LUND UNIVERSITY

Exploring the genetic basis of migratory traits in Phylloscopus warblers

Caballero-Lopez, Violeta

2025

Document Version:
Publisher's PDF, also known as Version of record

Link to publication

Citation for published version (APA):
Caballero-Lopez, V. (2025). *Exploring the genetic basis of migratory traits in Phylloscopus warblers*. Lund University.

Total number of authors:
1

General rights
Unless other specific re-use rights are stated the following general rights apply:
Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.
- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

Read more about Creative commons licenses: https://creativecommons.org/licenses/

Take down policy
If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

LUND UNIVERSITY

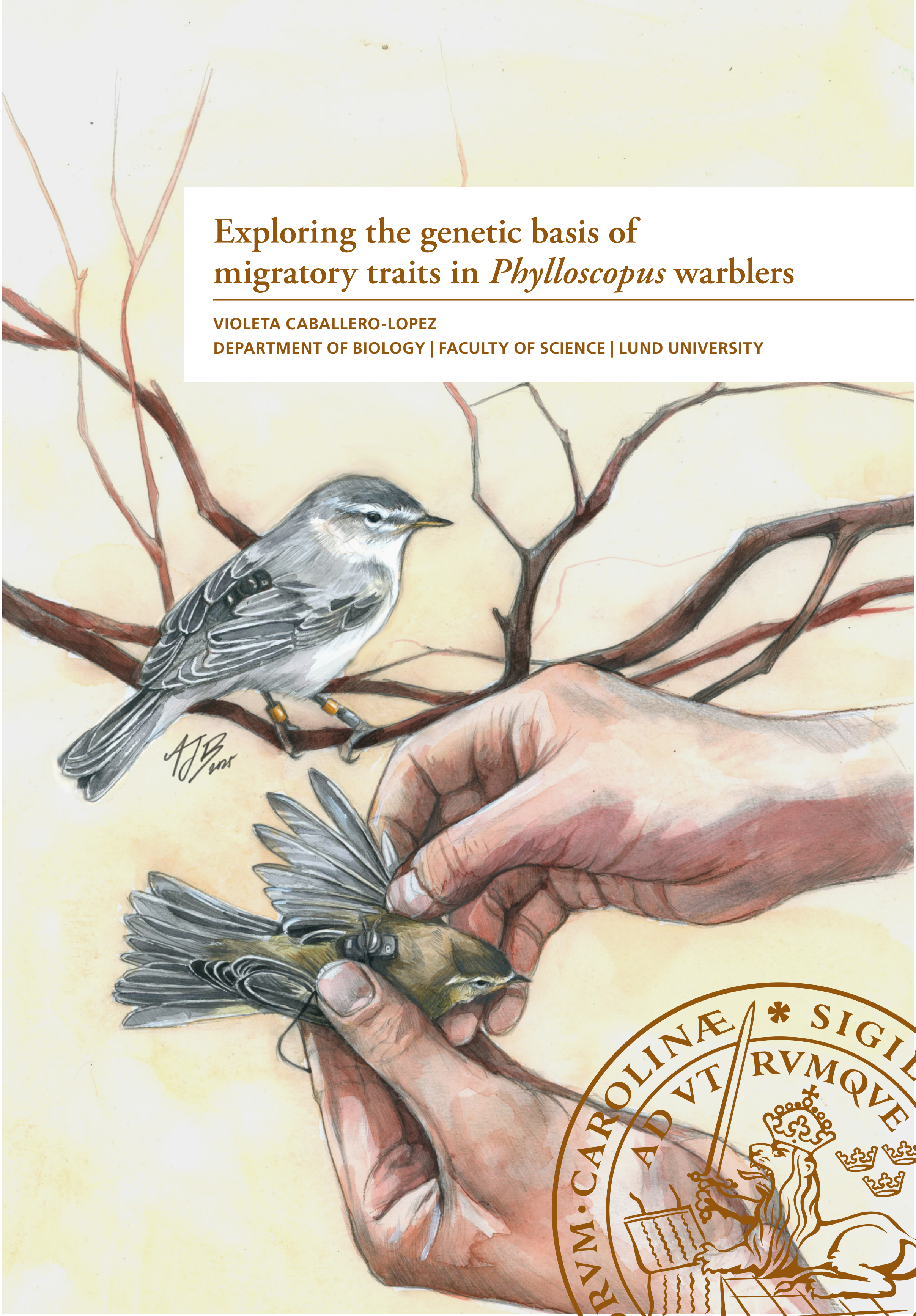
PO Box 117
221 00 Lund
+46 46-222 00 00

Download date: 31. May. 2026

Exploring the genetic basis of migratory traits in *Phylloscopus* warblers

VIOLETA CABALLERO-LOPEZ

DEPARTMENT OF BIOLOGY | FACULTY OF SCIENCE | LUND UNIVERSITY



Exploring the genetic basis of migratory traits in *Phylloscopus* warblers

Exploring the genetic basis of migratory traits in *Phylloscopus* warblers

Violeta Caballero-López

LUND
UNIVERSITY

DOCTORAL DISSERTATION

Doctoral dissertation for the degree of Doctor of Philosophy (PhD) at the Faculty of Science at Lund University to be publicly defended on the 28th of November at 09.00 in the Blue Hall, Department of Biology, Ecology building, Kontaktvägen 10, Lund.

Faculty opponent
Prof. Carles Vilà

Estación Biológica de Doñana - CSIC

Organization: LUND UNIVERSITY

Document name: Doctoral dissertation **Date of issue:** 2025-11-04

Author: Violeta Caballero-López

Title and subtitle: Exploring the genetic basis of migratory traits in *Phylloscopus* warblers

Abstract:

Each year as the seasons turn, the skies fill with millions of travellers. From the tundra to the tropics, birds embark on remarkable journeys guided by an innate programme and perform one of nature's most remarkable phenomena: migration. In this thesis, I tackle the study of the genetic basis of migratory behaviour in several *Phylloscopus* species with a multimodal approach. Here, I combine geolocator data (Papers II, V and VI) with molecular analyses (Papers I, II, IV, V and VI), cytogenetics (Paper IV) and genomic exploration (Papers I, IV and V) in order to identify and dissect genomic regions that may influence the migratory phenotype. In Paper I, we described a repeat-rich region (named MARB) that segregates across two migratory phenotypes of willow warblers *P. trochilus* with a high density of transposable elements (TEs) and other repetitive sequences. We developed a qPCR-based protocol that enabled us to genotype birds in further studies. In Paper II, we tracked 72 willow warblers throughout Sweden overlapping the hybrid zone, and genotyped them using the protocol from Paper I. We then studied the correlation between the migratory route (phenotype) and divergent genomic regions (genotype) in the willow warbler genome. In Paper III, we reviewed the current state of the field and provided hypotheses for the genetic basis of migratory traits across species. In Paper IV, we generated a willow warbler karyotype to locate the MARB region, which explains most variation in migratory direction. We screened the genome of two other migratory *Phylloscopus* taxa, the common chiffchaff *P. collybita* and the greenish warbler *P. trohiloides*, for comparative analyses. Such analyses also revealed a high amount of intact olfactory receptor sequences, posing the question whether olfaction may play a role in migratory direction. In Paper V we combine geolocator data and genomic analyses in the closest relative to willow warbler, the common chiffchaff, and we built a model that best explains the demographic history of two of its subspecies. In Paper VI we studied migratory differences between two chiffchaff species, which are sister taxa, the Iberian chiffchaff *P. ibericus* and the common chiffchaff, which occur in northern Spain. We use pressure geolocators which provide us with high resolution tracks, allowing for a more detailed comparison of their very distinct migratory behaviour. Hence, my thesis constitutes a big leap in the understanding of the proximal mechanisms behind migratory behaviour in birds, especially in relation to complex genomic regions and migratory routes.

Keywords: bird migration, geolocator, migratory phenotype, gene regulation, migratory divide

Language: English **Number of pages**: 65

ISBN (print): 978-91-8104-736-3 **ISBN (electronic):** 978-91-8104-737-0

I, the undersigned, being the copyright owner of the abstract of the above-mentioned dissertation, hereby grant to all reference sources permission to publish and disseminate the abstract of the above-mentioned dissertation.

Signature Date 2025-11-04

Exploring the genetic basis of migratory traits in *Phylloscopus* warblers

Violeta Caballero-López

LUND
UNIVERSITY

Cover illustration by Annie Booker

Cover pictures for Papers I, II, IV, V, VI: Harald Ris

Cover picture for Paper III: Violeta Caballero-López

Copyright pp 1-65 Violeta Caballero-López

Paper 1 © The authors. Published by Wiley (licensed under CC BY-NC-ND 4.0).

Paper 2 © The authors. Published by Springer Nature (licensed under CC BY 4.0)

Paper 3 © The authors. Published by Wiley (licensed under CC BY 3.0)

Paper 4 © 2025 The authors (Manuscript unpublished).

Paper 5 © 2025 The authors (Manuscript unpublished).

Paper 6 © 2025 The authors (Manuscript unpublished).

Faculty of Science

Department of Biology

ISBN: 978-91-8104-736-3 (print)

ISBN: 978-91-8104-737-0 (electronic)

Printed in Sweden by Media-Tryck, Lund University
Lund, 2025

NORDIC SWAN ECOLABEL
Printed matter
3041 0903

Media-Tryck is a Nordic Swan Ecolabel
certified provider of printed material.
Read more about our environmental
work at www.mediatryck.lu.se

MADE IN SWEDEN

“Tiger got to hunt, bird got to fly;
Man got to sit and wonder ‘why, why, why?’
Tiger got to sleep, bird got to land;
Man got to tell himself he understand.”

- Kurt Vonnegut, Cat’s Cradle.

Table of Contents

Abstract

Each year as the seasons turn, the skies fill with millions of travellers. From the tundra to the tropics, birds embark on remarkable journeys guided by an innate programme and perform one of nature's most remarkable phenomena: migration. In this thesis, I tackle the study of the genetic basis of migratory behaviour in several *Phylloscopus* species with a multimodal approach. Here, I combine geolocator data (Papers II, V and VI) with molecular analyses (Papers I, II, IV, V and VI), cytogenetics (Paper IV) and genomic exploration (Papers I, IV and V) in order to identify and dissect genomic regions that may influence the migratory phenotype. In Paper I, we described a repeat-rich region (named MARB) that segregates across two migratory phenotypes of willow warblers *P. trochilus* with a high density of transposable elements (TEs) and other repetitive sequences. We developed a qPCR-based protocol that enabled us to genotype birds in further studies. In Paper II, we tracked 72 willow warblers throughout Sweden, overlapping the hybrid zone and genotyped them using the protocol from Paper I. We then studied the correlation between the migratory route (phenotype) and divergent genomic regions (genotype) in the willow warbler genome. In Paper III, we reviewed the current state of the field and provided hypotheses for the genetic basis of migratory traits across species. In Paper IV we generated a willow warbler karyotype to locate the MARB region, which explains most variation in migratory direction. We screened the genomes of two other migratory *Phylloscopus* taxa, the common chiffchaff *P. collybita* and the greenish warbler *P. trohiloides*, for comparative analyses. Such analyses also revealed a high amount of intact olfactory receptor sequences, posing the question of whether olfaction may play a role in migratory direction. In Paper V we combine geolocator data and genomic analyses in the closest relative to the willow warbler, the common chiffchaff, and we built a model that best explains the demographic history of two of its subspecies. In Paper VI we studied migratory differences between two chiffchaff species which are sister taxa, the Iberian chiffchaff *P. ibericus* and the common chiffchaff, which occur in northern Spain. We use pressure geolocators which provide us with high-resolution tracks, allowing for a more detailed comparison of their very distinct migratory behaviour. Hence, my thesis constitutes a big leap in the understanding of the proximal mechanisms behind migratory behaviour in birds, especially in relation to complex genomic regions and migratory routes.

Popular science summary

The year was 1822. As every other morning, the white stork watched the first rays of sun flare out over the Congo Basin. Yet this day felt different. Thermal updrafts were powerful, the stork had been eating for long enough, and despite the annoying wooden stick stuck in its neck, it felt the urge to ascend in the skies. Joining others of its kind, the stork initiated a long journey across the vastness of the Sahara and over the Mediterranean Sea, back to the valley in Central Europe where it had been born. When nearing the familiar landscapes of home, the last thing the stork heard was a loud blow, and then everything turned black. This stork was pierced twice, once in Africa by hunters with a spear, and once again in Germany by villagers with a rifle. The unlucky bird, without knowing it, had just proved migration between continents.

Ever since, scientific ringing, the use of radar, radio transmission and satellite tracking have greatly improved our understanding of the impressive journeys migratory birds undertake. Some migrants, like the white stork, travel in flocks and rely on social learning from experienced individuals to reach wintering grounds. However, it remains a mystery to us how an 8-gram bird, resembling a fluffball, flies alone for thousands of kilometres to a place where it has never been before. When did this hatchling learn to climb to a height of 4500 meters in the sky before a storm? How can it fly for 37 hours non-stop across a desert, or over the sea? How can this solitary migrant read the stars? And most impressively, how does it know where to go for the first time? The answer lies in its DNA.

In this thesis, I studied several species of *Phylloscopus* warblers, small, greenish songbirds that migrate thousands of kilometres. I combined geolocators (small devices that record the birds' positions) with genomic analyses, molecular methods, and chromosome mapping to investigate how genetic information translates into a migratory route. I described a repetitive region in the genome of these migrants that sorts them into different migratory directions. Interestingly, such region is also full of olfactory receptor genes. This opens the question of whether birds can "smell their way" to wintering grounds. By comparing patterns between species, this work shows that, although migration is an ancient phenomenon, it might have evolved in a very flexible way. This flexibility could be possible due to regulatory mechanisms that allow the birds to develop different migration routes without necessarily rewriting the genetic code.

Texto de divulgación científica

Corría el año 1822. Como cualquier otra mañana, la cigüeña blanca observó los primeros rayos de sol expandirse sobre la cuenca del Congo. Pero ese día se sentía diferente. Las corrientes térmicas eran poderosas, había comido suficiente y a pesar del molesto palo de madera clavado en su cuello, sentía el impulso de ascender en el cielo. Uniéndose a otras de su especie, la cigüeña inició un largo viaje a través de la inmensidad del Sahara, sobre el mar Mediterráneo y de regreso al valle en Europa Central donde había nacido. Cuando sobrevolaba paisajes familiares, ya casi al final de su viaje, la cigüeña escuchó un disparo y todo se volvió negro. Esta ave fue alcanzada por dos proyectiles: una lanza en África que la hirió, y una bala en Europa que la mató. Sin saberlo, la desafortunada cigüeña acababa de demostrar la migración entre continentes.

Desde entonces el anillamiento científico, el uso de radares y localizadores que funcionan con señales de radio o satélite han mejorado nuestra comprensión de los impresionantes viajes que emprenden las aves migratorias. Algunos migrantes como aquella cigüeña blanca viajan en bandadas y aprenden siguiendo a individuos experimentados para llegar a las zonas de invernada. Sin embargo, sigue siendo un misterio como un pajarillo de 8 gramos del tamaño de una pelusa, vuela solo durante miles de kilómetros hacia un lugar donde nunca ha estado. ¿Cuándo aprendió a ascender a 4500 metros de altura antes de una tormenta? ¿Cómo puede volar durante 37 horas sin parar, cruzando mares y desiertos? ¿Cómo puede este migrante solitario orientarse con las estrellas? Y lo más intrigante para mí: ¿cómo sabe a dónde ir por primera vez? La respuesta está en su ADN.

En esta tesis he estudiado varias especies de mosquiteros del género *Phylloscopus*, pequeños pájaros marrón-verdoso que migran miles de kilómetros. He combinado rastreo con geolocalizadores (pequeños dispositivos que registran la posición del pájaro) y análisis genómicos, métodos moleculares y mapeo cromosómico para investigar cómo la información genética se materializa en la ruta migratoria. Descubrí una región repetitiva en el genoma que influye la dirección de migración y curiosamente, dicha región contiene muchos genes de receptores olfativos. Esto nos hace plantearnos si estas especies pueden "oler" su camino hacia las zonas de invernada. Al comparar entre especies, mi tesis muestra que, siendo la migración un proceso muy antiguo, podría haber evolucionado de manera muy flexible. Esta flexibilidad sería posible gracias a mecanismos reguladores que permiten a las aves desarrollar diferentes rutas sin necesidad de reescribir el código genético.

List of papers

I. **Caballero-López, V.**, Lundberg, M., Sokolovskis, K., & Bensch, S. (2022). Transposable elements mark a repeat-rich region associated with migratory phenotypes of willow warblers (*Phylloscopus trochilus*). *Molecular Ecology*, *31*(4), 1128-1141. https://doi.org/10.1111/mec.16292

II. Sokolovskis, K., Lundberg, M., Åkesson, S., Willemoes, M., Zhao, T., **Caballero-Lopez, V.**, & Bensch, S. (2023). Migration direction in a songbird explained by two loci. *Nature Communications*, 14(1), 165. https://doi.org/10.1038/s41467-023-35788-7

III. **Caballero-Lopez, V.**, & Bensch, S. (2024). The regulatory basis of migratory behaviour in birds: different paths to similar outcomes. *Journal of Avian Biology*, 2024(11-12), e03238. https://doi.org/10.1111/jav.03238

IV. **Caballero-Lopez, V.**, Dedukh, D., Ekman, D., Kauzál, O., Lundberg, M., Odenthal-Hesse, L., Proux-Wéra, E., Reifová, R., Reif, J., Altmanová, M., Trifonov, V., Bensch, S. A songbird karyotype: cytogenetic confirmation of a migration-associated region rich in olfactory receptor genes. *Submitted.*

V. **Caballero-Lopez, V.**, Mackintosh, A., Ekman, D., Proux-Wéra, E., Lundberg, M., Malmiga, G., Shipilina, D., Polakowski, M., Berdougo, M., Jankowiak, L., Bensch, S. Common chiffchaffs (*Phylloscopus collybita*) diverge in a genomic region associated with migration differences in willow warblers (*Phylloscopus trochilus*). *Submitted.*

VI. **Caballero-Lopez, V.**, Ris, H., Strehmann, F., Bensch, S. Same direction, different journeys: migratory strategies in two chiffchaff species. Manuscript.

Additional published papers during this thesis

I. Bensch, S., **Caballero-López, V.**, Cornwallis, C. K., & Sokolovskis, K. (2023). The evolutionary history of "suboptimal" migration routes. *Iscience*, 26(11). https://doi.org/10.1016/j.isci.2023.108266

II. Sokolovskis, K., **Caballero-Lopez, V.**, Åkesson, S., Lundberg, M., Willemoes, M., Zhao, T., & Bensch, S. (2023). Diurnal migration patterns in willow warblers differ between the western and eastern flyways. *Movement Ecology*, 11(1), 58. https://doi.org/10.1186/s40462-023-00425-x

Author contributions

I. Conceptualization: V.C-L., S.B. Laboratory work: V.C-L. Bioinformatic analysis: V.C-L., M.Lu. Field data collection: V.C-L, K.S., and S.B. Writing – first draft: V.C-L. Review and editing: all authors. (2022) *Molecular Ecology,* 31(4), 1128-1141. https://doi.org/10.1111/mec.16292

II. Conceptualization: S.B., K.S., and S.Å. Tracking data analysis: K.S. and M.W. Laboratory work: V.C-L., T.Z. Field data collection: K.S., M.Lu., S. Å., M.W., T.Z., V.C-L., and S.B. Writing—original draft: K.S. with input from S.B. Writing—review and editing: all authors. (2023) *Nature Communications*, 14:165. https://doi.org/10.1038/s41467-023-35788-7

III. Conceptualization: V.C-L., S.B. Writing – first draft: V.C-L. Review and editing: V.C-L., and S.B. (2024) *Journal of Avian Biology*, 2024(11-12), e03238. https://doi.org/10.1111/jav.03238

IV. Conceptualization: V.C-L., S.B. Field data collection: O.K., J.R., V.C-L., S.B., Laboratory work: V.C-L., D.D. Laboratory work support: L.O-H, R.R, V.T., M.A. Bioinformatic analyses: D.E., E.P-W., M.Lu. Writing – first draft: V.C-L. Review and editing: all authors

V. Conceptualization: V.C-L., S.B. Field data collection: V.C-L., S.B., G.M., M.P., L.J., M.B. Laboratory work: V.C-L., M.B. Tracking data analysis: V.C-L. Bioinformatic analyses: A.M., D.E., E.P-W., M.Lu. Writing – first draft: V.C-L. Review and editing: all authors

VI. Conceptualization: V.C-L., S.B. Tracking data analysis: V.C-L. Field data collection: V.C-L., H.R., F.S., and S.B. Writing – first draft: V.C-L. Review and editing: all authors.

Violeta Caballero-Lopez (V.C-L), Staffan Bensch (S.B.), Max Lundberg (M.Lu.), Dmitrij Dedukh (D.D), Linda Odenthal-Hesse (L.O-H), Radka Reifová (R.R), Jiří Reif (J.R), Ondřej Kauzál (O.K), Estelle Proux-Wéra (E.P-W)., Diana Ekman (D.E)., Marie Altmanová (M.A), Vladimir Trifonov (V.T), Michal Polakowski (M.P), Łukasz Jankowiak (L.J), Michaëla Berdougo (M.B), Finja Strehmann (F.S), Harald Ris (H.R), Daria Shipilina (D.S), Gintaras Malmiga (G.M)., Kristaps Sokolovskis (K.S.), Susanne Åkesson (S.Å.), Mikkel Willemoes (M.W.), Tianhao Zhao (T.Z.).

Abbreviations

TE	Transposable Element
CNV	Copy Number Variation
NGS	Next Generation Sequencing
OR	Olfactory Receptor
Mya	Million Years Ago
GRC	Germline Restricted Chromosomes
SV	Structural Variant
qPCR	Quantitative Polymerase Chain Reaction
AFLP	Amplified Fragment Length Polymorphism
MARB	Migration Associated Repeat Block
InvP	Inversion Polymorphism
Mb/Mbp	Mega base pair
FISH	Fluorescence In Situ Hybridisation
MDS	Multidimensional Scaling
ASL	Above Sea Level

Introduction

Migration is an extraordinary phenomenon widespread across many animal groups, including fish (Thorpe, 1988), reptiles (Avise & Bowen, 1994), insects (Warrant et al., 2016), mammals (Williamson et al., 1988), and, at a smaller scale, even amphibians (Semlitsch, 2008). It enables individuals to exploit favourable conditions for survival and reproduction year-round (Winger et al., 2019). But migratory birds are especially captivating to us, given the diversity of routes they display and the journeys they perform. A striking example is the Arctic tern *Sterna paradisaea,* which yearly flies more than 80,000 km between both poles, undertaking the longest recorded migratory journey (Egevang et al., 2010). Equally impressive, the bar-tailed godwit *Limosa lapponica* performs the longest non-stop known migratory flight from Alaska to New Zealand, covering more than 11000 km (Battley et al., 2012).

To perform such migratory feats, birds have developed a set of integrated adaptations collectively referred to as the migratory syndrome (Dingle, 2006). Broadly, these comprise endogenous clocks for accurate timing (Gwinner & Helm, 2003), navigation systems based on the position of the sun (Muheim et al., 2018), the stars (Emlen, 1975) and the Earth's magnetic field (Wiltschko & Wiltschko, 2002), as well as metabolic mechanisms for endurance flights, efficient fuel deposition (McWilliams & Karasov, 2001) and behavioural strategies for optimal migration (Hedenström, 2007).

Extensive evidence shows that the genetic basis of the expression of this complex behaviour is likely quantitative and follows a single threshold model (Pulido, 2011). Originally, this model was proposed by Wright (1934) and later applied to bird migration by Pulido et al. (1996). It poses that an underlying, normally distributed continuous trait called "liability" (in this case, a set of genetic mechanisms), influences a binary trait (migration/residency). When an individual's liability exceeds a threshold, the migratory phenotype is expressed (Figure 1). These thresholds are not fixed and depend on both environmental and genetic stimuli.

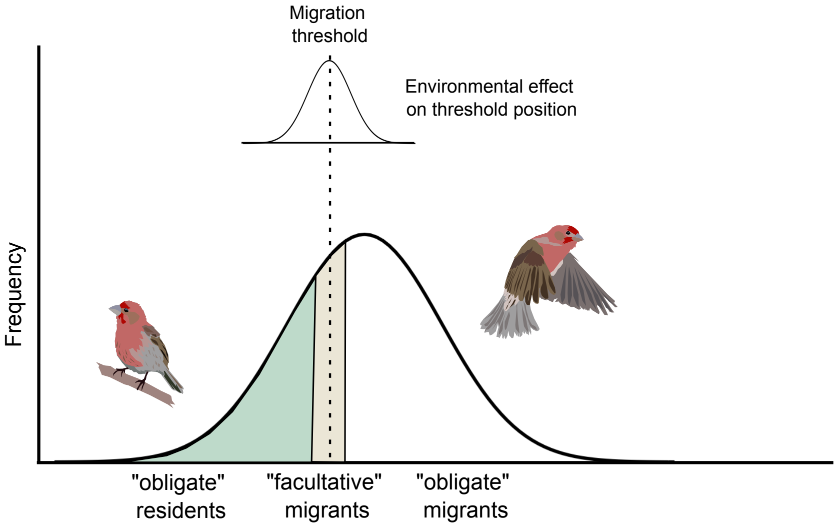


Figure 1. Adapted from Pulido (2011). This illustration depicts the environmental threshold model of migration for a given trait. The trait shown is migratory propensity in a partially migratory population, defined by a threshold that is not fixed but responsive to the environment. A population of facultative migrants might remain resident if they are below the threshold. Environmental cues such as, for example, an unusually cold autumn, can shift this threshold to the left and induce migratory behaviour in individuals that would otherwise remain sedentary.

This model defines migration as a highly dynamic, adaptable strategy. However, if migratory traits are not expressed for extended periods, how does selection maintain them in a population? In other words, how can a resident bird retain the ability to migrate if the species has not done so for thousands of years?

From a molecular perspective, this is possible because the genetic machinery for migratory behaviour can coexist with resident behaviour within a species (Pulido & Berthold, 2003). Many genes involved in migration have functional significance in other ecological contexts (Dingle, 2006). For instance, genes that have been associated with migration such as *CLOCK* and *ADCYAP1* may play roles in seasonal timing and behavioural plasticity while also being used in resident species (Mueller et al., 2011; Lugo Ramos et al., 2017). This flexibility allows birds to switch between migratory and sedentary lifestyles within a few generations. This was empirically demonstrated by Pulido et al. (1996) who selected for resident and migratory behaviour in blackcaps *Sylvia atricapilla* through breeding experiments, and showed high heritability for migratoriness and timing of migration.

Field evidence also supports this evolutionary plasticity. For instance, cattle egrets *Bubulcus ibis ibis* colonised North America in the late 19th century and have since then developed both resident and migratory populations (Browder, 1973). Migratory common quails *Coturnix coturnix* seem to have colonised the Azores archipelago more than 0.8 mya, where they became resident (Ravagni et al., 2023). Similarly, house finches *Carpodacus mexicanus* in western North America are sedentary, but they rapidly became migratory after being introduced to the East Coast (Able & Belthoff, 1998). Ecological niche modelling across many long-distance migrants in North America further supports this flexibility, showing that species can change between sedentary and migratory strategies in each glacial cycle (Zink & Gardner, 2017). However, this pattern is not general across the world. Species distribution models combined with the fossil record indicate that Eurasia-Africa migration was not interrupted in many species during the last glaciation. This discrepancy is likely due to differences in the distribution of ice sheets between America and Eurasia (Ponti et al., 2020).

Regardless of the migratory flyway (across the American Continent or Eurasia to Africa), the literature underscores that partial migration, i.e. the existence of both migratory and resident individuals in a population, is a necessary intermediate state in the switch between residency and migration (Berthold et al., 1990; Pulido et al., 1996; Berthold, 1999; Bensch et al., 2023). Nevertheless, how migration has emerged might differ across species.

How it started: evolutionary pathways that led to the current migratory diversity

Phylogenetic research shows that migratory behaviour in birds is a polyphyletic trait that has evolved multiple times independently (Winger et al., 2012; Dufour et al., 2020). This repeated evolution is likely a response to common selection pressures such as seasonality and competition (Cox, 1985; Helbig, 2003; Outlaw & Voelker, 2006). However, the ultimate causes that triggered migration for the first time are a subject under debate.

To understand why birds migrate, we must begin with the well-established observation that most migrants breed in seasonal environments (Somveille et al., 2018; Winger et al., 2019). The literature broadly categorises them into two groups regarding the conditions they experience in a yearly cycle: “niche trackers” and “niche switchers” (Gómez et al., 2016). Niche trackers seek out similar environmental conditions year-round (Fandos et al., 2020). A study comprising more than 100 New World passerines showed that migrants tend to track conditions more consistently than residents (Gómez et al., 2016). An example of this is the Swainson’s flycatcher *Myiarchus swainsoni* whose seasonal movement closely matched the predictions from a temperature-based model (Joseph & Stockwell, 2000). In contrast, niche switchers winter in climates different from those in their breeding grounds, as is the case with the Magnolia warbler *Dendroica magnolia* (Nakazawa et al., 2004). This pattern is also supported in broader datasets: Dufour et al. (2020) performed a comprehensive phylogenetic analysis including nearly all extant bird species and showed that migratory species, especially long-distance migrants, often winter in warmer climates than would be expected if they were true niche trackers. Overall, the literature suggests that strategies vary and are taxon-specific, and that more complex ecological niche modelling is needed to make accurate predictions.

As for the question of where migration originated, the answer is equally complex, and there are two main competing paradigms in this regard. The northern-home hypothesis, initially proposed by Bell (2000), sustains that migration evolved from temperate to tropical latitudes as birds shifted wintering grounds to escape harsh conditions. This hypothesis also integrates the notion that partial migration (Berthold, 1999) is necessary for the species to transition from sedentary to long-distance migrant states. Fully migratory populations then emerge in either of two ways: 1) the extinction of sedentary behaviour in part of the breeding range due to harsh conditions, or 2) the colonisation of migrants from highly seasonal areas that outcompete the sedentary individuals. In contrast, the "southern home hypothesis," which is the most widely accepted, states that tropical species, also driven by competition, evolved migration to exploit seasonally available resources in higher latitudes (Levey & Stiles, 1992).

However, the selection pressures shaping the current patterns are likely more diverse. Salewski and Bruderer (2007) propose a migration-dispersal theory where, parting from a resident population, selection for better breeding grounds drives post-breeding dispersal. Simultaneously, individuals reaching new grounds that are unsuitable outside the breeding season will evolve regular migration under the threshold model. However, the origin appears to be different in each family depending on their unique evolutionary histories and ecological pressures (Dufour et al., 2020). For example, migration in Anseriformes seems to have tropical origins, in contrast to Charadriiformes, where they seem to have started migrating from temperate areas (Figure 2).

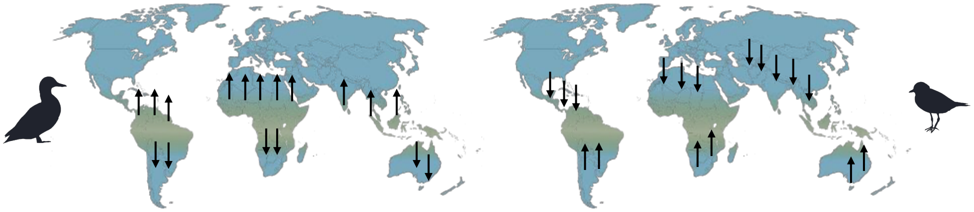


Figure 2. Hypotheses of the origin of migratory behaviour across different avian orders. Anseriformes (left) seem to have developed migration from tropical latitudes during the lower Miocene. Charadriiformes (right) started migrating from temperate latitudes during the upper Miocene (Dufour et al., 2020).

In the case of passerines, it is particularly striking that although most extant species (85%) are resident, phylogenetic analyses provide strong support for their common ancestor to be a long-distance migrant. It is suggested that current migratory patterns are most likely due to repeated loss of migratory behaviour which facilitated rapid radiation from two main centres of origin in South America and Australia 40 to 50 mya (Dufour et al., 2020).

Mechanisms shaping migratory routes: learning versus genetic programs

To complete a migration cycle, birds rely on both their innate genetic programme and a learning process (Pulido & Berthold, 2003; Yoda et al., 2017; Abrahms et al., 2021; Züst et al., 2023). The relative influence of genetic mechanisms and learning in migratory behaviour follows a spectrum that varies across species and has been a topic of debate for a long time (Lack, 1968; Piersma et al., 2005).

Juveniles of species that are typically long-lived and social, rely on experienced individuals to successfully migrate (Teitelbaum et al., 2016). Soaring migrants (those leveraging thermals to fly) also rely more on visual cues from topography and seem to benefit from social information provided by experienced conspecifics, for instance, to cross barriers (Panuccio et al., 2012). An iconic flag species that illustrates learning strategies is the white stork *Ciconia Ciconia*. Juveniles naturally migrate in large conspecific flocks together with experienced adults but are unable to reach wintering grounds when displaced (Chernetsov et al., 2004). Similar experiments in black-tailed godwits *Limosa limosa limosa,* claim that translocated juvenile birds have more similar migratory routes to those of their foster population, than their origin population and therefore heavily rely on social cues to migrate (Loonstra et al., 2023). This species forages, roosts and migrates in groups (Piersma et al., 1990) and consequently social influence is expected to be large. However, there are several caveats to consider. First, translocation was conducted between populations that followed a similar south-westerly direction, masking any potential genetic effects on orientation. Second, translocated individuals show greater variation than birds from either population. In fact, a translocated bird reached the same wintering grounds as its source population. This variation was even more evident in spring migration, hinting at individual differences unlikely to be explained by social influence alone.

On the opposite end of the spectrum of migratory strategies, solitary species (many of them songbirds) that fly mostly at night are often considered the epitome of genetically determined routes (Berthold & Helbig, 2008). A famous representative of this group is the common cuckoo *Cuculus canorus* which, despite being raised by other species, still reaches their species-specific wintering grounds without conspecific guidance (Vega et al., 2016; Thorup et al., 2020). However, recent discussions re-evaluate this view, claiming that the co-occurrence of songbird species during migration sets the grounds for inter-specific interactions through calling, which could potentially influence migratory routes (Aikens et al., 2022; Van Doren et al., 2025). It has been previously observed that indeed, calls from other species provide valuable information and can, for instance, influence breeding site choice once migration is completed (Szymkowiak et al., 2017). However, the extent to which different species influence each other remains unclear. Studies in the Palearctic system show that the those who indeed utter flight calls during migration are mostly *Turdus* species (Hüppop & Hilgerloh, 2012) and some *Emberiza* buntings. Up to 50% of nocturnally migrating passerines remain undetected by acoustic monitoring despite being recorded by radar (Weisshaupt et al., 2024). Some of the taxa that rarely call during night migration are the Old World flycatchers (*Muscicapidae*) and Old World warblers (*Sylviidae*) (Farnsworth, 2005), perhaps to avoid predation (Alerstam, 2009). Thus, it is difficult to envision how the many solitary species that reportedly produce no calls during migration nights rely on each other to reach a destination.

But the evolutionary processes behind complex traits are seldom black or white and there are several examples showing that many species, especially long-lived ones, could rely on both learning and genetic programming to migrate. For instance, juveniles of streaked shearwaters *Calonectris leucomelas* follow an innate southward orientation crossing landmasses in their first migration, whereas adults make detours that allow them to fly over water, overriding compass navigation (Yoda et al., 2017). Similarly, only a few translocated juvenile lesser spotted eagles *Clanga pomarina* from Latvia to Germany successfully reached wintering grounds (Meyburg et al., 2017). Yet, most translocated individuals headed south, which is where the Bosphorus crossing would have been if they had parted from their source populations in Latvia. Many then perished in the Mediterranean crossing, and this is interpreted by the authors as evidence of the importance of observing experienced individuals during migration. This argues for an inherited sense of direction. In line with this, hybrids between lesser spotted eagles and greater spotted eagles *C. clanga* inherited timing from *C. pomarina* but reached the wintering grounds of *C. clanga*, highlighting the genetic determination of these traits (Väli et al., 2018). These examples illustrate that migration strategies often emerge from the complex interplay between genetic programming and learning through experience or social interactions.

The genetics behind different migratory traits: a lack of consensus

The earliest proof of genetic determination of migratory behaviour was obtained in common garden experiments on the well-studied blackcaps, where migratory traits such as incidence, direction, timing and intensity can be selected for across a few generations (Helbig, 1991; Pulido et al., 1996; Berthold, 1999; Berthold & Helbig, 2008).

Since then, the progressive miniaturisation of tracking methods combined with the advancements in sequencing technologies has enabled numerous correlational studies in wild populations. A particularly informative approach has been the study of hybrid zones where populations with distinct migratory behaviours interbreed, forming migratory divides (Helbig, 1991; Veen et al., 2006; Delmore & Irwin, 2014). These constitute natural crossbreeding experiments that can be explored to uncover the genetic architecture and inheritance patterns of different migratory traits.

To illustrate this, the tracking and sequencing of hybrid individuals of Swainson's thrushes *Catharus ustulatus* show that SNPs in chromosome 4 associate with wintering longitude (Delmore & Irwin, 2014; Delmore et al., 2016). In contrast, this trait associates with the *VPS13A* gene in two species of *Vermivora* warblers (Toews et al., 2019). The blackcap system has yielded surprisingly little in terms of fixed polymorphisms associated with traits in the spectrum of migratory populations (Delmore et al., 2020), perhaps due to recent diversification (Pérez-Tris et al., 2004). However, recent studies suggest a possible role of structural variants in chromosome 27 on migratory direction (Delmore et al., 2023).

Regarding timing, which is largely heritable (Lamers et al., 2023), increased methylation of the photoperiodic *CLOCK* genes predicted spring migration phenology in barn swallows *Hirundo rustica* (Saino et al., 2017). In American kestrels, *Falco sparverius,* though, different *CLOCK*-linked genes correlate with migratory timing (Bossu et al., 2022). An association between the *ADCY8* gene and migratory distance in peregrine falcons *Falco peregrinus* suggests a role of long-term memory in the establishment of longer migratory routes (Gu et al., 2021).

The repertoire of genetic signatures behind different traits (Table 1) has led researchers to challenge the long-held hypothesis of a common genetic basis. Instead, attention is shifting toward the study of regulatory mechanisms over coding polymorphisms (Delmore et al., 2020; Louder et al., 2024). In line with this, a recent study comparing different populations of Common Yellowthroat *Geothlypis trichas* across North America, found that most identified loci were in non-coding regions of time-keeping genes (Zamudio-Beltrán et al., 2025). Interestingly, selection seems to target the same regions across populations, but the SNPs involved within each region differ, showing convergence at a finer scale to modulate migration.

Table 1. Representative bird studies that attempt migratory phenotype-genotype associations.

Species	Trait	Genetic region(s)	Function	Methods
Blackcap	Direction, migratory activity	Chromosome 27, *CLOCK* gene	Regulatory, neuropeptide synthesis, circadian rhythms	Tracking, genomic analyses, microsatellite typing
***Vermivora* warblers**	Wintering longitude	*VPS13A* gene	Unknown in birds	Tracking, genomic analyses
Swainson's Thrush	Wintering longitude, Migratory activity	Chromosome 4, *gad1,*	Clock-controlled gene	Tracking, genomic analyses, expression analyses
Willow warbler	Direction, distance	InvP in Chromosomes 1 and 5	Lipid metabolism	SNP array genotyping, whole-genome resequencing
Peregrine falcon	Distance	*ADCY8*	Long-term memory	Satellite tracking, sequencing
Barn swallow	Timing	*CLOCK POLY-Q*	Transcriptional trans-activation domain	Methylation analyses
American Kestrel	Timing	*top1*, *phlpp1*, *cpne4, peak1*	Clock regulator-light input pathway	RAD-seq
White-crowned sparrow	Migratory incidence	*GLUT1, heat shock protein family**	Glucose transporter, unfolded protein response	Expression analyses (microarray)
Common Yellowthroat	Timing	*Npas3, bmal, gria2, camk4, ntrk2, hivep2 * …*	Clock regulator-light input and metabolic pathway	Genomic analyses

*For a complete list of genes, see Zamudio-Beltrán et al. (2025) and Jones et al. (2008).

Navigation: an intriguing ability

One of the most captivating traits in solitary migrants is navigation, as it enables a juvenile bird without prior experience to follow a specific direction with remarkable determination and accuracy. It has been hypothesized that birds can do this relying on either of two orientation strategies, known as "clock and compass" and "goal-area navigation". Understanding which strategy birds employ helps us answer a fundamental question: do birds inherit a detailed internal map or just a set of navigational cues?

The clock and compass model states that young birds rely on an innate program indicating direction and length of journey, without any knowledge of a goal area. Therefore, they inherit a vector, or a set of time-specific vectors. This was shown in a classic and prominent experiment on common starlings *Sturnus vulgaris* (Perdeck, 1958) where 11000 birds were displaced southeast during autumn migration, perpendicular to their trajectory. Only adults compensated for the displacement and reached their wintering grounds, whereas juveniles ended up in more southerly latitudes. This was later challenged (Piersma et al., 2020) with the criticism that Perdeck did not account for the possibility that the translocated juveniles could be guided by local adults, which would rule out the inherited cues. However, shortly after, Pot et al. (2024) analysed historical recovery data and provided strong evidence that juveniles did not follow adults nor local birds after displacement, supporting the inherited vector navigation. For several decades now, evidence for inherited restlessness (correlated with distance) and specific direction cues is well established (Berthold, 1973; Helbig, 1991). Further experiments show that birds use magnetic cues (Kishkinev et al., 2015), celestial rotation (Emlen, 1970), and their combined integration (Able & Able, 1990) to calibrate this compass sense.

The goal-area navigation hypothesis, also known as "true navigation" by Rabøl (1978), proposed that a specific goal point is inherited, a safer and more precise mechanism for the bird itself. Proving this concept unequivocally is quite challenging, as it would require egg translocation experiments in solitary migrants, in order to avoid maternal effects or potential imprinting at the birthplace. Nevertheless, satellite telemetry in wandering albatrosses *Diomedea exulans* shows that they were able to navigate as good as adults (Åkesson & Weimerskirch, 2005). Similarly, satellite tracks of common cuckoos show that both juveniles and adults corrected for displacement towards their goal area (Thorup et al., 2020).

The clock and compass model of inheritance might appear more intuitive and simpler, but it raises evolutionary questions. The rapid changes in migratory routes that many migrants have experienced since the last glaciation (Hull & Girman, 2005; Gu et al., 2021) would require equally rapid changes in the underpinning genetic mechanisms. This is possible under a quantitative basis model as populations could adjust routes relatively quickly by shifting allele frequencies across many loci. However, direction specifically seems to be controlled by a few loci that follow Mendelian inheritance (Helbig, 1991; Väli et al., 2018; Sokolovskis et al., 2023), where changes depend on rare mutations on major-effect alleles. Therefore, the rapid changes in migratory direction that some species experience could seem hard to understand. For instance, novel northwestern directions have been recorded in blackcaps that recently started wintering in England (Berthold et al., 1992), and barn swallows changed timing and orientation in less than 35 years and now breed in Argentina (Winkler et al., 2017). In addition, presumably novel southwestern routes are being established by Richard's pipits *Anthus richardi*, (Dufour et al., 2021). Nevertheless, there is a possible explanation behind such shifts: phylogenetic analyses show that quick changes in direction might need a state of residency to exist, whereas strict, long-distance migrants are unlikely to develop novel routes (Bensch et al., 2023). This is because residents can experience relaxed selection in the locus behind orientation, allowing alternative alleles to persist. When environmental conditions change, these alleles can change in frequency, leading to a "novel" direction. This hypothesis supports the idea of an evolutionarily constrained migration program in strict migrants (Liedvogel et al., 2011) while acknowledging relatively rapid direction shifts.

Altogether, it is worth mentioning that while "clock and compass" and "goal-area navigation" are often presented as opposing hypotheses, there is likely an integration of both systems in solitary migrants. During the first migration, direction might be innate, but this can be overruled by navigation towards a goal once it has been experienced (Thorup et al., 2007; Yoda et al., 2017).

Aims

Despite the advancements in the field of bird migration, many questions remain unanswered regarding the genetic underpinnings of migratory traits. In a broad sense, the migratory behaviour has a quantitative genetic basis, but some of the traits involved seem to be the result of few loci or genetic elements of strong effects that, integrated, give rise to the migratory routes. The diversity of mechanisms proposed in the literature highlights the complexity of the migratory behaviour, and gene regulation or structural variation are rapidly gaining attention. The study of hybrid zones between closely related taxa with different migratory phenotypes provides an ideal natural framework to establish phenotype-genotype associations. To this end, I leverage several *Phylloscopus* species breeding in Europe, which display distinct migratory routes.

Two willow warbler subspecies with divergent migratory routes inhabit Sweden and meet in migratory divides around the Baltic (Hedenström & Petterson, 1987; Bensch et al., 1999; Lundberg et al., 2017). Before my studies, it was known that their genomes were virtually undifferentiated except for three divergent regions within inversion polymorphisms (InvP) in chromosomes 1, 3, and 5 (Lundberg et al., 2017) though only InvP1 and InvP5 are related to migration (Larson et al., 2014). In addition, a marker identified by AFLP (Amplified Fragment Length Polymorphism) had highly different frequencies in the two migratory phenotypes (Bensch, Åkesson, et al., 2002; Bensch et al., 2009). Similarly, ringing data suggested that two chiffchaff subspecies show parallel migratory directions to those exhibited by willow warbler subspecies and that these would also form hybrid zones on both sides of the Baltic Sea. Using these systems, the aims of this thesis are:

1. **To identify and describe genomic regions influencing migratory behaviour**

In **Paper I** we explore the AFLP-derived marker (previously known as WW2) to describe a complex, repeat-rich region, later known as MARB (Migration Associated Repeat Block) that associates with migratory phenotypes in the willow warbler. Due to a high GC and repeat content, this region is challenging to assemble. We combine genomic and molecular data to discern whether MARB is physically linked to any of the other divergent regions in the genome or is, instead, an independent locus.

2. **To establish phenotype-genotype correlations in migratory traits**

In **Paper II,** we use tracking data from 72 willow warblers across both subspecies' ranges and the migratory divide together with molecular methods, in order to establish phenotype-genotype correlations. We aim to assess the influence of candidate loci (MARB and the inversions on chromosomes 1 and 5) on several migratory traits and determine their inheritance pattern.

3. **To synthesize current knowledge and develop hypotheses on the evolution of genetic mechanisms behind migratory traits**

With the improvements of sequencing technologies, regions that have been traditionally overlooked can now be considered as candidates for migration traits. In **Paper III,** we aim to highlight the importance of such complex regions to study traits in the context of the current literature. We intend to propose hypotheses on how such regions and regulatory mechanisms, rather than just coding polymorphisms, can act as regulatory switches and influence migratory traits.

4. **To generate and analyse a willow warbler karyotype to locate a complex region underpinning migratory direction, and to investigate homology across closely related taxa.**

In **Paper IV,** we intend to visualise the chromosome location of MARB on a willow warbler karyotype to confirm that it is a single locus and estimate the length of this region. Leveraging on improved genome assemblies, we intend to characterize the genetic elements present in MARB and to understand how widespread it is across the *Phylloscopus* tree. For that, we investigate the greenish warbler (a basal taxon), and a sister species to the willow warbler, the common chiffchaff.

5. **To investigate the divergence of MARB across migratory phenotypes in other species.**

In **Paper V**, we aim to understand if MARB also diverges across chiffchaff subspecies that migrate differently. We hypothesize that, although different species seem to diverge in the genetic mechanisms behind migratory traits, the willow warbler and the common chiffchaff might share commonalities given that they are closely related.

6. To investigate migratory strategies across species and set the grounds for future phenotype-genotype studies

In **Paper VI,** we aim to establish the basis for studying the genetics behind migratory traits in two hybridising sister chiffchaff species. For that, we track common chiffchaffs and Iberian chiffchaffs which are presumed to diverge in migratory distance. We investigate how different challenges related to being short or long-distance migrants have led to divergent migratory strategies.

Willow warbler perching on an oak tree. Artist: Elsie (Ye Xiong).

General methodology

Study species

Two *Phylloscopus* species that breed in Sweden

Two *Phylloscopus* warbler species, the willow warbler *P. trochilus* and the common chiffchaff *P. collybita* breed around the Baltic Sea in abundant numbers and display parallel migratory phenotypes. This makes them ideal candidates to perform comparative migration studies.

The willow warbler is a long-distance migrant with two subspecies breeding in Sweden. The southern subspecies, also common throughout central Europe, *P. t. trochilus*, is generally smaller with a shorter wing length, presents an overall yellower plumage tone and follows a western migratory route to West Africa. In contrast, the northern subspecies which spreads further east into Russia, *P. t. acredula*, is larger, more long-winged and greyer, and migrates eastward towards East and Southern Africa (Hedenström & Petterson, 1987; Chamberlain et al., 2000).

Despite these average differences in plumage and size, the two subspecies show substantial overlap (Bensch et al., 2009) and so their distinct migratory routes constitute the main phenotypic difference between them. *Trochilus* and *acredula* meet and interbreed without signs of assortative mating (Liedvogel et al., 2014), forming at least three hybrid zones and migratory divides (Figure 3), one in central Scandinavia, one east of the Baltic (Bensch et al., 2009) and one in the Åland archipelago (Andersson et al., 2024). The narrowness of these contact zones despite the random mating suggests potential selection against hybrids, perhaps due to maladapted migration routes (Zhao et al., 2020).

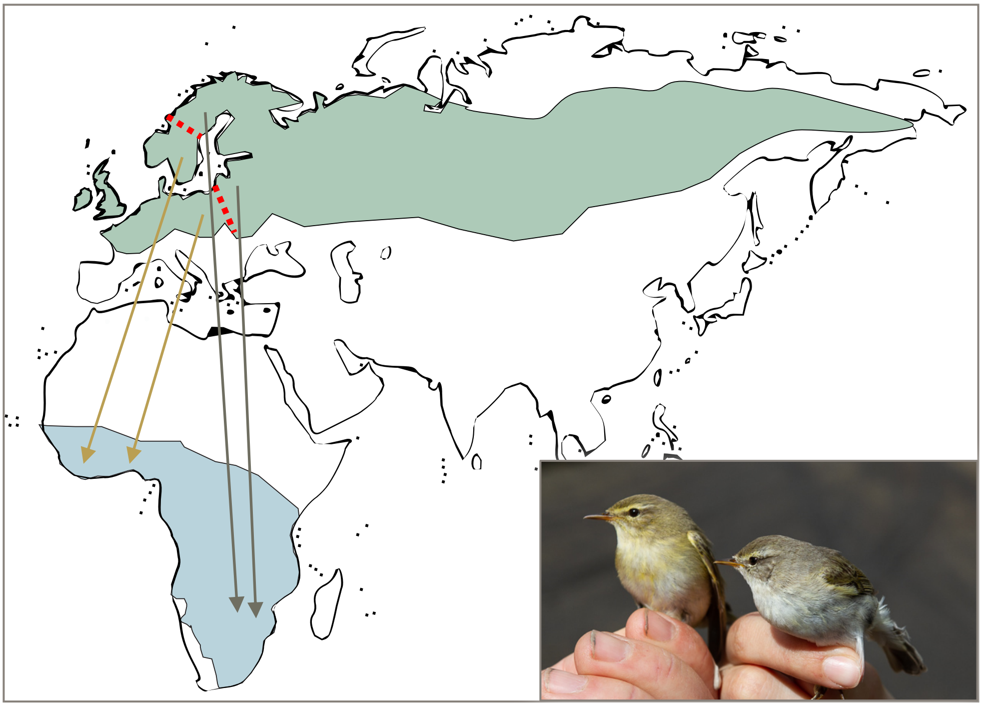


Figure 3. Willow warbler distribution map showing breeding grounds (green) and wintering grounds (blue). Migratory divides are depicted as dashed lines on both sides of the Baltic. The western routes of *trochilus* are depicted in brown, and the eastern routes of *acredula* are depicted in grey. The subspecies *acredula* is replaced in central Siberia by the subspecies *yakutensis*, which also winters in southern Africa (Sokolovskis et al., 2018). The picture shows both phenotypes side by side (*trochilus* to the left and *acredula* to the right). Photo: Harald Ris.

Previous studies identified three divergent regions between *trochilus* and *acredula* birds (Bensch, Åkesson, et al., 2002; Bensch et al., 2009; Lundberg et al., 2017). By mapping re-sequenced individuals to a short-read Illumina reference genome, the authors could identify the highly differentiated regions resulting from three inversion polymorphisms (InvP) in chromosomes 1 (11.6 Mb), 3 (13.2 Mb) and 5 (4.0 Mb). However, only the inversions in chromosomes 1 and 5 strictly segregate with the two migratory phenotypes. Another region that showed differentiation was an AFLP-derived marker named WW2 (Bensch, Åkesson, et al., 2002; Bensch et al., 2009) that occurs in narrow clines across migratory divides but failed to be detected in the Illumina genome.

The common chiffchaff split from the willow warbler lineage approximately 5 million years ago (Alström et al., 2018). It is described as part of a cryptic species complex, presently containing at least eight taxa with species or subspecies status (Clement & Helbig, 1998; Alström et al., 2018; Rheindt et al., 2025). It is considered to be a facultative migrant as a fraction of individuals in some populations spend the winter in breeding grounds, whereas others are medium and long-distance migrants (Hahn et al., 2009; Lampila et al., 2009). Two subspecies breed in Scandinavia, *P. c. collybita* in the south (and most of continental Europe) and *P. c. abietinus* in the north (and East towards the Ural Mountains). They present subtle plumage and biometric differences (Hansson et al., 2000) and ringing recoveries suggest that *collybita* birds have a more western component in their migratory route, whereas *abietinus* follow an eastern route (Lindström et al., 2007). Like willow warblers, these chiffchaff subspecies meet in two contact zones (Figure 4), both in South-central Scandinavia and East of the Baltic (Hansson et al., 2000). However, the densities in the Swedish contact zone are still low as *collybita* birds have been recently colonising Sweden from the south (Lindström et al., 2007).

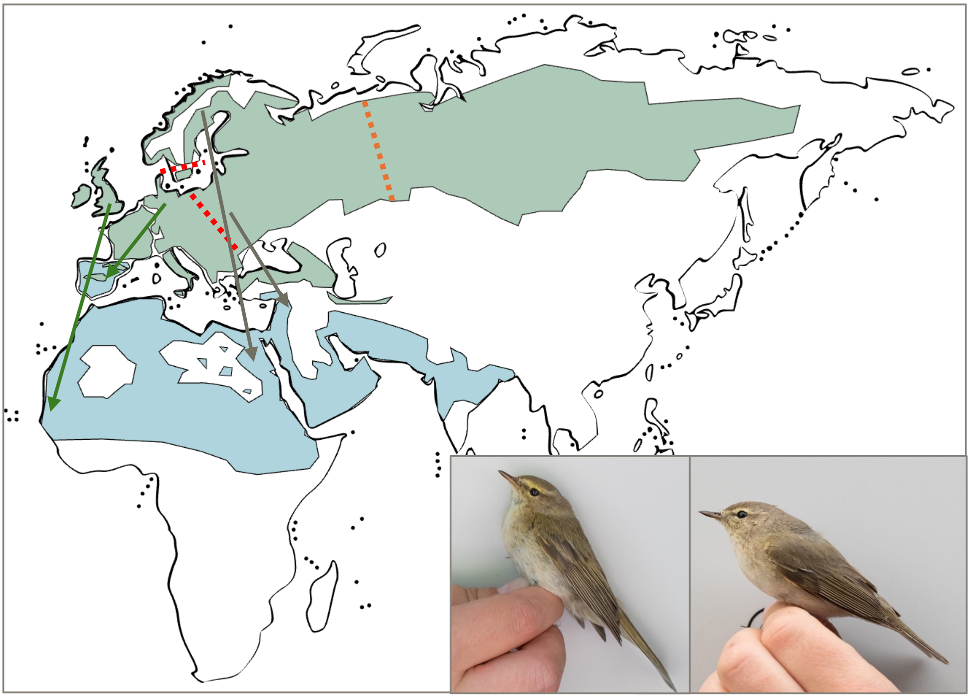


Figure 4. Common chiffchaff distribution map showing breeding grounds (green) and wintering grounds (blue). Migratory divides are depicted as dashed red lines on both sides of the Baltic. *Collybita* directions are depicted in green arrows and *abietinus* directions are depicted in grey arrows. Dashed orange lines show the split between breeding ranges of *abietinus* and *tristis* subspecies, which winters in India (Salvin & Strickland, 1882). The picture shows both phenotypes side by side (*collybita* to the left and *abietinus* to the right). Photos: Michaëla Berdougo.

In contrast to the willow warbler subspecies that do not differ in mtDNA (Bensch et al., 1999) the two chiffchaff subspecies carry slightly divergent (0.7%) mitochondrial haplotypes (Helbig et al., 1996; Raković et al., 2019). A study based on sequences from three nuclear loci failed to find any difference between *collybita* and *abietinus* (Bensch et al., 2006) but whether this low level of divergence is representative for the rest of the genome was not known at the start of my studies.

Two *Phylloscopus* that breed in Spain

In the Iberian Peninsula, the common chiffchaff (subspecies *collybita*) and the Iberian chiffchaff *Phylloscopus ibericus* (Figure 5) have distinct breeding grounds. *Collybita* birds have a dispersed breeding distribution mostly restricted to the northern plateau and the Pyrenees (Balmori et al., 2002; Shirihai & Svensson, 2018), whereas *ibericus* breed throughout north and northwestern regions, Andalusia and Portugal (Salomon et al., 2003). Wing morphology, isotope data and field observations (Catry et al., 2005; de la Hera et al., 2020) suggest that *ibericus* is a long-distance migrant that winters in sub-Saharan Africa, although the migratory route remains unknown. In contrast, *collybita* birds breeding in Spain are considered shorter distance migrants with ringing recoveries that show a range of wintering grounds within the Iberian Peninsula, Morocco and Senegal (Pagani-Núñez et al., 2014; https://migrationatlas.org/node/1842). These two species also differ in song and call notes (Salomon, 1989; Hansson et al., 2000), and in genotype with a mitochondrial divergence of 4.6% in the cytochrome b gene (Helbig et al., 1996). However, there is substantial overlap in plumage and morphology (Gordo et al., 2017). Relevant for the research on migration genetics, they meet in a narrow migratory divide in the western Pyrenees where they hybridise (Bensch, Helbig, et al., 2002a).

Figure 5. The Iberian chiffchaff *P. ibericus* was previously considered a subspecies (*P. collybita brehmii)* part of the common chiffchaff complex. It acquired species status in 2003 and can be distinguished primarily by its song. Morphologically, they have a longer wing and yellower tone in the plumage. Photo: Ralph Martin.

Study sites

We have sampled individuals from different populations in a range of habitats across their breeding grounds in Europe using male song playback and mist nets. The data used in this study spans more than 20 years, with blood samples dating back to the late 90s (Figure 6).

Willow warblers can be found in a wide range of habitats and prefer early seral stages of forest, often open and linked to human activity, with low tree heights (Sæther, 1983). They are found in both deciduous and coniferous forests (Stostad & Menéndez, 2014; Lapshin et al., 2020). The common chiffchaffs have a considerable habitat overlap with willow warblers, though they prefer a well-structured understory (Cody, 1978; Sæther, 1983). The Iberian chiffchaff is more restricted to deciduous, slopy oak forest (Onrubia & Copete, 2022).

In Sweden, birds (willow warblers and common chiffchaffs) were trapped in a latitudinal gradient that comprises subspecies in allopatric populations and the contact zones where the two subspecies and their hybrids live in sympatry. East of the Baltic, birds were trapped within and around the contact zone, from western Poland to central Lithuania. In Spain, birds were sampled in two locations in the north (*ibericus*) and northwest (*collybita*) of the country (Figure 6).

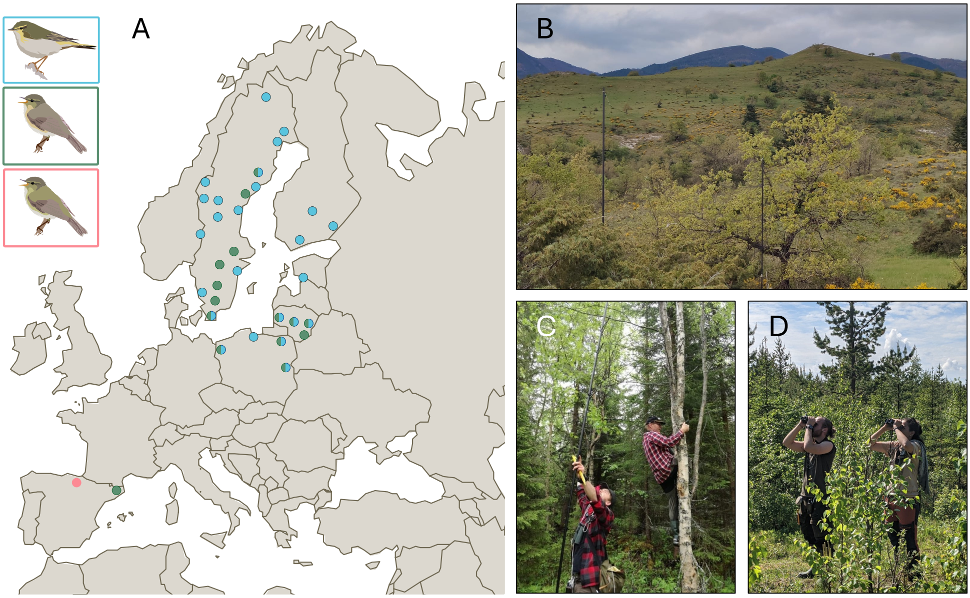


Figure 6. A) Sampling sites for the willow warbler (blue), common chiffchaff (green), and Iberian chiffchaff (pink) included in this thesis. Mixed circles indicate shared sampling locations between species. Each point contains more than one location. B) Typical net setup (Álava, Spain). C) Staffan Bensch and Kristaps Sokolovskis setting up an unnecessarily difficult net in Jämtland (2019). D) Harald and I scouting for returning tagged willow warblers in Jämtland (2020). Photos B, C: author. Photo D: Kristaps Sokolovskis.

From phenotype to genotype

Throughout this thesis, I employed four complementary approaches to link migratory traits to genomic regions.

Tracking

We tagged a total of 597 adult male birds across the 3 species included in this thesis (466 willow warblers in Sweden, 70 common chiffchaffs around the Baltic Sea, 31 Iberian chiffchaffs and 30 common chiffchaffs in Spain). Given the mass of our target species (7,5-10g on average), we used the smallest possible tracking devices, a combination of light-level geolocators (Intigeo-W30Z11-DIP 12 × 5 × 4 mm, 0.32 g; **Paper II** and **V**) and pressure geolocators (Intigeo, BARW30Z9-DIP, 0.38 g; **Paper VI**). These tags comprise 3 - 4,75% of the average species' lean body mass. They were attached using the leg-loop harness method (Figure 7; Naef-Daenzer, 2007). We programmed them to measure ambient light levels every 5 minutes, and atmospheric pressure (through a barometer) every 20 minutes. Data was recovered upon retrieval the following year, downloaded and processed. Light level geolocators estimate the approximate position of a bird based on day length (latitude) and sunrise/sunset times (longitude) (https://migratetech.co.uk/geolocation_9.html). Pressure geolocators estimate positions through a combination of measurements: pressure likelihood is obtained by querying the pressure measured by the device against the ERA5 reanalysis data of atmospheric pressure across the globe (https://raphaelnussbaumer.com/GeoPressureManual/). Light data is then implemented to narrow down the position probabilities, and a movement model is created with wind patterns, also obtained from the ERA5 data bank.

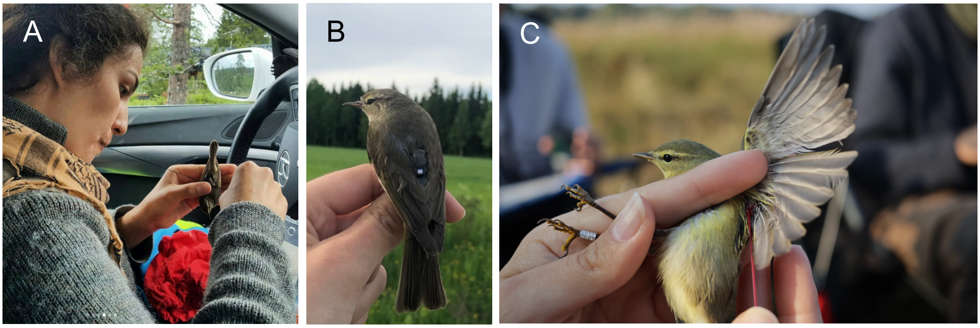


Figure 7. Process of geolocator attachment (A, B) and blood sampling (C) across species. Photo A: Kristaps Sokolovskis. Photo B: author. Photo C: Harald Ris.

Molecular work

Blood samples were collected in SET buffer from the brachial vein in the field (Figure 7) and stored at -20°C until DNA extraction. Feathers (inner-most primary) were also collected and stored in envelopes. DNA extraction was performed in the lab following the ammonium acetate protocol (Richardson et al., 2001) and used for Quantitative Polymerase Chain Reaction (qPCR; both for measuring copy number variation and for genotyping). This technique amplifies specific DNA sequences and quantifies them in real time by detecting fluorescent signals. In addition, samples were also used for sexing, microsatellite typing, mitochondrial genotyping and genome resequencing.

Cytogenetics

Fresh testes were collected from *trochilus* breeding males in Czechia and used to generate the spermatocyte spreads. Then, we performed Fluorescence *in situ* Hybridisation (FISH) on them with a specific probe designed to bind to the region of interest (Figure 8; **Paper IV**).

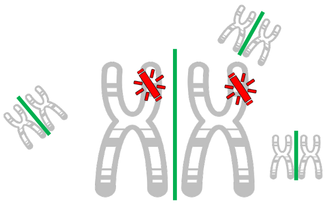


Figure 8. The principle behind FISH on a karyotype. The synaptonemal complex is labelled with green, fluorescent antibodies. The size of each synaptonemal complex is used as a proxy for chromosome size. The probe binds to MARB specifically and it is labelled with a contrasting colour (red).

Genome analyses

Throughout the thesis, we capitalize on resequencing data (Illumina) mapped against four high-quality genome assemblies. These genomes were previously generated *de novo* using a combination of long-read sequencing, linked-read sequencing and optical mapping. The oldest genome belongs to a male *P. t. acredula*, with 496 scaffolds (N50 = 17 Mb). The *P. t. trochilus* genome (male) contains 547 scaffolds (N50 = 34 Mb) and the *P. c. collybita* genome (female) is a contig-level assembly consisting of 517 contigs (N50 = 28 Mb). All three genomes are available at NCBI under bioproject PRJNA550489. The *P. t. viridanus* genome is the latest assembly and consists of 555 contigs (N50 = 34.5 Mb).

We additionally re-sequenced 76 willow warblers and 24 common chiffchaffs belonging to the different subspecies. Such data was used to produce population statistics (**Papers IV** and **V**) and to build models of demographic inference between subspecies (**Paper V**).

Contributions to the field

A repeat-rich, complex region correlates with migratory phenotypes in willow warblers

The two willow warbler subspecies breeding in Europe (*P. t. trochilus* and *P. t. acredula*) have been the target of several studies investigating the genetic basis for their distinct migratory behaviours (Bensch et al., 2009; Bensch, Åkesson, et al., 2002; Larson et al., 2014; Lundberg et al., 2017). Before sequencing technologies became accessible, the AFLP method was commonly employed to identify closely related taxa or genomic regions that may be under selection (Gobert et al., 2002; Joly & Bruneau, 2007). Bensch et al. (2002) identified the WW2 marker in willow warblers, a 5-base pair duplication which segregated across both migratory divides (Bensch et al., 2009). Once the first willow warbler genome assembly was available (Illumina, Bioproject PRJNA319295), such marker, surprisingly, could not be detected.

In **Paper I**, we capitalised on the first long-read PacBio *acredula* genome (under Bioproject PRJNA550489). There, WW2 was indeed present, not in one copy as it was expected from the AFLP study, but in multiple copies and only in unmapped scaffolds that were not captured in the Illumina genome. Using qPCR techniques, we were able to quantify the WW2 copy number variation (CNV) between east-migrating *acredula*, and west-migrating *trochilus* birds from populations surrounding the Baltic. Given the bimodal distribution of the copy numbers across both subspecies (Figure 9), we were able to infer that this region was likely inherited as one block. This was further supported by the inheritance patterns of the WW2 copy numbers (Table S5 in **Paper II**) and by a *trochilus* karyotype (**Paper IV**).

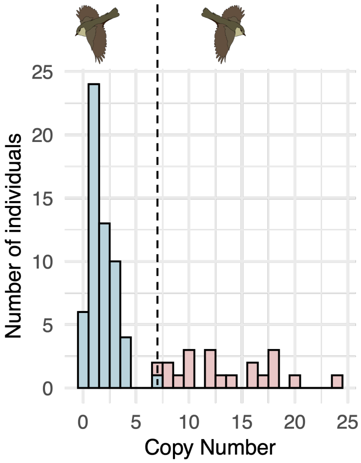


Figure 9. Copy number variation of the WW2 marker across pure willow warbler subspecies (i.e., excluding the hybrid zone). The dashed line represents the migratory divide in central Scandinavia. Copy numbers of this transposon on each bird are our only aid to determine if the haplotype is MARB-a (*acredula;* pink) or MARB-t (*trochilus;* blue) in the absence of a correct assembly of the region.

We therefore described such scaffolds as part of a region rich in transposable elements (TEs) and olfactory receptor sequences (ORs) of unknown functionality. WW2 itself was part of the Long Terminal Repeat (LTR) region of a transposon inserted during an ancient infection by an endogenous retrovirus (ERV) that contained the 5-bp duplication as a derived state. Whether this TE has a direct effect on migration routes is unlikely given that this marker only shows copy number variation across willow warbler subspecies, but not other taxa, as later seen in **Papers IV** and **V**. We highlight the importance of regions that are unresolved due to technological limitations. Such complex regions have traditionally been neglected and treated as "junk" DNA. However, they could be involved in speciation processes as important as the radiation of Oscine passerines into thousands of species (Suh et al., 2018). A very important outcome of this study was the development of the qPCR-based genotyping protocol of MARB that enabled us to understand how this region is linked to migration (**Paper II**).

Genetics behind migratory direction

In **Paper II**, we combine tracking data from 72 male willow warblers with molecular analyses to establish genotype-phenotype correlations. Birds were sampled across the full latitudinal range of Sweden, encompassing pure subspecies populations and the hybrid zone. We typed each bird for markers previously linked to migratory phenotype, these being the Inversion polymorphisms in Chromosomes 1 and 5 (Lundberg et al., 2017), and the repeat-rich region described in **Paper I** (Caballero-López et al., 2022), which we named MARB (Migration Associated Repeat Block). Our analyses reveal that MARB is the primary region segregating east and west migrants, explaining 64% of the variation in migratory direction. MARB appears to have an epistatic interaction with the inversion polymorphism in chromosome 1 (InvP1). More specifically, the MARB-a haplotype (*acredula* birds) seems to have a dominant effect over InvP1 and is strongly associated with eastward migration (Figure 10). These findings align with results from the classic blackcap breeding experiments which concluded that direction was controlled by one or several loci of large effect (Helbig, 1991). Contrary to expectations, the return rates of hybrids were comparable to those of pure subspecies populations. Whether this indicates an absence of hybrid disadvantage or reflects survivor bias towards returning individuals remains unresolved.

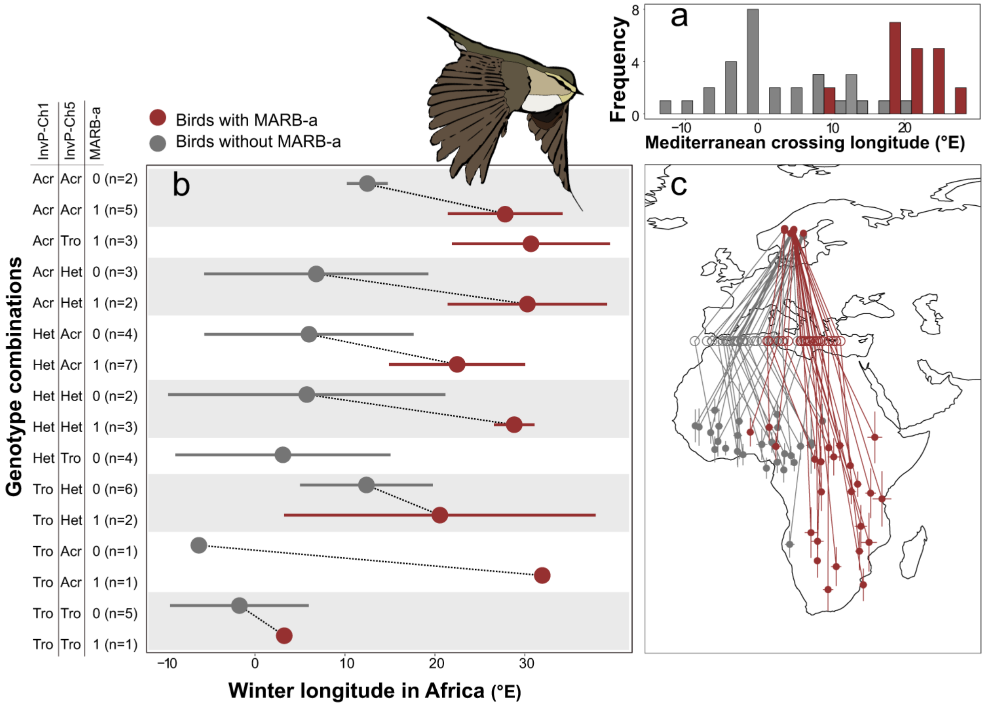


Figure 10. a Histogram depicting bimodality in the frequencies of where birds from the migratory divide crossed the Mediterranean. **b** Mean (whiskers depict ± standard deviations) winter longitudes for each of the nine combined genotypes of InvP-Ch1 and InvP-Ch5, illustrated separately for birds with (red) and without (dark gray) the MARB-a. On the Y-axis, the labels stand for genotype on InvP-Ch1, InvP-Ch5 (Acr homozygote for acredula allele, Het heterozygote, Tro homozygote for trochilus allele) and whether MARB-a is absent “0” or present “1”. Dotted lines connect the genotypes of both chromosomal inversions that have or do not have MARB-a. **c** Breeding and winter locations for birds from the hybrid zone with (red) and without (dark gray) the MARB-a. Hollow circles show estimates of longitudes where birds crossed the Mediterranean Sea. The lines connect the locations of each individual. Error bars of locations in Africa show standard deviations in longitude and latitude of the main winter site of each bird.

A comprehensive review of the field of genetic mechanisms behind migratory traits

Despite innovations in both sequencing technologies and tracking devices, phenotype-genotype associations remain difficult to establish when studying complex behaviours. An increasing number of studies identify different genomic regions behind migratory traits, which is perhaps not unexpected, given that migration has been gained and lost several times across the avian tree. This has shifted the focus towards studying other aspects of the genome besides sequence polymorphisms, such as regulatory mechanisms, which offer flexible and rapid means of evolutionary change. They can affect behaviours like migration, which require dynamic responses to dynamic environmental pressures. Regulatory networks facilitate fine-tuned control over gene activity and can evolve faster than coding sequences, facilitating quick phenotypic shifts (Dsilva & Galande, 2024; Zamudio-Beltrán et al., 2025).

In **Paper III** we review the state of the field and provide hypotheses on how different migrant species might display similar behaviours through a diverse range of regulatory mechanisms of expression. This emphasises the importance of the often-neglected non-coding regions of the genome, epigenetic modifications and structural variants (SVs). We also present several hypotheses of how such wide array of mechanisms may work in different species. We conclude that this regulatory basis is likely species-specific at a fine scale but results in similar strategies as a response to similar environmental pressures.

The MARB region is in a medium-sized chromosome that contains most olfactory receptor sequences (ORs) in the genome

Given the limitations of sequence-only approaches commonly encountered in our field, in **Paper IV** we employ cytogenetics to identify MARB. Using MARB-specific probes, we conducted *in situ* hybridisation on spermatocyte cells and visually identified the region in a male willow warbler karyotype. The probe binds along 80% of the 11th largest chromosome, which has an estimated size of 34,4 Mbp. We further characterised MARB in two other *Phylloscopus* species (Figure 11), the common chiffchaff *P. c. collybita* and the greenish warbler *P. trochiloides viridanus* which is a basal species of this genus.

We further discuss the high density of intact ORs across MARB in all analysed species. We highlight the importance of complex genomic regions that are often neglected in other genome projects, particularly those with high OR content, which seem to be captured only in the most complete assemblies (Driver & Balakrishnan, 2021).

Research on avian olfaction has traditionally focused on foraging behaviour, homing ability or conspecific recognition (Bang & Cobb, 1968; Grubb, 1973; Hutchison & Wenzel, 1980; Wenzel, 2007). However, the evidence suggests a broader role, perhaps in the successful execution of migratory journeys. Translocation experiments on lesser black-backed gulls, *Larus fuscus fuscus*, manipulated through olfactory nerve section, show that they rely on olfaction to correct for displacement during migration (Wikelski et al., 2015). Similarly, a study of olfaction in navigation of a songbird, the catbird *Dumetella carolinensis* showed that anosmic adults treated with zinc sulphate could not orient as well as controls (Holland et al., 2009).

Our findings in this paper provide evidence that MARB is present in probably all *Phylloscopus*. We raise the question of whether olfaction plays a more significant role in avian migration than previously appreciated, potentially contributing to the evolution and diversity of migratory routes.

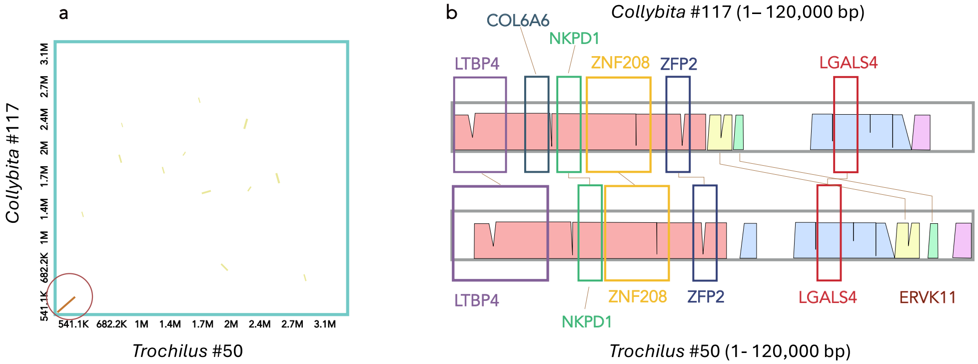


Figure 11. Schematic representation of a comparison of MARB scaffolds in trochilus (#50) and collybita (#117). Dot plot of full length (**a**) and *Mauve* alignment over the first 120 kb. (**b**) Annotated genes illustrated in coloured boxes. Despite shared features across *Phylloscopus* (repeat families, OR, pseudogene density and GC content), the MARB region seems to have been through numerous rearrangements, resulting in divergent sequence architecture.

MARB correlates with migratory phenotype in chiffchaff subspecies

In **Paper V** we integrate genome resequencing, molecular and tracking data to investigate genetic differences associated with migratory phenotype in two common chiffchaff subspecies, *P. c. collybita* and *P. c. abietinus*. We demonstrate that this system mirrors the migratory divergence seen in *P. t. trochilus* and *P. t. acredula* with parallel contact zones in Scandinavia and across the Baltic, making these chiffchaff subspecies an ideal target for comparative analyses.

Population statistics and demographic modelling show that *abietinus* and *collybita* are still in early stages of divergence. Their highest differentiation ($F_{ST} > 0.6$), however, occurs in mitonuclear and fertility-related genes, suggesting that selection might be driving subspecies divergence. Notably, the MARB contigs also show high differentiation, although uncertainty in their assembly may affect population statistics. Nevertheless, the clear clustering by multidimensional scaling analyses (MDS) also supports that different migratory phenotypes present distinct MARB haplotypes. This turns MARB into the only region divergent between east and west migrants that is common to chiffchaffs and willow warblers.

This has crucial implications for the understanding of the genetic basis of migratory behaviour across species. If MARB regulates migratory direction in chiffchaffs, it does so within a different genomic context than in willow warblers. These findings align with studies in common yellowthroats where populations with different migratory behaviours showed parallel evolution at the gene level —same genes repeatedly involved— but convergent evolution at the SNP level (different mutations within such genes; Zamudio-Beltrán et al., 2025). Importantly, many of the variants were found in noncoding regions, suggesting that control of gene expression plays a central role in shaping migratory phenotypes. This shows that different species may adapt to similar migratory challenges through distinct, yet partially predictable genetic pathways.

Short and long-distance migrants differ in migratory traits

Despite belonging to a cryptic species complex, the Iberian chiffchaff and common chiffchaff have been considered separate species for over two decades (Salomon et al., 2003). In the final chapter of this thesis, **Paper VI**, we deployed pressure geolocators on 61 chiffchaffs in the Iberian Peninsula (30 *P. c. collybita* and 31 *P. ibericus*) to investigate differences in migratory strategies. Our findings confirm that *P. ibericus* are indeed long-distance migrants, wintering in West Africa. They fly higher, faster and longer than the sympatric Spanish *P. collybita,* which remain in the Iberian Peninsula year-round (Figure 12). These results pave the way for future studies in the narrow hybrid zone between the two species in the western Pyrenees (Bensch, Helbig, et al., 2002). Combining resequencing data with geolocator tracks will enable us to study genetic differences behind the strategies of long and short-distance migrants.

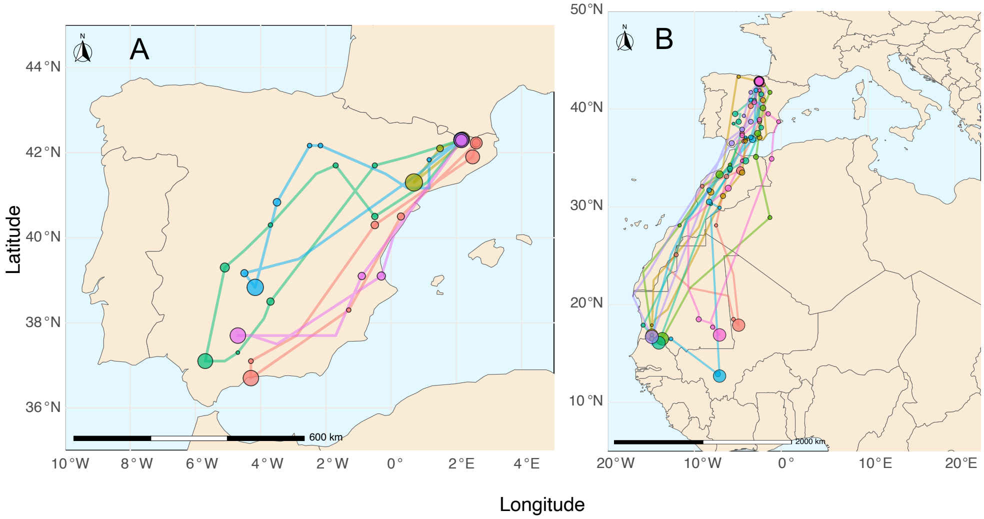


Figure 12. Modelled trajectories from *P. c. collybita* (A) and *P. ibericus* (B) captured in Spain. Each individual is depicted with a different colour. Circles show stationary periods: breeding grounds, wintering grounds and stopover sites. The size of the circle is proportional to the time spent in the stationary period.

Conclusions and future directions

This thesis constitutes a big leap in the study of the genetic architecture behind migratory behaviour and has implications that extend beyond species-specific insights. We identified a large, repetitive region (MARB) which explains most variation in migratory direction in European willow warblers and demonstrates that complex regions, often dismissed as junk-DNA, can play central roles in behavioural divergence. Our comparative analyses reveal that MARB is likely present in all *Phylloscopus* species, and it seems to correlate with migratory strategies in chiffchaff subspecies. The different genomic context in which MARB seems to have evolved across species suggests that similar behavioural traits may have emerged through convergent genetic pathways. An increasing number of studies support this, emphasizing the role of regulatory mechanisms, particularly in non-coding regions (Merlin & Liedvogel, 2019; Delmore et al., 2023; Louder et al., 2024; Zamudio-Beltrán et al., 2025). With the integration of cytogenetics, genomic, molecular and tracking data, we provide a robust framework to link genotype and phenotype even in such complex regions that remain unresolved in genome assemblies.

Nevertheless, there are gaps in the field that still need to be addressed. We are aware that our data is male-biased, due to several reasons. First, in monogamous bird species, males are typically more philopatric than females (Liberg & von Schantz, 1985) which ensures a larger retrieval of geolocators. Second and most importantly, females are substantially harder to relocate and recapture after migration (McKinnon & Love, 2018), as they remain inconspicuous among the vegetation and don't react to playback; thus, targeted recapture would require relocating nests. This can mask patterns such as differential migration. This is a poorly understood phenomenon in birds that has been, for example, detected in chiffchaffs, blackbirds or northern flickers where males and females seem to exhibit distinct migratory strategies (Catry et al., 2005; Fudickar et al., 2013; Gow & Wiebe, 2014). From a population genetics perspective, male-biased sampling can skew allele frequency estimates (and therefore gene flow estimates) and reduce the detection power of sex-linked loci (Prugnolle & De Meeus, 2002). Future studies should aim to incorporate balanced sex ratios and explore sex-specific genomic and behavioural variation to fully capture the complexity of migratory systems.

Another caveat of using geolocator data is that, as we only retrieve loggers from birds that survived migration at least twice, our inferences are inevitably survivor-biased. This hinders the estimation of potential hybrid disadvantage as our data does not represent individuals that might have lower survival due to maladapted intermediate routes (Rushing et al., 2021). However, if we want to test the selection against willow warbler hybrids (estimated to be a 10% difference in survival per generation) we would need survival data for more than 1000 individuals to confirm hybrid disadvantage (Zhao et al., 2020).

Currently, tracking studies on juveniles of larger species show differences in timing (McKinnon et al., 2014; Patchett et al., 2022) and tortuosity (less direct routes) of migration (Mellone et al., 2013; Vega et al., 2016). A major tipping point for the field will take place when satellite tracking devices are small enough to be carried by small, solitary migrants. This will ensure life data input without the need of retrieval, and will provide us with first-time migrants and female migratory patterns, and overall mortality rates across different routes.

Finally, the work with complex genomic regions is also challenging by itself. Despite using highly contiguous assemblies that combine long-read sequencing (PacBio Hi-Fi), link-read sequencing (10X Chromium) and optical mapping (Bionano Genomics), the MARB region remains challenging to map. In future assemblies we will attempt combining long read sequencing with Ultra-Long read sequencing (Oxford Nanopore) and Trio-sequencing with sequences from parents and offspring to resolve haplotypes and complex regions (Figure 13). These approaches have proved successful in resolving regions of comparable complexity in chicken that might indeed be homologous to MARB (Huang et al., 2023).

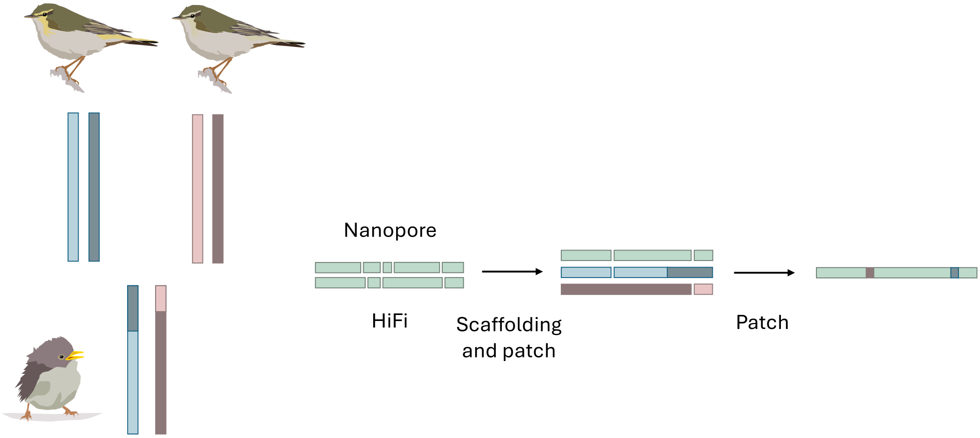


Figure 13. Trio-based genome assembly strategy for a willow warbler family including parental individuals from the hybrid zone with different MARB haplotypes and their hybrid offspring. Paternal and maternal haplotypes can be used to fill the gaps in primary contigs.

Our findings challenge traditional approaches that focus on coding sequences and highlight the need to explore underrepresented genomic regions. We also emphasize the value of studying cryptic species and hybrid zones to uncover the genetic basis of several migratory traits. With an integrative approach, this thesis contributes to the understanding of the genetic basis of migration in birds.

Figure 14. After eight days of torrential downpour, the clouds finally part one morning in Ribes de Freser, Spain — one of the many trapping sites for *Phylloscopus* species in this thesis. Photo: Harald Ris.

Acknowledgements

If there is something that has kept me in this harsh latitude, it is our department. I have been in the Ecology building for 8 years, much less than many of you. But I have met a lot of people coming and going, so my acknowledgements section will not be short. Everything good in me as a researcher is because each one of you has touched my life, so the least I can do is thank you properly.

Staffan, thank you for your calm guidance, for always making the best of every situation, for believing in me when I did not, and for *always* having my back. As the true diplomat you are, you show that choosing to be kind and solution-oriented will always bring out the best in others. Thank you for your patience, you handled my Mediterranean temperament like no one else could. Most of all, thank you for your generosity as a scientist. I hope that one day I can trust my instincts while taking nothing for granted in science, just like you do.

Thank you, **Dennis**, for the funniest lectures I have ever attended, for always having a positive mindset, for your enthusiasm, and for keeping me alive with cava during the tough Kvismaren summers. **Helena**, thank you for keeping an eye on me all these years, for being such a reassuring presence in every ISP meeting, and for your sharp look through my kappa. **Charlie**, I think it is a good sign that I have not needed you as a mentor, but thank you for always being there, and for trying to explain Bayesian Phylogenetic Mixed Models to us, though I am afraid that it crossed my brain leaving an echo behind. Thank you **Eric Warrant** for being my opponent in my half-time, it prepared me well for what´s to come.

The former willow warbler team members: **Tianhao**, the Beast from the East, thank you for always being willing to discuss qPCR or pressure logger analysis with me, and for remembering all my birthdays. **Mikkel**, thank you for showing me how to "control" birds with a speaker so they fall in the net. **Kristaps**, thank you for teaching me the neanderthal ways to catch a bird. **Max**, thank you for explaining the same thing again and again until I no longer have the empty look of a confused capybara. Thank you, **Alex M**, for your brightness and your patience in explaining demographic inference to all of us. Many times.

Thank you, **Alexander Suh** and **Nathalie Feiner**, for discussing transposon matters with me. For you, it was maybe one hour of your time; for me, it ended in a few years of work, many ideas, and the first paper in this thesis. Thank you, **Diana E.** and **Estelle P-W.**, for your invaluable help with bioinformatic analyses across the years.

Thank you **Lars,** for so many ringing mornings, your acid sense of humour, and your sharp insights in the MEEL discussions. **Jan-Åke**, thank you for making the department a better place, for your contagious laughter, for appreciating my paintings, for always asking how I am, you make us all feel at home. To the people that have organised so many cool workshops that ended up in Spas: thank you **Emily**, **Bengt** and **Olof**, this really took the PhD experience to another level. But also thank you for your insightful questions and discussions in the MEEL meetings. **Michi**, thank you for always keeping an eye on me, before and during the PhD. Thank you for appreciating my art, and for all the moth talk. **Susanne** for teaching us almost all there is about compass and orientation. **Anders**, for your sense of humour and your calm nature. **Thomas**, the Swedish Attenborough, I always learn something after each conversation with you. Your lectures left us with hands itchy for an applause every time they ended. Thank you for always checking on me and for making me feel valuable. **Sissel**, thank you for always discussing migration with me and for your loud laughter. Your strength and character as a scientist inspire me every day.

To the SACT team, especially **Erik Selander**, **Dimitri** and **Nathalie**. Thank you for everything you do for the department seminars, for the ctenophore micro photography and for the fungi knowledge.

To the Max Planck team: **Elena**, **Karem** and **Karen**. Thank you for adopting me in Plön, I do not know how I would have kept my sanity otherwise. Thank you, **Linda**, for showing me karyotyping for the first time and for welcoming in your Hobbiton home.

To the Czech team: **Carlos**, amigo mío, te fuiste muy pronto pero siempre me quedará tu conocimiento experto de memes, tu sonrisa inmensa, tus chistes malos, tu ética de trabajo, tu calidez y tu inmenso corazón. **Radka** and **Stephen**, thank you for our discussions about probes and genomes. **Tomas**, **Eleonora** and **Marie**: thank you for taking care of me with Czech beer and cake, and for making sure I did not inhale too much formamide in the lab. **Vladimir**, thank you for your genuine interest in my project, and for helping me even when I was too embarrassed to ask. But mainly, thank you for your friendship. **Dima**, my dear friend. Thank you for not giving up on me and my project, and for finding the time when you had none. But mostly, thank you for laughing instead of defenestrating me when I broke my slides at 12 am.

A mis estrellas fugaces españolas: **Jesús Veiga**, gracias por enseñarme a hacer qPCRs como una pro, me adoptaste y siempre lo recordaré. **Jesús Ortega**, gracias por todas las risas y el acuario con las quisquillas. Eres un ejemplo de "científico de la leche que sabe hablar de otras cosas que no son ciencia". Desafortunadamente esta tesis no se caga en las monjas de un colegio católico, eso te lo dejo a ti. **Dani Truchado**, por tus dibujos y tu presencia cálida. A **Jessi**, por tardes de chicas que no he tenido ni antes ni después, a **Lucía J.** y **Luz** por vuestra dulzura. **Ainara,** eskerrik asko por los paseos y las charlas cuando mi corasonsito no estaba bien. **Javi Pinilla** gracias por siempre ayudarme con estadística y por ser tan bueno. A **Juan Diego** (y familia), me sacas de quicio, pero nos lo hemos pasado bien. Gracias **Paula** por traer todo el color de Andalucía hasta aquí arriba.

Thank you to the gang from the glorious old days: **Samantha**, for your big heart and for teaching me so many things in the lab when no one else could! **Mridula**, for your bright smile and laughter. **Mariana**, for all the Kvismaren adventures and for keeping an eye on me always. **Hongkai**, for your calmness and for being always willing to help me with bioinformatic questions. **Linus** for being an inspiring territory mapper, and for the good talks about bird ecology, you always made me see the bigger picture. **Ann-Katrin**, for your bright smile. **Tamara**, for your caring presence and all your crafty contributions through the years. **Angela** and **Theo**, for all the fun chats. **Pedro Rosero,** gracias por tu gran corazón, por siempre ofrecer tu ayuda y por el honor que fue dibujar tu portada. **J. Pablo** y **Micaela**, por bailar conmigo mago de oz y el meneito en las defensas. **Carlos** y **Pablo Arellano**, por toda la salsa, las parrilladas, las navidades varados aquí, la poesía y los buenos libros. **Philip** and **Hanna**, thank you for the amazing chats. **Julian Melgar**, gracias por tu presencia, siempre me relaja, y por dejarme dibujar tu portada, fue un honor.

Carolina, obrigada pelo cochicho e por me explicar a genética populacional, por tua personalidade brilhante, por tua atenção, por tua doçura e a tua força. **Amparo**, por todas las galletas de oficina que *tu* traes y *yo* me como, y por tu naturaleza cuidadora. **Ximena**, la otra Caballero, la princesa andina, por todos los perreos en las fiestas y en las clases de estadística. **Susana**, por tu amabilidad y dulzura, **Agnes**, for being so helpful, for your sharp insights and amazingly evil mind (please have mercy on me). **Jesper** for always being willing to help and chat about loggers with me, your huge heart, your patience and endless curiosity, I really admire you. **Sonja**, thank you for teaching me to be a fearless knitter, and **Cecilia**, thank you for all the knitting afternoons and the migration chats. **Lucia**, for the mushroom foraging and subsequent parasite grooming. **Sofie** the karate kid, for being always such a bright presence, I always leave our conversations with a smile. **Jöran**, I could listen to you speaking about orchids and wool the whole day, thank you for all the cheese. **Shridar**, thank you for your contagious laughter and your amazing curry. **Emma K**, for always receiving me with the biggest smile and the sweetest Spanska and for coming to all the moth expeditions; many more to come! **Quentin**, thank you for your big heart, your frog stickers and for being so noble. **Simon**, for always being willing to help me with bioinformatics and genome evolution discussions. Also, for your inspiring craftiness and knowledge about the most random things. **Kalle**, for running your expert eyes through my kappa, and your calming energy. Since we took our masters together, you have always inspired me to be the best scientist version of myself and to do things properly. **Elsie**, for so many

gin tonics, laughter, tears and plant passion throughout the years, you are a big presence in the department and in my life. **Arne A**, for your calm presence, your exquisite taste for a good jersey and your craftiness. **Kat**, thank you for the endless fly supply and all the reality checks. **Zack**, thank you for your kindness, your predisposition to help and your amazing sense of humour. **Homa**, for always chatting about programming with me, for raising your voice when it needs to be done, and for taking care of my geckos when I am not around. **Rae**, for your amazing pumpkin pies and thanksgivings, for your good nature and soothing presence. **Guillaume**, for saying things as you see them, no ornaments, no beating around the bush, just passion. **Niko**, for your enthusiasm and kindness. **Daniel Tajmel**, thank you for all the plant expertise, cozy Malmö evenings and your sensitivity. **Zsofia**, thank you for not smashing us against a red kangaroo or a buffalo in Australia, and for teaching me Hungarian dog language. **Ernö,** travelling with you is like travelling with a human encyclopaedia, thank you for coming along to Bangkok, and the Great Barrier Reef. **Alessia**, thank you for your sweetness, for our Australian birding expeditions, and for showing me the frogmouth and the platypus. I am amazed by your journey since you started the PhD, you are brilliant already. **Grace**, you dolphin lady, your time here was short but intense, always back like a boomerang. Thank you for the tuna trip and many other expeditions, wait for me down under! **Michaela** and **Bucur**, for taking care of my animals when I was not around, for the book discussions and for all the cozy evenings in our caves. **Amandine**, thank you for always hyping me up during our masters, for all the times you cooked for me when I was coming back home late from work, and for being such a caring and generous friend.

Qinyang, you're one of the people with the biggest heart -and brain- I have met. Thank you for our biking trips, for your insightful comments in this kappa, for teaching me stats before I went ahead and pretended to know what I was saying in front of the students. For your amazing sense of humour and the ability to laugh at everything, including yourself. **Jane**, thank you for so many years of leaving "anonymous" chocolates, cards and little gifts in my desk when you thought I was stressed. For always receiving our surprise visits through Anderslöv with berries, plums, stews and coffee. Thank you for your big heart and your sensitivity. But mostly, thank you for your courage and honesty, I will always admire that from you. **Finja,** it is impressive how you make every animal calm around yourself, including us humans. Thank you for your *chauffeur* services, for all the ferments, for showing me how to use a sewing machine, for your patience, your sensitivity to beautiful things, and for always feeding us all. **Hamid**, gracias por siempre ayudarme con lo que necesito, ya sea trayendo aceite de oliva y huesos de jamón en coche desde España, llevándome a sitios, cuidando mis stinky rabbits y mis peces, o discutiendo bayesian methods y filogenias. Siempre estás ahí. ممنون. **Yedra,** por tu dulzura, por cuidarnos a todos tan bien a base de empanada y tortilla de patata, por ser tan generosa y por todas las historias de campo. Personas como tú nos da buen nombre a los madracas. **Juanita,** la paisa más chula, es imposible

no estar de buen humor después de hablar contigo. Gracias por alegrarme todas las comidas, por apuntarte a misiones desastrosas por el bosque y aunque el tópico sea un poco… trambólico, espero que te quedes en migración por mucho tiempo.

To **Emma E, Yohan, Hanna W, Erica, Iain, Elin, Robin, Alex L, Ruben, André, Arne H., Evelina, Ana, Jana, Lila, Jamie, Zaide, Karla, Sara P.**, you all made this trip so much fun!

Gintaras slash *moose*, slash *amber*. Thank you for your help, on either side of the Baltic. For the funniest summers of my life and your big heart (I think it might actually be moose-sized). Thank you for teaching me the ways of the reeds and for risking your life in a Ford Mondeo with me. I cannot say more to avoid liability.

Sara and **Amir**, I am so lucky to live next door from you. Thank you for keeping an eye on me when I disappeared in my thesis-writing frenzies, or when I was sick, feeding me the most amazing Persian food. The strength to write this book came out of that. ممنون

To my Swedish family, especially **Johanna R.** and **Dani G**, who came to see me talk in my first big conference in Stockholm. I was so scared I gave that talk drunk, but you gave me strength. I shall never forget it.

Ana, gracias por guiarnos por los Pirineos y por contar los mosquiteros en *ebird*. Gracias a ti, el último capítulo de esta tesis existe. **Joan**, gracias a tu carpacho de corzo, yo existo. Gracias a los dos por acogernos a todos y por ser tan buenos.

Juan, dende a primeira vez que viñeches a Lund, foi imposible non quererte. Escoitarte é mellor que escoitar á Cadena Ser. Aprendo de ti en cada conversa, e sempre marcho coa intención de poñerme máis no lugar do outro. Grazas por traer a filosofía á miña vida. Con un pouco de sorte, farei que che gustemos un pouco máis os fodechinchos.

Pablo, compañero de gracias y desgracias. Gracias por dedicarme tiempo con todas mis preguntas de Geopressure, incluso cuando no tenías ni para ti; por llevarme a capturar ruiseñores, por enseñarme el buen vivir de Copenhague (gracias a **Blanca** también); por siempre responder a todo con una sonrisa gigante de Pennywise, pero sobre todo gracias "Por" todo el JAMÓN. Es mi posesión más preciada. Ha sido un honor luchar a tu lado. Ahora, el patíbulo nos espera. Te veré al otro lado.

Javi, eres la mejor medicina para este clima. Cada vez que vienes me dejas los abdominales bien fuertes. Gracias por las muchas excursiones improvisadas en el bosque, por aguantar mis "despotricamientos", por ser tan buen narrador de historias, por reírte de mí tantas veces, me ha hecho mucho bien. Gracias por enseñarme tantas cosas de comportamiento animal (incluido el humano), por tu empatía y por contagiar tu respeto y admiración por todos los seres vivos, sin importar cómo de diminutos o "simples" sean. Pero lo siento, seguiré comiendo vacas veganas. Ya sabes que "en el barro se está bien" (Ábalos, 2025).

David, alma de cántabro. No hay papel en el Amazonas para escribir todo lo que debería, pero haré un sumario. Fuiste "Hue, saturation and intensity" en este gris lugar que es Lund 8 meses al año. Vas a ser el origen de mis patas de gallo (y de alguna cana) cuando aparezcan. Gracias por 5 años de humor muy censurable que no puedo reproducir por escrito, por enseñarme a moverme en el barrizal de Kvismaren (en diversos tipos de vehículo), por llegar gritando coplas de Joselito conmigo sin miedo a ser cancelado, por curarme a base de puzles y workouts, por los chanchullos mafiosos para vender mi arte, por cebarme con sobaos pasiegos y pipas Tijuana cuando no me acuerdo de mi nombre ni yo. Por aguantar regateos eternos en bazares de Estambul conmigo (al final creo que pagamos más de lo que pedían). Pero sobre todo, gracias por tu lealtad. Si hay otra vida después de ésta espero cruzarme contigo otra vez; si no, nos vemos en el infierno seguro.

A mi familia. A **Marisa** por ayudarme con el inglés, que me dio las alas para volar. A **Jose**, por todos los consejos de academia y por cuidarme desde la distancia. A **mamá,** gracias por todas las tardes ayudándome con las malditas matemáticas, por aguantar mis lloreras antes de todos y cada uno de mis exámenes, por mostrarme todas las cosas en las que podría convertirme si quería desde pequeña, por dejarme elegir siempre y por enseñarme que con esfuerzo casi todo se puede en esta vida, a pesar de "la maldición de las López". **Papá**, gracias por cebarme a documentales de la 2, por hacer que me guste dibujar, el campo, la lluvia, los truenos y los animales; si he elegido biología es por todo eso. **Daniel**, gracias por venir a capturar pájaros conmigo y por los baños en las ciénagas suecas. Eres la persona más resistente que conozco y tu nobleza hace que yo quiera ser mejor persona.

To **Harald.** I really think you have tagged more birds in this thesis than anyone else. One of the first things you taught me is the *one and only* proper way to fold a net, and since then, you have never stopped. You have taught me to ID skuas flying far away, and to drive (legally). Because of you, I look at nature with better eyes. There is beauty in a golden plover flying over a mountain top, but also in the old greater black-backed gull reigning over a rusty pier for years, or a common *blåvinge* fluttering by the roadside. You make me look outwards. Thank you for lifting me in the middle of a storm in northern Spain after days of no birds and no hot meals. Thank you for embracing my culture and for sharing yours, for adding colour to my life, for handling my 90 personalities with infinite patience and for enduring all my podcasts (you know I don't do silence). Thank you for being my biggest fan — I am definitely yours.

Reference list

Able, K. P., & Able, M. A. (1990). Calibration of the magnetic compass of a migratory bird by celestial rotation. *Nature*, *347*(6291), 378–380. https://doi.org/10.1038/347378a0

Able, K. P., & Belthoff, J. R. (1998). Rapid 'evolution' of migratory behaviour in the introduced house finch of eastern North America. *Proceedings of the Royal Society B: Biological Sciences*, *265*(1410), 2063–2071. https://doi.org/10.1098/rspb.1998.0541

Abrahms, B., Teitelbaum, C. S., Mueller, T., & Converse, S. J. (2021). Ontogenetic shifts from social to experiential learning drive avian migration timing. *Nature Communications*, *12*(1), 7326. https://doi.org/10.1038/s41467-021-27626-5

Aikens, E. O., Bontekoe, I. D., Blumenstiel, L., Schlicksupp, A., & Flack, A. (2022). Viewing animal migration through a social lens. *Trends in Ecology & Evolution*, *37*(11), 985–996. https://doi.org/10.1016/j.tree.2022.06.008

Åkesson, S., & Weimerskirch, H. (2005). Albatross Long-Distance Navigation: Comparing Adults And Juveniles. *Journal of Navigation*, *58*(3), 365–373. https://doi.org/10.1017/S0373463305003401

Alerstam, T. (2009). Flight by night or day? Optimal daily timing of bird migration. *Journal of Theoretical Biology*, *258*(4), 530–536. https://doi.org/10.1016/j.jtbi.2009.01.020

Alström, P., Rheindt, F. E., Zhang, R., Zhao, M., Wang, J., Zhu, X., Gwee, C. Y., Hao, Y., Ohlson, J., Jia, C., Prawiradilaga, D. M., Ericson, P. G. P., Lei, F., & Olsson, U. (2018). Complete species-level phylogeny of the leaf warbler (Aves: Phylloscopidae) radiation. *Molecular Phylogenetics and Evolution*, *126*, 141–152. https://doi.org/10.1016/j.ympev.2018.03.031

Andersson, J. E., Lehikoinen, P., Berdougo, M., Jolkkonen, J., & Bensch, S. (2024). A hybrid population of Willow Warblers in the Åland Archipelago. *Journal of Ornithology*, *165*(3), 835–840. https://doi.org/10.1007/s10336-024-02149-0

Avise, J. C., & Bowen, B. W. (1994). Investigating sea turtle migration using DNA markers. *Current Opinion in Genetics & Development*, *4*(6), 882–886. https://doi.org/10.1016/0959-437X(94)90074-4

Balmori, A., Cuesta, M. Á., & Caballero, J. M. (2002). Distribución de los mosquiteros ibérico (*Phylloscopus brehmii*) y europeo (*Phylloscopus collybita)* en los bosques de ribera de Castilla y León (España). *M. A.*

Bang, B. G., & Cobb, S. (1968). The Size of the Olfactory Bulb in 108 Species of Birds. *The Auk*, *85*(1), 55–61. https://doi.org/10.2307/4083624

Battley, P. F., Warnock, N., Tibbitts, T. L., Gill Jr, R. E., Piersma, T., Hassell, C. J., Douglas, D. C., Mulcahy, D. M., Gartrell, B. D., Schuckard, R., Melville, D. S., & Riegen, A. C. (2012). Contrasting extreme long-distance migration patterns in bar-tailed godwits *Limosa lapponica*. *Journal of Avian Biology*, *43*(1), 21–32. https://doi.org/10.1111/j.1600-048X.2011.05473.x

Bensch, S., Åkesson, S., & Irwin, D. E. (2002). The use of AFLP to find an informative SNP: Genetic differences across a migratory divide in willow warblers. *Molecular Ecology*, *11*(11), 2359–2366. https://doi.org/10.1046/j.1365-294X.2002.01629.x

Bensch, S., Andersson, T., & Åkesson, S. (1999). Morphological and molecular variation across a migratory divide in willow warblers, *Phylloscopus trochilus*. *Evolution*, *53*(6), 1925–1935. https://doi.org/10.1111/j.1558-5646.1999.tb04573.x

Bensch, S., Caballero-Lopez, V., Cornwallis, C. K., & Sokolovskis, K. (2023). The evolutionary history of “suboptimal” migration routes. *iScience*, 108266. https://doi.org/10.1016/j.isci.2023.108266

Bensch, S., Grahn, M., MÜller, N., Gay, L., & Åkesson, S. (2009). Genetic, morphological, and feather isotope variation of migratory willow warblers show gradual divergence in a ring. *Molecular Ecology*, *18*(14), 3087–3096. https://doi.org/10.1111/j.1365-294X.2009.04210.x

Bensch, S., Helbig, A. J., Salomon, M., & Seibold, I. (2002a). Amplified fragment length polymorphism analysis identifies hybrids between two subspecies of warblers. *Molecular Ecology*, *11*(3), 473–481. https://doi.org/10.1046/j.0962-1083.2001.01455.x

Bensch, S., Irwin, D. E., Irwin, J. H., Kvist, L., & Åkesson, S. (2006). Conflicting patterns of mitochondrial and nuclear DNA diversity in *Phylloscopus* warblers. *Molecular Ecology*, *15*(1), 161–171. https://doi.org/10.1111/j.1365-294X.2005.02766.x

Berthold, P. (1973). Relationships Between Migratory Restlessness and Migration Distance in Six Sylvia Species. *Ibis*, *115*(4), 594–599. https://doi.org/10.1111/j.1474-919X.1973.tb01998.x

Berthold, P. (1999). A comprehensive theory for the evolution, control and adaptability of avian migration. *Ostrich*. https://www.tandfonline.com/doi/abs/10.1080/00306525.1999.9639744

Berthold, P., & Helbig, A. J. (2008). The genetics of bird migration: Stimulus, timing, and direction. *Ibis*, *134*, 35–40. https://doi.org/10.1111/j.1474-919X.1992.tb04731.x

Berthold, P., Helbig, A. J., Mohr, G., & Querner, U. (1992). Rapid microevolution of migratory behaviour in a wild bird species. *Nature*, *360*(6405), 668–670. https://doi.org/10.1038/360668a0

Berthold, P., Mohr, G., & Querner, U. (1990). Steuerung und potentielle Evolutionsgeschwindigkeit des obligaten Teilzieherverhaltens: Ergebnisse eines Zweiweg-Selektionsexperiments mit der Mönchsgrasmücke *(Sylvia atricapilla). Journal für Ornithologie, 131(1), 33–45. https://doi.org/10.1007/BF01644896*

Bossu, C. M., Heath, J. A., Kaltenecker, G. S., Helm, B., & Ruegg, K. C. (2022). Clock-linked genes underlie seasonal migratory timing in a diurnal raptor. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1974), 20212507. https://doi.org/10.1098/rspb.2021.2507

Browder, J. A. (1973). Long-Distance Movements of Cattle Egrets. *Bird-Banding*, *44*(3), 158–170. https://doi.org/10.2307/4511956

Caballero-López, V., Lundberg, M., Sokolovskis, K., & Bensch, S. (2022). Transposable elements mark a repeat-rich region associated with migratory phenotypes of willow warblers (*Phylloscopus trochilus*). *Molecular Ecology*, *31*(4), 1128–1141. https://doi.org/10.1111/mec.16292

Catry, P., Lecoq, M., Araújo, A., Conway, G., Felgueiras, M., King, J. M. B., Rumsey, S., Salima, H., & Tenreiro, P. (2005). Differential migration of chiffchaffs *Phylloscopus collybita* and *P. ibericus* in Europe and Africa. *Journal of Avian Biology*, *36*(3), 184–190. https://doi.org/10.1111/j.0908-8857.2005.03445.x

Chamberlain, C. p., Bensch, S., Feng, X., Åkesson, S., & Andersson, T. (2000). Stable isotopes examined across a migratory divide in Scandinavian willow warblers (*Phylloscopus trochilus trochilus* and *Phylloscopus trochilus acredula*) reflect their African winter quarters. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*(1438), 43–48. https://doi.org/10.1098/rspb.2000.0964

Chernetsov, N., Berthold, P., & Querner, U. (2004). Migratory orientation of first-year white storks (*Ciconia ciconia*): Inherited information and social interactions. *Journal of Experimental Biology*, *207*(6), 937–943. https://doi.org/10.1242/jeb.00853

Clement, P., & Helbig, A. J. (1998). Taxonomy and identification of chiffchaffs in the Western Palearctic. *British Birds*, *91*(9).

Cody, M. L. (1978). Habitat Selection and Interspecific Territoriality among the Sylviid Warblers of England and Sweden. *Ecological Monographs*, *48*(4), 351–396. https://doi.org/10.2307/2937239

Cox, G. W. (1985). The Evolution of Avian Migration Systems between Temperate and Tropical Regions of the New World. *The American Naturalist*, *126*(4), 451–474. https://doi.org/10.1086/284432

de la Hera, I., Gómez, J., Dillane, E., Unanue, A., Pérez-Rodríguez, A., Pérez-Tris, J., & Torres-Sánchez, M. (2020). Wintering grounds, population size and evolutionary history of a cryptic passerine species from isotopic and genetic data. *Journal of Avian Biology*, *51*(9). https://doi.org/10.1111/jav.02559

Delmore, K. E., & Irwin, D. E. (2014). Hybrid songbirds employ intermediate routes in a migratory divide. *Ecology Letters*, *17*(10), 1211–1218. https://doi.org/10.1111/ele.12326

Delmore, K. E., Toews, D. P. L., Germain, R. R., Owens, G. L., & Irwin, D. E. (2016). The Genetics of Seasonal Migration and Plumage Color. *Current Biology*, *26*(16), 2167–2173. https://doi.org/10.1016/j.cub.2016.06.015

Delmore, K. E., Van Doren, B. M., Ullrich, K., Curk, T., van der Jeugd, H. P., & Liedvogel, M. (2023). Structural genomic variation and migratory behavior in a wild songbird. *Evolution Letters*, qrad040. https://doi.org/10.1093/evlett/qrad040

Delmore, K., Illera, J. C., Pérez-Tris, J., Segelbacher, G., Lugo Ramos, J. S., Durieux, G., Ishigohoka, J., & Liedvogel, M. (2020). The evolutionary history and genomics of European blackcap migration. *eLife*, *9*, e54462. https://doi.org/10.7554/eLife.54462

Dingle, H. (2006). Animal migration: Is there a common migratory syndrome? *Journal of Ornithology*, *147*(2), 212–220. https://doi.org/10.1007/s10336-005-0052-2

Doren, B. M. V., DeSimone, J. G., Firth, J. A., Hillemann, F., Gayk, Z., Cohen, E., & Farnsworth, A. (2025). Social associations across species during nocturnal bird migration. *Current Biology*, *35*(4), 898-904.e4. https://doi.org/10.1016/j.cub.2024.12.033

Driver, R. J., & Balakrishnan, C. N. (2021). Highly Contiguous Genomes Improve the Understanding of Avian Olfactory Receptor Repertoires. *Integrative and Comparative Biology*, *61*(4), 1281–1290. https://doi.org/10.1093/icb/icab150

Dsilva, G. J., & Galande, S. (2024). From sequence to consequence: Deciphering the complex cis-regulatory landscape. *Journal of Biosciences*, *49*(2), 46. https://doi.org/10.1007/s12038-024-00431-0

Dufour, P., de Franceschi, C., Doniol-Valcroze, P., Jiguet, F., Guéguen, M., Renaud, J., Lavergne, S., & Crochet, P.-A. (2021). A new westward migration route in an Asian passerine bird. *Current Biology*, *31*(24), 5590-5596.e4. https://doi.org/10.1016/j.cub.2021.09.086

Dufour, P., Descamps, S., Chantepie, S., Renaud, J., Guéguen, M., Schiffers, K., Thuiller, W., & Lavergne, S. (2020). Reconstructing the geographic and climatic origins of long-distance bird migrations. *Journal of Biogeography*, *47*(1), 155–166. https://doi.org/10.1111/jbi.13700

Egevang, C., Stenhouse, I. J., Phillips, R. A., Petersen, A., Fox, J. W., & Silk, J. R. D. (2010). Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proceedings of the National Academy of Sciences*, *107*(5), 2078–2081. https://doi.org/10.1073/pnas.0909493107

Emlen, S. T. (1970). Celestial Rotation: Its Importance in the Development of Migratory Orientation. *Science*, *170*(3963), 1198–1201.

Emlen, S. T. (1975). The Stellar-Orientation System of a Migratory Bird. *Scientific American*, *233*(2), 102–111.

Fandos, G., Rotics, S., Sapir, N., Fiedler, W., Kaatz, M., Wikelski, M., Nathan, R., & Zurell, D. (2020). Seasonal niche tracking of climate emerges at the population level in a migratory bird. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1935), 20201799. https://doi.org/10.1098/rspb.2020.1799

Farnsworth, A. (2005). Flight Calls and Their Value for Future Ornithological Studies and Conservation Research. *The Auk*, *122*(3), 733–746. https://doi.org/10.1093/auk/122.3.733

Fudickar, A. M., Schmidt, A., Hau, M., Quetting, M., & Partecke, J. (2013). Female-biased obligate strategies in a partially migratory population. *Journal of Animal Ecology*, *82*(4), 863–871. https://doi.org/10.1111/1365-2656.12052

Gobert, V., Moja, S., Colson, M., & Taberlet, P. (2002). Hybridization in the section Mentha (Lamiaceae) inferred from AFLP markers. *American Journal of Botany*, *89*(12), 2017–2023. https://doi.org/10.3732/ajb.89.12.2017

Gómez, C., Tenorio, E. A., Montoya, P., & Cadena, C. D. (2016). Niche-tracking migrants and niche-switching residents: Evolution of climatic niches in New World warblers (Parulidae). *Proceedings of the Royal Society B: Biological Sciences*, *283*(1824), 20152458. https://doi.org/10.1098/rspb.2015.2458

Gordo, O., Arroyo, J. L., Rodríguez, R., & Martínez, A. (2017). Inability of Biometry to Discriminate Iberian and Common Chiffchaffs During the Autumn Migration Period. *Ardeola*, *64*(1), 49. https://doi.org/10.13157/arla.64.1.2017.ra4

Gow, E. A., & Wiebe, K. L. (2014). Males migrate farther than females in a differential migrant: An examination of the fasting endurance hypothesis. *Royal Society Open Science*, *1*(4), 140346. https://doi.org/10.1098/rsos.140346

Grubb, T. C. (1973). Colony Location by Leach's Petrel. *The Auk*, *90*(1), 78–82.

Gu, Z., Pan, S., Lin, Z., Hu, L., Dai, X., Chang, J., Xue, Y., Su, H., Long, J., Sun, M., Ganusevich, S., Sokolov, V., Sokolov, A., Pokrovsky, I., Ji, F., Bruford, M. W., Dixon, A., & Zhan, X. (2021). Climate-driven flyway changes and memory-based long-distance migration. *Nature*, *591*(7849), 259–264. https://doi.org/10.1038/s41586-021-03265-0

Gwinner, E., & Helm, B. (2003). Circannual and Circadian Contributions to the Timing of Avian Migration. In P. Berthold, E. Gwinner, & E. Sonnenschein (Eds.), *Avian Migration* (pp. 81–95). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-662-05957-9_5

Hahn, S., Bauer, S., & Liechti, F. (2009). The natural link between Europe and Africa – 2.1 billion birds on migration. *Oikos*, *118*(4), 624–626. https://doi.org/10.1111/j.1600-0706.2008.17309.x

Hansson, M. C., Bensch, S., & Brännström, O. (2000). Range expansion and the possibility of an emerging contact zone between two subspecies of Chiffchaff *Phylloscopus collybita* ssp. *Journal of Avian Biology*, *31*(4), 548–558. https://doi.org/10.1034/j.1600-048X.2000.1310414.x

Hedenström, A. (2007). Adaptations to migration in birds: Behavioural strategies, morphology and scaling effects. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1490), 287–299. https://doi.org/10.1098/rstb.2007.2140

Hedenström, A., & Petterson, J. (1987). Migration routes and wintering areas of willow warblers *Phylloscopus trochilus* (L.) ringed in Fennoscandia. *Ornis Fennica*, *64*(4), 137–143.

Helbig, A. J. (1991). Inheritance of migratory direction in a bird species: A cross-breeding experiment with SE- and SW-migrating blackcaps (*Sylvia atricapilla*). *Behavioral Ecology and Sociobiology*, *28*(1), 9–12. https://doi.org/10.1007/BF00172133

Helbig, A. J. (2003). Evolution of Bird Migration: A Phylogenetic and Biogeographic Perspective. In P. Berthold, E. Gwinner, & E. Sonnenschein (Eds.), *Avian Migration* (pp. 3–20). Springer. https://doi.org/10.1007/978-3-662-05957-9_1

Helbig, A. J., Martens, J., Seibold, I., Henning, F., Schottler, B., & Wink, M. (1996). Phylogeny and species limits in the Palaearctic chiffchaff *Phylloscopus collybita* complex: Mitochondrial genetic differentiation and bioacoustic evidence*. *Ibis*, *138*(4), 650–666. https://doi.org/10.1111/j.1474-919X.1996.tb04767.x

Holland, R. A., Thorup, K., Gagliardo, A., Bisson, I. A., Knecht, E., Mizrahi, D., & Wikelski, M. (2009). Testing the role of sensory systems in the migratory heading of a songbird. *Journal of Experimental Biology*, *212*(24), 4065–4071. https://doi.org/10.1242/jeb.034504

Huang, Z., Xu, Z., Bai, H., Huang, Y., Kang, N., … Xu, L. (2023). Evolutionary analysis of a complete chicken genome. *Proceedings of the National Academy of Sciences*, *120*(8), e2216641120. https://doi.org/10.1073/pnas.2216641120

Hull, J. M., & Girman, D. J. (2005). Effects of Holocene climate change on the historical demography of migrating sharp-shinned hawks (*Accipiter striatus velox*) in North America. *Molecular Ecology*, *14*(1), 159–170. https://doi.org/10.1111/j.1365-294X.2004.02366.x

Hüppop, O., & Hilgerloh, G. (2012). Flight call rates of migrating thrushes: Effects of wind conditions, humidity and time of day at an illuminated offshore platform. *Journal of Avian Biology*, *43*(1), 85–90. https://doi.org/10.1111/j.1600-048X.2011.05443.x

Hutchison, L. V., & Wenzel, B. M. (1980). Olfactory Guidance in Foraging by Procellariiforms. *The Condor*, *82*(3), 314–319. https://doi.org/10.2307/1367400

Joly, S., & Bruneau, A. (2007). Delimiting Species Boundaries in *Rosa* Sect. *Cinnamomeae* (Rosaceae) in Eastern North America. *Systematic Botany*, *32*(4), 819–836. https://doi.org/10.1600/036364407783390863

Jones, S., Pfister-Genskow, M., Cirelli, C., & Benca, R. M. (2008). Changes in brain gene expression during migration in the white-crowned sparrow. *Brain Research Bulletin*, *76*(5), 536–544. https://doi.org/10.1016/j.brainresbull.2008.03.008

Joseph, L., & Stockwell, D. (2000). Temperature-Based Models of the Migration of Swainson's Flycatcher (*Myiarchus swainsoni*) across South America: A New Use for Museum Specimens of Migratory Birds. *Proceedings of the Academy of Natural Sciences of Philadelphia*, *150*, 293–300.

Kishkinev, D., Chernetsov, N., Pakhomov, A., Heyers, D., & Mouritsen, H. (2015). Eurasian reed warblers compensate for virtual magnetic displacement. *Current Biology*, *25*(19), R822–R824. https://doi.org/10.1016/j.cub.2015.08.012

Lack, D. (1968). Bird Migration and Natural Selection. *Oikos*, *19*(1), 1–9. https://doi.org/10.2307/3564725

Lamers, K. P., Nilsson, J.-Å., Nicolaus, M., & Both, C. (2023). Adaptation to climate change through dispersal and inherited timing in an avian migrant. *Nature Ecology & Evolution*, *7*(11), 1869–1877. https://doi.org/10.1038/s41559-023-02191-w

Lampila, P., Mönkkönen, M., & Rajasärkkä, A. (2009). The ability of forest reserves to maintain original fauna–why has the Chiffchaff (*Phylloscopus collybita abietinus*) disappeared from eastern central Finland?. *Ornis Fennica*, *86*(2), 71–80.

Lapshin, N. V., Matantseva, M. V., & Simonov, S. A. (2020). Nest Site Selection and Nest Construction in the Willow Warbler (*Phylloscopus trochilus* L., 1758) (Sylviidae, Aves) in the Taiga Zone of Northwestern Russia. *Biology Bulletin*, *47*(10), 1378–1384. https://doi.org/10.1134/S1062359020100155

Larson, K. W., Liedvogel, M., Addison, B., Kleven, O., Laskemoen, T., Lifjeld, J. T., Lundberg, M., Åkesson, S., & Bensch, S. (2014). Allelic Variation in a Willow Warbler Genomic Region Is Associated with Climate Clines. *PLOS ONE*, *9*(5), e95252. https://doi.org/10.1371/journal.pone.0095252

Levey, D. J., & Stiles, F. G. (1992). Evolutionary Precursors of Long-Distance Migration: Resource Availability and Movement Patterns in Neotropical Landbirds. *The American Naturalist*, *140*(3), 447–476. https://doi.org/10.1086/285421

Liberg, O., & von Schantz, T. (1985). Sex-Biased Philopatry and Dispersal in Birds and Mammals: The Oedipus Hypothesis. *The American Naturalist*, *126*(1), 129–135.

Liedvogel, M., Åkesson, S., & Bensch, S. (2011). The genetics of migration on the move. *Trends in Ecology & Evolution*, *26*(11), 561–569. https://doi.org/10.1016/j.tree.2011.07.009

Liedvogel, M., Larson, K. W., Lundberg, M., Gursoy, A., Wassenaar, L. I., Hobson, K. A., Bensch, S., & Åkesson, S. (2014). No evidence for assortative mating within a willow warbler migratory divide. *Frontiers in Zoology*, *11*(1), 52. https://doi.org/10.1186/s12983-014-0052-2

Lindström, Å., Svensson, S., Green, M., & Ottvall, R. (2007). Distribution and population changes of two subspecies of Chiffchaff *Phylloscopus collybita* in Sweden. *Ornis Svecica*, *17*(3–4), 137–147. https://doi.org/10.34080/os.v17.22684

Loonstra, A. H. J., Verhoeven, M. A., Both, C., & Piersma, T. (2023). Translocation of shorebird siblings shows intraspecific variation in migration routines to arise after fledging. *Current Biology*, *33*(12), 2535-2540.e3. https://doi.org/10.1016/j.cub.2023.05.014

Louder, M. I. M., Justen, H., Kimmitt, A. A., Lawley, K. S., Turner, L. M., Dickman, J. D., & Delmore, K. E. (2024). Gene regulation and speciation in a migratory divide between songbirds. *Nature Communications*, *15*(1), Article 1. https://doi.org/10.1038/s41467-023-44352-2

Lugo Ramos, J. S., Delmore, K. E., & Liedvogel, M. (2017). Candidate genes for migration do not distinguish migratory and non-migratory birds. *Journal of Comparative Physiology A*, *203*(6), 383–397. https://doi.org/10.1007/s00359-017-1184-6

Lundberg, M., Liedvogel, M., Larson, K., Sigeman, H., Grahn, M., Wright, A., Åkesson, S., & Bensch, S. (2017). Genetic differences between willow warbler migratory phenotypes are few and cluster in large haplotype blocks. *Evolution Letters*, *1*(3), 155–168. https://doi.org/10.1002/evl3.15

McKinnon, E. A., Fraser, K. C., Stanley, C. Q., & Stutchbury, B. J. M. (2014). Tracking from the Tropics Reveals Behaviour of Juvenile Songbirds on Their First Spring Migration. *PLOS ONE*, *9*(8), e105605. https://doi.org/10.1371/journal.pone.0105605

McKinnon, E. A., & Love, O. P. (2018). Ten years tracking the migrations of small landbirds: Lessons learned in the golden age of bio-logging. *The Auk*, *135*(4), 834–856. https://doi.org/10.1642/AUK-17-202.1

McWilliams, S. R., & Karasov, W. H. (2001). Phenotypic flexibility in digestive system structure and function in migratory birds and its ecological significance. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *128*(3), 577–591. https://doi.org/10.1016/S1095-6433(00)00336-6

Mellone, U., López-López, P., Limiñana, R., Piasevoli, G., & Urios, V. (2013). The trans-equatorial loop migration system of Eleonora's falcon: Differences in migration patterns between age classes, regions and seasons. *Journal of Avian Biology*, *44*(5), 417–426. https://doi.org/10.1111/j.1600-048X.2013.00139.x

Merlin, C., & Liedvogel, M. (2019). The genetics and epigenetics of animal migration and orientation: Birds, butterflies and beyond. *Journal of Experimental Biology*, *222*(Suppl_1), jeb191890. https://doi.org/10.1242/jeb.191890

Meyburg, B.-U., Bergmanis, U., Langgemach, T., Graszynski, K., Hinz, A., Börner, I., Meyburg, C., & Vansteelant, W. M. G. (2017). Orientation of native versus translocated juvenile lesser spotted eagles (*Clanga pomarina*) on the first autumn migration. *Journal of Experimental Biology*, *220*(15), 2765–2776. https://doi.org/10.1242/jeb.148932

Mueller, J. C., Pulido, F., & Kempenaers, B. (2011). Identification of a gene associated with avian migratory behaviour. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1719), 2848–2856. https://doi.org/10.1098/rspb.2010.2567

Muheim, R., Schmaljohann, H., & Alerstam, T. (2018). Feasibility of sun and magnetic compass mechanisms in avian long-distance migration. *Movement Ecology*, *6*(1), 8. https://doi.org/10.1186/s40462-018-0126-4

Naef-Daenzer, B. (2007). An allometric function to fit leg-loop harnesses to terrestrial birds. *Journal of Avian Biology*, *38*(3), 404–407. https://doi.org/10.1111/j.2007.0908-8857.03863.x

Nakazawa, Y., Peterson, A. T., Martínez-Meyer, E., & Navarro-Sigüenza, A. G. (2004). Seasonal niches of nearctic-neotropical migratory birds: implications for the evolution of migration. *The Auk*, *121*(2), 610–618. https://doi.org/10.1642/0004-8038(2004)121[0610:snonmb]2.0.co;2

Onrubia, A., & Copete, J. (2022). *Mosquitero ibérico Phylloscopus ibericus*.

Outlaw, D. C., & Voelker, G. (2006). Phylogenetic Tests of Hypotheses for the Evolution of Avian Migration: A Case Study Using the Motacillidae. *The Auk*, *123*(2), 455–466. https://doi.org/10.1093/auk/123.2.455

P. Bell, C. (2000). Process in the evolution of bird migration and pattern in avian ecogeography. *Journal of Avian Biology*, *31*(2), 258–265. https://doi.org/10.1034/j.1600-048X.2000.310218.x

Panuccio, M., Agostini, N., & Premuda, G. (2012). Ecological barriers promote risk minimisation and social learning in migrating short-toed snake eagles. *Ethology Ecology & Evolution*. https://www.tandfonline.com/doi/full/10.1080/03949370.2011.583692

Patchett, R., Kirschel, A. N. G., King, J. R., Styles, P., & Cresswell, W. (2022). Age-related changes in migratory behaviour within the first annual cycle of a passerine bird. *PLOS ONE*, *17*(10), e0273686. https://doi.org/10.1371/journal.pone.0273686

Perdeck, A. C. (1958). Two Types of Orientation in Migrating Starlings, *Sturnus vulgaris* L., and Chaffinches, Fringilla coelebs L., as Revealed by Displacement Experiments. *BioOne*. https://doi.org/10.5253/arde.v1i2.p1

Pérez-Tris, J., Bensch, S., Carbonell, R., Helbig, A. J., & Tellería, J. L. (2004). Historical diversification of migration patterns in a passerine bird. *Evolution*, *58*(8), 1819–1832. https://doi.org/10.1554/03-731

Piersma, T., Loonstra, A. H. J., Verhoeven, M. A., & Oudman, T. (2020). Rethinking classic starling displacement experiments: Evidence for innate or for learned migratory directions? *Journal of Avian Biology*, *51*(5). https://doi.org/10.1111/jav.02337

Piersma, T., Pérez-Tris, J., Mouritsen, H., Bauchinger, U., & Bairlein, F. (2005). Is There a "Migratory Syndrome" Common to All Migrant Birds? *Annals of the New York Academy of Sciences*, *1046*(1), 282–293. https://doi.org/10.1196/annals.1343.026

Piersma, T., Zwarts, L., & Bruggemann, J. H. (1990). Behavioural aspects of the departure of waders before long-distance flights: flocking, vocalizations, flight paths and diurnal timing. *Ardea*, *78*(2), 157-184

Ponti, R., Arcones, A., Ferrer, X., & Vieites, D. R. (2020). Lack of evidence of a Pleistocene migratory switch in current bird long-distance migrants between Eurasia and Africa. *Journal of Biogeography*, *47*(7), 1564–1573. https://doi.org/10.1111/jbi.13834

Pot, M. T., Visser, M. E., Helm, B., von Rönn, J. A. C., & van der Jeugd, H. P. (2024). Revisiting Perdeck's massive avian migration experiments debunks alternative social interpretations. *Biology Letters*, *20*(7), 20240217. https://doi.org/10.1098/rsbl.2024.0217

Prugnolle, F., & De Meeus, T. (2002). Inferring sex-biased dispersal from population genetic tools: A review. *Heredity*, *88*(3), 161–165. https://doi.org/10.1038/sj.hdy.6800060

Pulido, F. (2011). Evolutionary genetics of partial migration—The threshold model of migration revis(it)ed. *Oikos*, *120*(12), 1776–1783. https://doi.org/10.1111/j.1600-0706.2011.19844.x

Pulido, F., & Berthold, P. (2003). Quantitative Genetic Analysis of Migratory Behaviour. In P. Berthold, E. Gwinner, & E. Sonnenschein (Eds.), *Avian Migration* (pp. 53–77). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-662-05957-9_4

Pulido, F., Berthold, P., & Van Noordwijk, A. J. (1996). Frequency of migrants and migratory activity are genetically correlated in a bird population: Evolutionary implications. *National Acad Sciences*, *93*, 14642–14647.

Rab l, J. (1978). One-Direction Orientation versus Goal Area Navigation in Migratory Birds. *Oikos*, *30*(2), 216–223. https://doi.org/10.2307/3543481

Raković, M., Neto, J. M., Lopes, R. J., Koblik, E. A., Fadeev, … & Drovetski, S. V. (2019). Geographic patterns of mtDNA and Z-linked sequence variation in the Common Chiffchaff and the 'chiffchaff complex'. *PLOS ONE*, *14*(1), e0210268. https://doi.org/10.1371/journal.pone.0210268

Ravagni, S., Sanchez-Donoso, I., Jiménez-Blasco, I., Andrade, P., Puigcerver, M., Chorão Guedes, A., Godinho, R., Gonçalves, D., Leitão, M., Leonard, J. A., Rodríguez-Teijeiro, J. D., & Vilà, C. (2023). Evolutionary history of an island endemic, the Azorean common quail. *Molecular Ecology*, *n/a*(n/a). https://doi.org/10.1111/mec.16997

Rheindt, F. E., Donald, P. F., Donsker, D. B., Gerbracht, J. A., Iliff, M. J.,… Christidis, L. (2025). AviList: A unified global bird checklist. *Biodiversity and Conservation*, *34*(10), 3359–3376. https://doi.org/10.1007/s10531-025-03120-y

Richardson, D. S., Jury, F. L., Blaakmeer, K., Komdeur, J., & Burke, T. (2001). Parentage assignment and extra-group paternity in a cooperative breeder: The Seychelles warbler (*Acrocephalus sechellensis*). *Molecular Ecology*, *10*(9), 2263–2273. https://doi.org/10.1046/j.0962-1083.2001.01355.x

Rushing, C. S., Van Tatenhove, A. M., Sharp, A., Ruiz-Gutierrez, V., Freeman, M. C., … & Sillett, T. S. (2021). Integrating tracking and resight data enables unbiased inferences about migratory connectivity and winter range survival from archival tags. *Ornithological Applications*, *123*(2), duab010. https://doi.org/10.1093/ornithapp/duab010

Sæther, B.-E. (1983). Habitat selection, foraging niches and horizontal spacing of Willow Warbler *Phylloscopus trochilus* and Chiffchaff *P. collybita* in an area of sympatry. *Ibis*, *125*(1), 24–32. https://doi.org/10.1111/j.1474-919X.1983.tb03080.x

Saino, N., Ambrosini, R., Albetti, B., Caprioli, M., De Giorgio, B., …& Rubolini, D. (2017). Migration phenology and breeding success are predicted by methylation of a photoperiodic gene in the barn swallow. *Scientific Reports*, *7*(1), Article 1. https://doi.org/10.1038/srep45412

Salewski, V., & Bruderer, B. (2007). The evolution of bird migration—A synthesis. *Naturwissenschaften*, *94*(4), 268–279. https://doi.org/10.1007/s00114-006-0186-y

Salomon, M. (1989). Song as a Possible Reproductive Isolating Mechanism between Two Parapatric Forms. The Case of the Chiffchaffs *Phylloscopus c. Collybit*a and *P. c. Brehmii* in the Western Pyrenees. *Behaviour*, *111*(1/4), 270–290.

Salomon, M., Voisin, J.-F., & Bried, J. (2003). On the taxonomic status and denomination of the Iberian Chiffchaffs. *Ibis*, *145*(1), 87–97. https://doi.org/10.1046/j.1474-919X.2003.00122.x

Salvin, O., & Strickland, H. E. (1882). *A Catalogue of the Collection of Birds Formed by the Late Hugh Edwin Strickland*. University Press.

Semlitsch, R. D. (2008). Differentiating Migration and Dispersal Processes for Pond-Breeding Amphibians. *The Journal of Wildlife Management*, *72*(1), 260–267. https://doi.org/10.2193/2007-082

Shirihai, H., & Svensson, L. (2018). *Handbook of Western Palearctic Birds, Volume 1: Passerines: Larks to Warblers*. Bloomsbury Publishing.

Sokolovskis, K., Bianco, G., Willemoes, M., Solovyeva, D., Bensch, S., & Åkesson, S. (2018). Ten grams and 13,000 km on the wing – route choice in willow warblers *Phylloscopus trochilus yakutensis* migrating from Far East Russia to East Africa. *Movement Ecology*, *6*(1), 20. https://doi.org/10.1186/s40462-018-0138-0

Sokolovskis, K., Lundberg, M., Åkesson, S., Willemoes, M., Zhao, T., Caballero-Lopez, V., & Bensch, S. (2023). Migration direction in a songbird explained by two loci. *Nature Communications*, *14*(1), Article 1. https://doi.org/10.1038/s41467-023-35788-7

Somveille, M., Rodrigues, A. S. L., & Manica, A. (2018). Energy efficiency drives the global seasonal distribution of birds. *Nature Ecology & Evolution*, *2*(6), 962–969. https://doi.org/10.1038/s41559-018-0556-9

Stostad, H. N., & Menéndez, R. (2014). Woodland structure, rather than tree identity, determines the breeding habitat of Willow Warblers *Phylloscopus trochilus* in the northwest of England. *Bird Study*, *61*(2), 246–254. https://doi.org/10.1080/00063657.2014.901293

Suh, A., Smeds, L., & Ellegren, H. (2018). Abundant recent activity of retrovirus-like retrotransposons within and among flycatcher species implies a rich source of structural variation in songbird genomes. *Molecular Ecology*, *27*(1), 99–111. https://doi.org/10.1111/mec.14439

Szymkowiak, J., Thomson, R. L., & Kuczyński, L. (2017). Interspecific social information use in habitat selection decisions among migrant songbirds. *Behavioral Ecology*, *28*(3), 767–775. https://doi.org/10.1093/beheco/arx029

Teitelbaum, C. S., Converse, S. J., Fagan, W. F., Böhning-Gaese, K., O'Hara, R. B., Lacy, A. E., & Mueller, T. (2016). Experience drives innovation of new migration patterns of whooping cranes in response to global change. *Nature Communications*, *7*(1), 12793. https://doi.org/10.1038/ncomms12793

Thorpe, J. E. (1988). Salmon migration. *Science Progress (1933-)*, *72*(3 (287)), 345–370.

Thorup, K., Bisson, I.-A., Bowlin, M. S., Holland, R. A., Wingfield, J. C., Ramenofsky, M., & Wikelski, M. (2007). Evidence for a navigational map stretching across the continental U.S. in a migratory songbird. *Proceedings of the National Academy of Sciences*, *104*(46), 18115–18119. https://doi.org/10.1073/pnas.0704734104

Thorup, K., Vega, M. L., Snell, K. R. S., Lubkovskaia, R., Willemoes, M., Sjöberg, S., Sokolov, L. V., & Bulyuk, V. (2020). Flying on their own wings: Young and adult cuckoos respond similarly to long-distance displacement during migration. *Scientific Reports*, *10*(1), 7698. https://doi.org/10.1038/s41598-020-64230-x

Toews, D. P. L., Taylor, S. A., Streby, H. M., Kramer, G. R., & Lovette, I. J. (2019). Selection on VPS13A linked to migration in a songbird. *Proceedings of the National Academy of Sciences*, *116*(37), 18272–18274. https://doi.org/10.1073/pnas.1909186116

Väli, Ü., Mirski, P., Sellis, U., Dagys, M., & Maciorowski, G. (2018). Genetic determination of migration strategies in large soaring birds: Evidence from hybrid eagles. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1884), 20180855. https://doi.org/10.1098/rspb.2018.0855

Veen, T., Svedin, N., Forsman, J. T., Hjernquist, M. B., Qvarnström, A., Hjernquist, K. A. T., Träff, J., & Klaassen, M. (2006). Does migration of hybrids contribute to post-zygotic isolation in flycatchers? *Proceedings of the Royal Society B: Biological Sciences*, *274*(1610), 707–712. https://doi.org/10.1098/rspb.2006.0058

Vega, M. L., Willemoes, M., Thomson, R. L., Tolvanen, J., Rutila, J., … & Thorup, K. (2016). First-Time Migration in Juvenile Common Cuckoos Documented by Satellite Tracking. *PLOS ONE*, *11*(12), e0168940. https://doi.org/10.1371/journal.pone.0168940

Warrant, E., Frost, B., Green, K., Mouritsen, H., Dreyer, D., Adden, A., Brauburger, K., & Heinze, S. (2016). The Australian Bogong Moth *Agrotis infusa*: A Long-Distance Nocturnal Navigator. *Frontiers in Behavioral Neuroscience*, *10*. https://doi.org/10.3389/fnbeh.2016.00077

Weisshaupt, N., Saari, J., & Koistinen, J. (2024). Evaluating the potential of bioacoustics in avian migration research by citizen science and weather radar observations. *PLOS ONE*, *19*(3), e0299463. https://doi.org/10.1371/journal.pone.0299463

Wenzel, B. M. (2007). Avian olfaction: Then and now. *Journal of Ornithology*, *148*(2), 191–194. https://doi.org/10.1007/s10336-007-0147-z

Wikelski, M., Arriero, E., Gagliardo, A., Holland, R. A., Huttunen, M. J., … & Wistbacka, R. (2015). True navigation in migrating gulls requires intact olfactory nerves. *Scientific Reports*, *5*(1), 17061. https://doi.org/10.1038/srep17061

Williamson, D., Williamson, J., & Ngwamotsoko, K. T. (1988). Wildebeest migration in the Kalahari. *African Journal of Ecology*, *26*(4), 269–280. https://doi.org/10.1111/j.1365-2028.1988.tb00979.x

Wiltschko, W., & Wiltschko, R. (2002). Magnetic compass orientation in birds and its physiological basis. *Die Naturwissenschaften*, *89*, 445–452. https://doi.org/10.1007/s00114-002-0356-5

Winger, B. M., Auteri, G. G., Pegan, T. M., & Weeks, B. C. (2019). A long winter for the Red Queen: Rethinking the evolution of seasonal migration. *Biological Reviews*, *94*(3), 737–752. https://doi.org/10.1111/brv.12476

Winger, B. M., Lovette, I. J., & Winkler, D. W. (2012). Ancestry and evolution of seasonal migration in the Parulidae. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1728), 610–618. https://doi.org/10.1098/rspb.2011.1045

Winkler, D. W., Gandoy, F. A., Areta, J. I., Iliff, M. J., Rakhimberdiev, E., Kardynal, K. J., & Hobson, K. A. (2017). Long-Distance Range Expansion and Rapid Adjustment of Migration in a Newly Established Population of Barn Swallows Breeding in Argentina. *Current Biology*, *27*(7), 1080–1084. https://doi.org/10.1016/j.cub.2017.03.006

Wright, S. (1934). An Analysis of Variability in Number of Digits in an Inbred Strain of Guinea Pigs. *Genetics*, *19*(6), 506–536.

Yoda, K., Yamamoto, T., Suzuki, H., Matsumoto, S., Müller, M., & Yamamoto, M. (2017). Compass orientation drives naïve pelagic seabirds to cross mountain ranges. *Current Biology*, *27*(21), R1152–R1153. https://doi.org/10.1016/j.cub.2017.09.009

Zamudio-Beltrán, L. E., Bossu, C. M., Bueno-Hernández, A. A., Dunn, P. O., Sly, N. D., Rayne, C., Anderson, E. C., Hernández-Baños, B. E., & Ruegg, K. C. (2025). Parallel and convergent evolution in genes underlying seasonal migration. *Evolution Letters*, *9*(2), 189–208. https://doi.org/10.1093/evlett/qrae064

Zhao, T., Ilieva, M., Larson, K., Lundberg, M., Neto, J. M., Sokolovskis, K., Åkesson, S., & Bensch, S. (2020). Autumn migration direction of juvenile willow warblers (*Phylloscopus t. Trochilus* and *P. t. Acredula*) and their hybrids assessed by qPCR SNP genotyping. *Movement Ecology*, *8*(1). https://doi.org/10.1186/s40462-020-00209-7

Zink, R. M., & Gardner, A. S. (2017). Glaciation as a migratory switch. *Science Advances*, *3*(9), e1603133. https://doi.org/10.1126/sciadv.1603133

Züst, Z., Mukhin, A., Taylor, P. D., & Schmaljohann, H. (2023). Pre-migratory flights in migrant songbirds: The ecological and evolutionary importance of understudied exploratory movements. *Movement Ecology*, *11*(1), 78. https://doi.org/10.1186/s40462-023-00440-y

Exploring the genetic basis of migratory traits in *Phylloscopus* warblers

PAPER I

Caballero-López, V., Lundberg, M., Sokolovskis, K., & Bensch, S. (2022). Transposable elements mark a repeat-rich region associated with migratory phenotypes of willow warblers (*Phylloscopus trochilus*). *Molecular Ecology, 31*(4), 1128-1141.

PAPER II

Sokolovskis, K., Lundberg, M., Åkesson, S., Willemoes, M., Zhao, T., Caballero-Lopez, V., & Bensch, S. (2023). Migration direction in a songbird explained by two loci. *Nature Communications*, 14(1), 165.

PAPER III

Caballero-Lopez, V., & Bensch, S. (2024). The regulatory basis of migratory behaviour in birds: different paths to similar outcomes. *Journal of Avian Biology*, 2024(11-12), e03238.

PAPER IV

Caballero-Lopez, V., Dedukh, D., Ekman, D., Kauzál, O., Lundberg, M., Odenthal-Hesse, L., Proux-Wéra, E., Reifová, R., Reif, J., Altmanová, M., Trifonov, V., Bensch, S. A songbird karyotype: cytogenetic confirmation of a migration-associated region rich in olfactory receptor genes. *Submitted*.

PAPER V

Caballero-Lopez, V., Mackintosh, A., Ekman, D., Proux-Wéra, E., Lundberg, M., Malmiga, G., Shipilina, D., Polakowski, M., Berdougo, M., Jankowiak, L., Bensch, S. Common chiffchaffs (*Phylloscopus collybita*) diverge in a genomic region associated with migration differences in willow warblers (*Phylloscopus trochilus*). *Submitted*.

PAPER VI

Caballero-Lopez, V., Ris, H., Strehmann, F., Bensch, S. Same direction, different journeys: migratory strategies in two chiffchaff species. Manuscript.

Printed by Media-Tryck, Lund 2025 NORDIC SWAN ECOLABEL 3041 0903

LUND UNIVERSITY

Faculty of Science
Department of Biology

ISBN 978-91-8104-736-3