pipits from the remaining Canary Islands – Lanzarote, La Graciosa, Gran Canaria, La Gomera, and El Hierro – during the course of this thesis. This effort resulted in the recording of more than 1000 Berthelot's Pipits, effectively covering the entire Canary Archipelago and almost the entire range of this species, with the exception of the Selvagen Islands and the Deserta Grande in the Madeira Archipelago (see section on "Conclusion and future directions" for details).

## CONCLUSIONS AND FUTURE DIRECTIONS

Our studies have improved the understanding of song variation in two sister pipit species, both with simple songs but different natural histories and migratory strategies, at multiple scales, from individual-level differences to geographic song variation across the species' distribution range.

We demonstrated that the songs of male and female Tawny Pipits are individually unique and suitable for IAM (**Chapter 1**). This less-intrusive monitoring approach should be preferred over traditional mark-recapture methods, which we found to negatively impact Tawny Pipit behaviour (**Chapter 2).** Although we demonstrated that both males and females have individual acoustic signatures, we could not distinguish between the sexes based on their song, either by direct observation in the field or quantitative analysis. However, the possibility that the birds themselves can distinguish between male and female songs remains, requiring further studies using playback experiments.

The IAM methodology we tested and successfully applied at our Czech coal mines field site (**Chapter 1**) has also been recently tested in another stable, isolated Tawny Pipit population in the gravel pits of the Pandorf Plain (ca. 60 km from the south-east of Vienna, Austria; Wendelin et al. 2022). Our preliminary results indicate that IAM can be easily implemented in this area and may be more efficient than traditional methods for estimating population density, territorial dynamics, and survival and return rates. Obtaining songs from this and other isolated populations will improve our understanding of how population isolation influences intraspecific song variation in Tawny Pipits.

Our IAM approach used a shotgun directional microphone connected to a Marantz PMD 661 recorder, providing high-resolution, accurate data on bird song. Such data allow researchers to capture the nuances of individual variations in song, resulting in a comprehensive acoustic profile of individuals within a species, as demonstrated for the Tawny and Berthelot's Pipits in **Chapters 1 and 3**, respectively. These detailed recordings are invaluable for training and calibrating passive acoustic recorders, which can then be deployed over larger areas and longer periods to collect data more efficiently. Additionally, the high-quality data obtained from directional microphones can be used as a reference for developing and fine-tuning automated or semi-automated analyses using machine learning (e.g. Stowell et al. 2019; Xie et al. 2019). Algorithms can be trained on these recordings to recognize the specific acoustic signatures of individual birds within a species, facilitating the detection and identification of individuals from passive recordings. In this way, machine learning models can improve the accuracy and reliability of monitoring efforts using passive acoustic recorders.

Moreover, individual acoustic monitoring helps in understanding the variability in vocalizations at the individual level, which is crucial for machine learning models to account for, when identifying individuals in different acoustic environments. This dual approach—using detailed directional microphone recordings as training sets for broader passive acoustic monitoring and machine learning analyses—provides a robust framework for studying and conserving bird populations across different species.

While we demonstrated that male Berthelot's Pipits have individually unique songs (**Chapter 3**), we could not assess the temporal stability of their songs within this thesis. However, we recorded songs from a subset of Berthelot's Pipits in several localities in Tenerife and La Gomera over multiple breeding seasons. A future study focusing on the temporal assessment of Berthelot's Pipit songs will provide further evidence to confirm their presumed stability over time. Within this chapter, we also suggested that the lack of region-specific song structures in Tawny and Berthelot's Pipits might result from high song variation at the individual level. Although we were unable to visually or quantitatively distinguish between songs from different geographic origins in our pipit species, it is possible that the birds themselves can detect these differences. Future studies on these species should use playback experiments to verify whether the birds can distinguish between songs from different geographic origins.

Migratory behaviour significantly influences geographic song variation at different scales in migratory and sedentary passerines (**Chapter 3**). However, other aspects of natural history and ecology differ between Tawny and Berthelot's Pipits and could have influenced our results. To ascertain that song variation is influenced by migratory strategies, comparing populations of the same species that differ in this respect is ideal. We propose two suitable candidates within the genus *Anthus* – the Meadow Pipit (*A. pratensis*) and the Rock Pipit (*A. petrosus*), both species with most populations being European migrants, but with some being year-round residents (Alström & Mild 2003). Additionally, as discussed in **Chapter 3**, the impact of migratory connectivity, site fidelity and natal philopatry on song variation in Tawny Pipit populations remains unclear. Further investigation is therefore needed to determine the extent to which these factors contribute to song variation within and between populations. Investigation into these aspects could also be extended to other avian species in which song is learned.

During this thesis, we also recorded Berthelot's Pipits in the five Canary Islands not included in Chapter 3 (La Gomera, El Hierro, Gran Canaria, Lanzarote, and La Graciosa), thus sampling across all the Canary Islands. Over 1000 Berthelot's Pipits were recorded, nearly covering the entire range of the species except for the Selvagens Islands and the island of Deserta Grande in the Madeira Archipelago. Although we briefly visited Deserta Grande, we were unable to record the songs of the pipits we encountered there. The original plan for this thesis included recording on Selvagem Grande, but COVID-19 restrictions and logistical challenges prevented us from obtaining the necessary permits.

Regardless of the feasibility of future data collection in the Selvagens archipelago, our current dataset is comprehensive, including songs from most islands within the species' range, including all major islands from two of the three archipelagos in Macaronesia (Canaries and Madeira). Using these data, we can compare islands along the Canary Archipelago, considering their varied degrees of isolation from the African continent. Future additions of recordings from Selvagem Grande would allow comparisons among three archipelagos (Canaries, Madeira and Selvagens), to test for acoustic differentiation. Moreover, we would be able to contrast the degree of song divergence with morphological divergence, as the populations from Selvagens and the Canaries have been assigned to different subspecies of *A. berthelotii* than those from the Madeira archipelago. This robust dataset will enable a detailed future study of the song of *Anthus berthelotii* and facilitate a comparison of geographic song variation across Macaronesia with the known colonization history based on genetic data.

While we have made significant progress in exploring acoustic individuality and geographic song variation in passerines, many aspects of these topics remain unresolved. Our findings provide a strong foundation for continued exploration into the relationships between avian song, ecology, and evolution, providing valuable insights for the scientific community.

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# Chapter 1

**Oñate-Casado, J**., Porteš, M., Beran, V., Petrusek, A., Petrusková, T. (2023). Guess who? Evaluating individual acoustic monitoring for males and females of the Tawny Pipit, a migratory passerine bird with a simple song. *Journal of Ornithology*, 164: 845–858.

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Male Tawny Pipit singing during the breeding season in the Gran Sasso and Laga Mountains National Park (Italy), 2020.

# Chapter 2

**Oñate-Casado, J**., Porteš, M., Beran, V., Petrusek, A., Petrusková, T. (2021). An experience to remember: lifelong effects of playback-based trapping on behaviour of a migratory passerine bird. *Animal Behaviour*, 182: 19–29.

A Tawny Pipit individual approaching a loudspeaker during a playback experiment conducted in a population in the coal mines near Most, Czechia.

# Chapter 3

**Oñate-Casado, J**., Porteš, M., Beran, V., Pérez-Granados, C., Traba, J., Barrero, A., Sakhalkar, S. P., Petrusek, A., Petrusková, T. (manuscript submitted). When individuality obscures geographic song variation: a comparison of two passerine sister species with different migratory strategies.

Berthelot's Pipit perching during sunset, Tenerife (Canary Islands, Spain), 2021.

Sunset at Playa de Cofete, Fuerteventura (Canary Islands, Spain).

**Oñate-Casado, J**. (2024). Patterns in geographic song variation in migratory and sedentary passerines: A comparison of two sister pipit species. Doctoral dissertation, Department of Ecology, Faculty of Science, Charles University, Viničná 7, 128 00 Prague, Czechia.

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