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

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DEPARTMENT OF BIOLOGY | FACULTY OF SCIENCE | LUND UNIVERSITY



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Violeta Caballero-López



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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.

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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. trochiloides*, 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.

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Violeta Caballero-López



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*“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	10
Popular science summary	11
Texto de divulgación científica.....	12
List of papers	13
Additional published papers during this thesis	14
Author contributions	15
Abbreviations.....	16
Introduction	17
How it started: evolutionary pathways that led to the current migratory diversity	19
Mechanisms shaping migratory routes: learning versus genetic programs	21
The genetics behind different migratory traits: a lack of consensus.....	23
Navigation: an intriguing ability	25
Aims	27
General methodology	30
Study species.....	30
Two <i>Phylloscopus</i> species that breed in Sweden	30
Two <i>Phylloscopus</i> that breed in Spain.....	33
Study sites.....	33
From phenotype to genotype	35
Tracking	35
Molecular work.....	36
Cytogenetics	36
Genome analyses.....	36
Contributions to the field.....	37
A repeat-rich, complex region correlates with migratory phenotypes in willow warblers	37
Genetics behind migratory direction.....	38

A comprehensive review of the field of genetic mechanisms behind migratory traits	40
The MARB region is in a medium-sized chromosome that contains most olfactory receptor sequences (ORs) in the genome.....	40
MARB correlates with migratory phenotype in chiffchaff subspecies.....	41
Short and long-distance migrants differ in migratory traits	42
Conclusions and future directions.....	44
Acknowledgements.....	47
Reference list	53

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. trochiloides*, 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., Berdugo, 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>

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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 (Awise & 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.

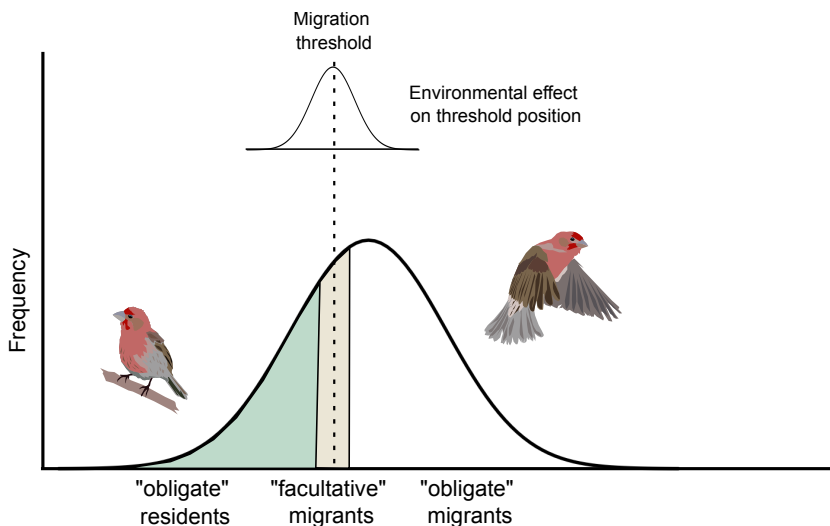


Figure 1. Adapted from Pulido (2011). This illustration depicts the environmental threshold model of migration for a given trait. The trait shown is migratory propensity in a partially migratory population, defined by a threshold that is not fixed but responsive to the environment. A population of facultative 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).

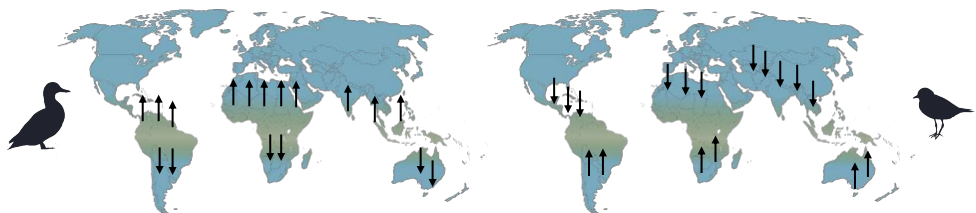


Figure 2. Hypotheses of the origin of migratory behaviour across different avian orders. Anseriformes (left) seem to have developed migration from tropical latitudes during the lower Miocene. Charadriiformes (right) started migrating from temperate latitudes during the upper Miocene (Dufour et al., 2020).

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 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, <i>CLOCK</i> gene	Regulatory, neuropeptide synthesis, circadian rhythms	Tracking, genomic analyses, microsatellite typing
Vermivora warblers	Wintering longitude	<i>VPS13A</i> gene	Unknown in birds	Tracking, genomic analyses
Swainson's Thrush	Wintering longitude, Migratory activity	Chromosome 4, <i>gad1</i> ,	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	<i>ADCY8</i>	Long-term memory	Satellite tracking, sequencing
Barn swallow	Timing	<i>CLOCK</i> <i>POLY-Q</i>	Transcriptional trans-activation domain	Methylation analyses
American Kestrel	Timing	<i>top1</i> , <i>phlpp1</i> , <i>cpne4</i> , <i>peak1</i>	Clock regulator-light input pathway	RAD-seq
White-crowned sparrow	Migratory incidence	<i>GLUT1</i> , <i>heat shock protein family</i> *	Glucose transporter, unfolded protein response	Expression analyses (microarray)
Common Yellowthroat	Timing	<i>Npas3</i> , <i>bmal</i> , <i>gria2</i> , <i>camk4</i> , <i>ntrk2</i> , <i>hivp2</i> * ...	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 & Pettersson, 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 & Pettersson, 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).

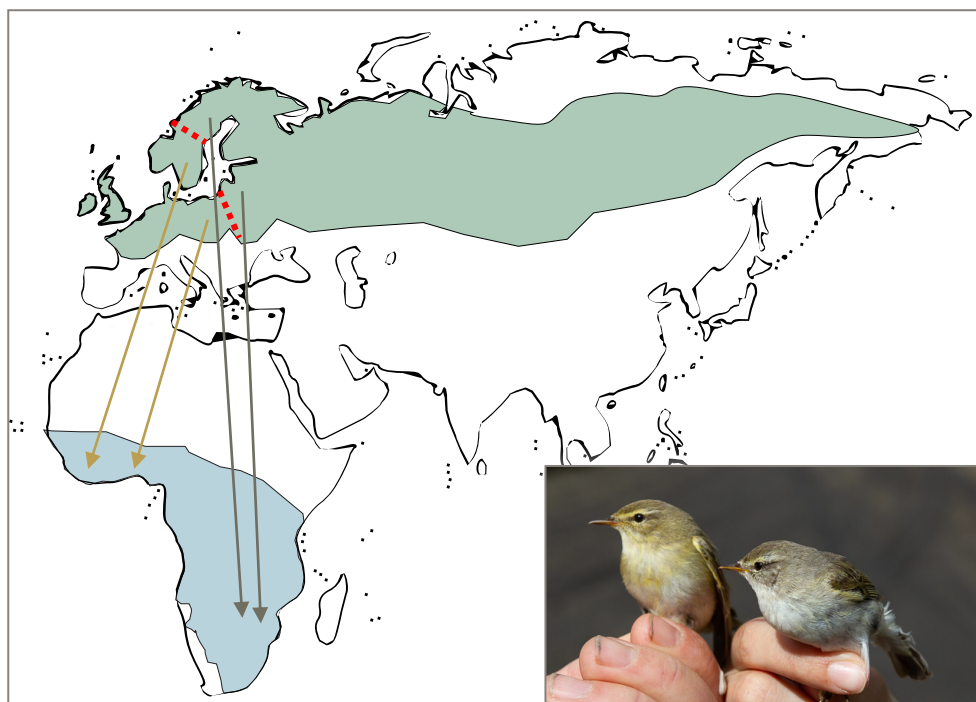


Figure 3. Willow warbler distribution map showing breeding grounds (green) and wintering grounds (blue). Migratory divides are depicted as dashed lines on both sides of the Baltic. The western routes of *trochilus* are depicted in brown, and the eastern routes of *acredula* are depicted in grey. The 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).

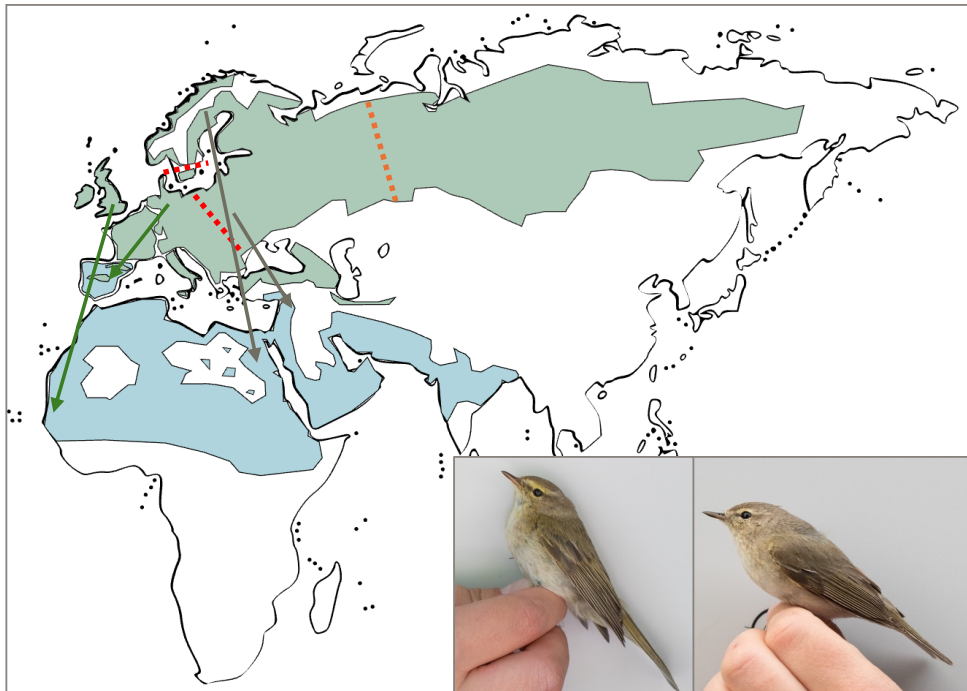


Figure 4. Common chiffchaff distribution map showing breeding grounds (green) and wintering grounds (blue). Migratory divides are depicted as dashed red lines on both sides of the Baltic. *Collybita* directions are depicted in green arrows and *abietinus* directions are depicted in grey arrows. Dashed 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; Shirihaï & 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).

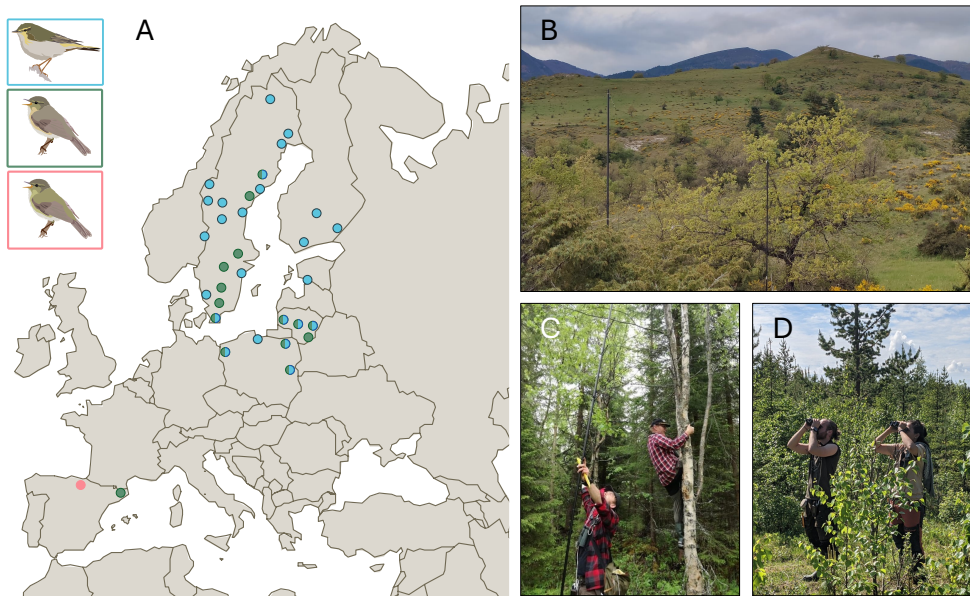


Figure 6. A) Sampling sites for the willow warbler (blue), common chiffchaff (green), and Iberian chiffchaff (pink) included in this thesis. Mixed circles indicate shared sampling locations between species. Each point contains more than one location. B) Typical net setup (Alava, Spain). C) Staffan Bensch 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 $12 \times 5 \times 4$ 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.

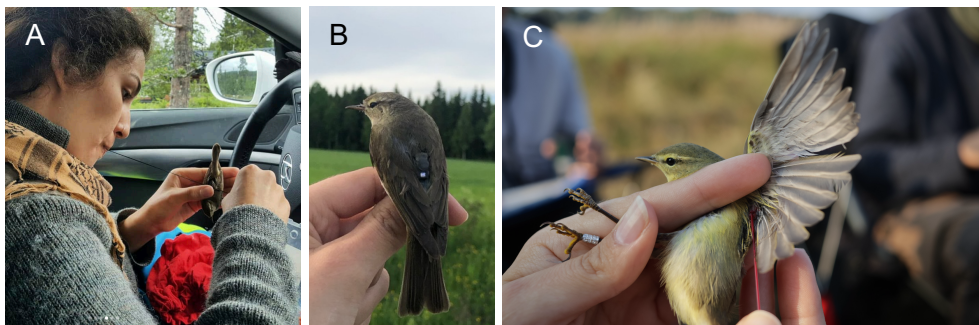


Figure 7. Process of geolocator attachment (A, B) and blood sampling (C) across species. Photo A: Kristaps Sokolovskis. Photo B: author. Photo C: Harald Ris.

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).

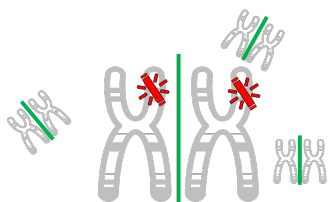


Figure 8. The principle behind FISH on a karyotype. The synaptonemal complex is labelled with green, fluorescent antibodies. The size of each synaptonemal complex is used as a proxy for chromosome size. The probe binds to MARB specifically and it is labelled with a contrasting colour (red).

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**).

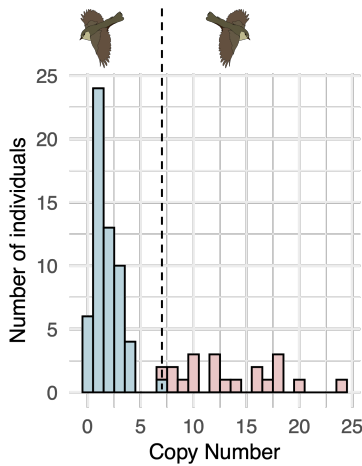


Figure 9. Copy number variation of the WW2 marker across pure willow warbler subspecies (i.e., excluding the hybrid zone). The dashed line represents the migratory divide in central Scandinavia. Copy numbers of this transposon on each bird are our only aid to determine if the haplotype is MARB-a (*acredula*;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

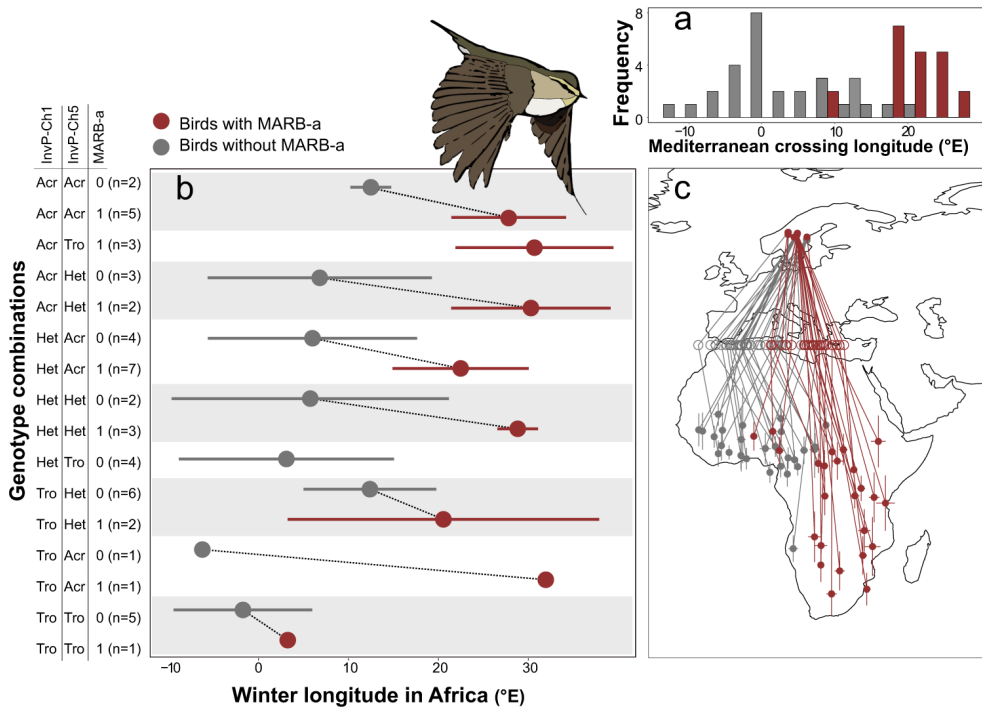


Figure 10. **a** Histogram depicting bimodality in the frequencies of where birds from the migratory divide crossed the Mediterranean. **b** Mean (whiskers depict $\pm$ standard deviations) winter longitudes for each of the nine combined genotypes of InvP-Ch1 and InvP-Ch5, illustrated separately for 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.

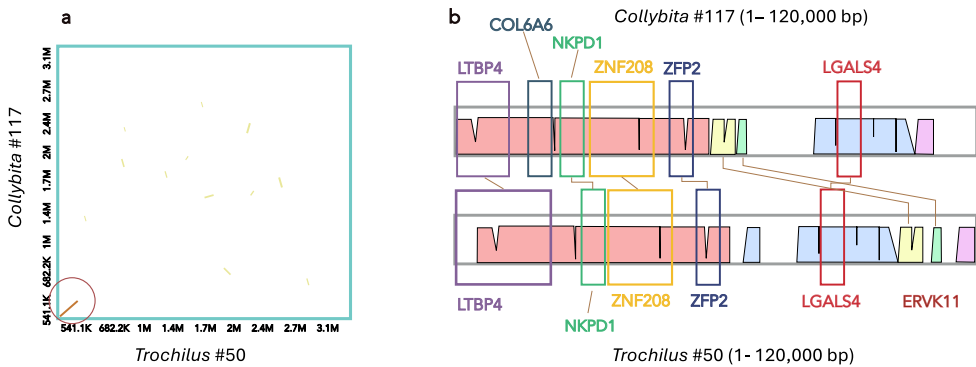


Figure 11. Schematic representation of a comparison of MARB scaffolds in trochilus (#50) and collybita (#117). Dot plot of full length (a) and Mauve alignment over the first 120 kb. (b) Annotated genes illustrated in coloured boxes. Despite shared features across *Phylloscopus* (repeat families, OR, 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.

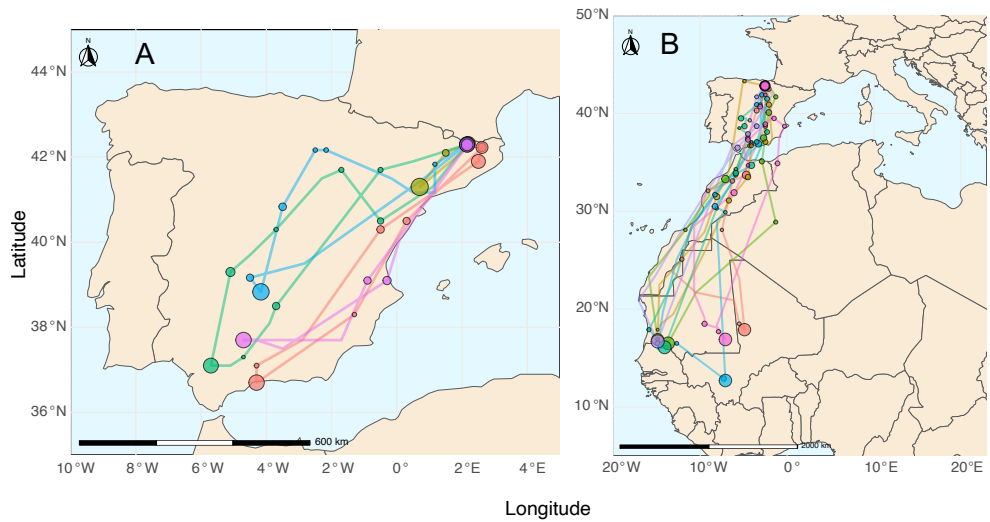


Figure 12. Modelled trajectories from *P. c. collybita* (A) and *P. ibericus* (B) captured in Spain. Each individual is depicted with a different colour. Circles show stationary periods: breeding grounds, wintering grounds and stopover sites. The size of the circle is proportional to the time spent in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

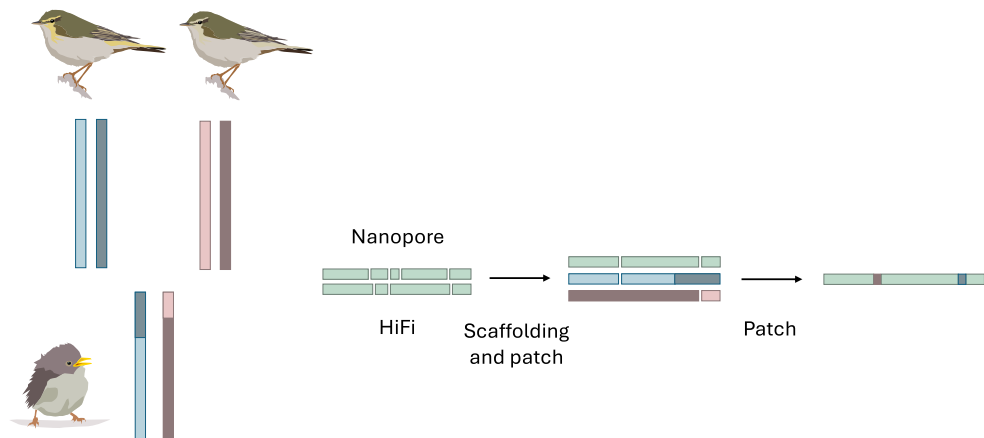


Figure 13. Trio-based genome assembly strategy for a willow warbler family including parental individuals from the hybrid zone with different MARB haplotypes and their hybrid offspring. Paternal and maternal haplotypes can be used to fill the gaps in primary contigs.

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.

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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

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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., Berdugo, 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*.