Flight energetics in migratory birds: integrating wind-tunnel measurements and migration ecology

Macías Torres, Pablo

2025

Citation for published version (APA):
Macías Torres, P. (2025). *Flight energetics in migratory birds: integrating wind-tunnel measurements and migration ecology*. Lunds universitet, Media-Tryck .

Total number of authors:
1

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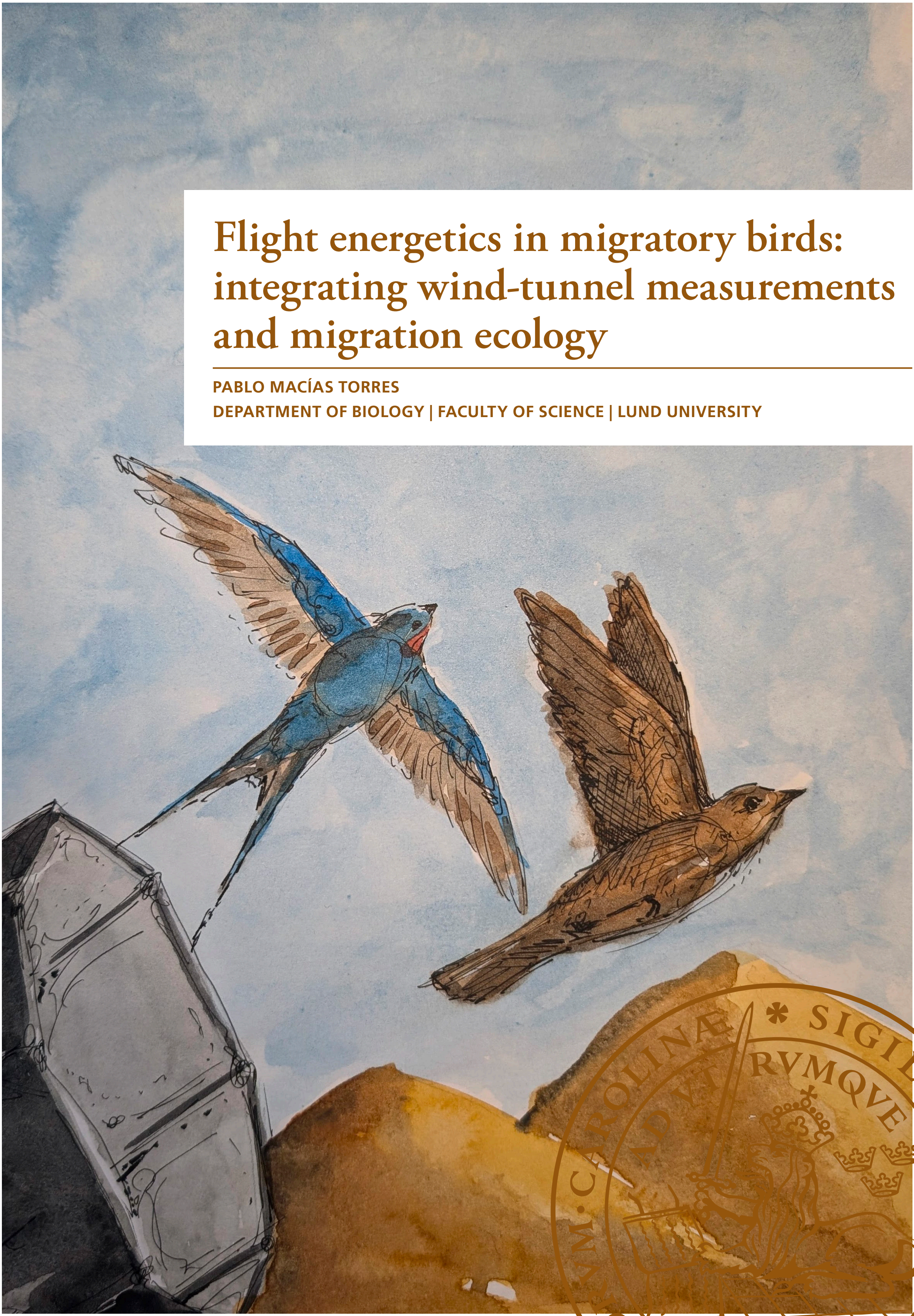

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PAPER I.

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PAPER II.

Macías-Torres, P., Friman, S. I., Johansson, L. C., Hedenström, A. (2025). Flight energetics of barn swallows across speeds: high aerodynamic efficiency, but low energy conversion efficiency. (manuscript)

PAPER III.

Macías-Torres, P., Hedenström, A. (2025). Within-season flexibility in migratory strategies in a long-distance migratory songbird. (submitted)

PAPER IV.

Macías-Torres, P., Hedenström, A. (2025). Time and energy budgets in a long-distance migratory songbird: The decisive role of daylength. (manuscript)

LUND
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ISBN 978-91-8104-738-7

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

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Pablo Macías Torres

LUND
UNIVERSITY

DOCTORAL DISSERTATION

by due permission of the Faculty of Science, Lund University, Sweden. To be publicly defended in the Blue Hall, Ecology Building, Kontaktvägen 10, Lund 223 62, Sweden, on Friday 21 November at 09.00

Faculty opponent
Dr. Jesko Partecke

Max Planck Institute of Animal Behaviour, Radolfzell, Germany.

Organization: LUND UNIVERSITY

Document name: DOCTORAL DISSERTATION **Date of issue:** 2025-10-28

Author(s): Pablo Macías Torres

Title and subtitle: Flight energetics in migratory birds: integrating wind-tunnel measurements and migration ecology

Abstract:

Birds migrate across the globe on their wings, a behavioural adaptation that allows birds to exploit seasonal environments. Their migrations are ultimately influenced by their ability to fly, a costly but high energy-efficient mode of locomotion that enables birds to travel far distances in a short amount of time. This thesis investigates bird migration from a flight energetic perspective, focusing on small passerines, to understand how birds complete their long-distance journeys. To address this, I have combined two complementary approaches: controlled wind-tunnel experiments and individual-based tracking across full migratory journeys.

In the wind tunnel, I quantified flight energetics in thrush nightingales *Luscinia luscinia* and barn swallows *Hirundo rustica*. Power–speed relationships were species-specific and followed the canonical U-shape in both cases. Crucially, energy conversion efficiency varied with speed, peaking at intermediate speeds aligned with ecologically relevant speed for sustained flight during migration. Importantly, conversion efficiency also differed between both species, suggesting a specialization-flexibility trade-off consistent with each species' flight ecology.

In parallel, individual tracking of thrush nightingales revealed their migration patterns from which we could infer their migration strategies under the scope of optimal migration theory. Thrush nightingales do not stick to single strategy throughout the migratory journey, but switch strategies depending on the environment. Ecological barriers shaped the behaviour seasonally: the Sahara crossing in autumn suggest a risk minimization strategy; Arabian Peninsula crossing in spring was followed by intensive daytime fuelling that sustained consecutive nocturnal migratory flights, consistent with a time minimization strategy. This was facilitated by an increasing daylength gradient as spring migration progressed.

Integrating both approaches allowed to explore bird migration energetics in detail. Pairing wind tunnel flight cost measurements with precise migratory flight durations from tracking yielded total time and energy required for the journey. In spring, time and energy budgets matched theoretical ratios; in autumn, both nearly doubled, indicating season-specific constraints on performance. Different daylength gradient on each season likely modulated the observed patterns, underscoring the importance of available fuelling time in the migration speed. Together, these studies highlight the synergy of complementary approaches in advancing our understanding of bird migration ecology.

Key words: migration pattern, migration strategy, flight power, long-distance migration, passerine, metabolic energy, energy conversion efficiency

Language: English **Number of pages**: 72

ISBN (print): 978-91-8104-738-7 **ISBN (electronic):** 978-91-8104-739-4

Signature Date 2025-10-28

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Cover illustration by Pablo Macías Torres

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ISBN 978-91-8104-738-7 (print)
ISSN 978-91-8104-739-4 (electronic)

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

Printed matter
3041 0903

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MADE IN SWEDEN

“No animal exists, or can exist, independently of an environment, and the animal that utilizes the resources of the environment must also be able to cope with the difficulties it presents.”

Knut Schmidt-Nielsen, 1997

Table of Contents

Abstract

Birds migrate across the globe on their wings, a behavioural adaptation that allows birds to exploit seasonal environments. Their migrations are ultimately influenced by their ability to fly, a costly but high energy-efficient mode of locomotion that enables birds to travel far distances in a short amount of time. This thesis investigates bird migration from a flight energetic perspective, focusing on small passerines, to understand how birds complete their long-distance journeys. To address this, I have combined two complementary approaches: controlled wind-tunnel experiments and individual-based tracking across full migratory journeys.

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Popular scientific summary

After flying for ten days without stopping, the bar-tailed godwit, with its energy loads nearly depleted, arrived at its destination. It was another successful autumn crossing of the entire Pacific Ocean, from the coast of Alaska to New Zealand, covering ~10 000 km. Meanwhile, on the other side of the world, a thrush nightingale of about 30 grams, finds itself in the middle of the Sahara Desert, waiting for nightfall to resume the migratory journey further south. These are just two examples of the remarkable journeys that migratory birds undertake each year: an adaptation that allows them to breed in highly seasonal environments at high latitudes.

Birds can cross the world because of their ability to fly. Flying, however, is expensive. Flapping continuously for hours, sometimes days without stopping, burns fuel at a high rate. However, flight allows birds and any other flying animal to cover large distances in a short amount of time. My thesis tackles the question: how do birds manage their flight energetics well enough to fly migrate such large distances around the world? To find out, I combined two complementary approaches: wind-tunnel experiments that measure the costs of flight under controlled conditions, and individual tracking of birds across their cross-continental migrations.

In the wind tunnel, we studied the flight energetics of thrush nightingales *Luscinia luscinia* and barn swallows *Hirundo rustica*. As expected, the power required to fly follows a classic U-shaped curve: very slow and very fast speed are costly; intermediate speeds are cheaper. Importantly, we also found that energy conversion efficiency, the ability to transform metabolic energy into mechanical flight power transferred into the air, is not constant: it peaks at intermediate speeds, the same speeds that would maximize efficient sustained transportation during migratory flights. This is because the metabolic power increased more steeply at slow and fast speeds than the mechanical power.

Additionally, energy conversion efficiency also differed between the two species, suggesting a specialization–flexibility trade-off: higher conversion efficiency over a narrow speed range versus lower efficiency spread across a broader range. The difference in energy conversion efficiency seems to be consistent with each species flight lifestyle: thrush nightingales (with a narrower but higher conversion efficiency) spend most of the year on the ground or perching, spending hundreds of hours airborne during migration; barn swallows (with a shallower but broader range in flight conversion efficiency) are adapted to an aerial lifestyle, flapping for much of the day year round. Our results suggest physiological adaptations that optimise flight energy use at the speeds most relevant to each species' ecology.

Because migration happens in the wild and not inside wind tunnels, we also tracked thrush nightingales throughout their entire migrations by tagging them with small electronic multisensor devices. From these sensors we inferred their migration patterns. This small passerine covers on average about 18 000 km every year and they only migrated at night, performing clusters of nocturnal flights separated by fuelling periods that provisioned enough energy to fuel the flights. The observed migratory behaviours were compared with predictions from optimal migration theory, which proposes that birds may prioritise time, energy, or risk (safety) depending on context. We found that nightingales did not follow a single strategy; they switched strategies as conditions changed. Ecological barriers were especially influential. During the autumn Sahara crossing, the birds migrated with nocturnal flights and stopped during daytime in the middle of the dessert remaining inactive until the next night. This was the behaviour showed for up to three to four days, until crossing the desert completely, when a several weeklong stopover took place. Our observations indicate that the thrush nightingales did not feed during daytime and thus minimized neither time nor energy when crossing this segment, consistent with survival-first behaviour in a harsh, food-poor environment. In spring, the birds showed a different behaviour when crossing the Arabian Peninsula. After crossing the barrier, the birds did not perform any long stopover but continued flying over multiple consecutive nights (up to 22). This was supported by indications of intensive diurnal feeding until the arrival at the breeding grounds, which indicated that enough fuel loads were gained on a daily basis to sustain each night migratory flight, a behaviour that fits a sprint time-minimisation strategy.

Importantly, we could link wind-tunnel flight energy measurements with precise migratory flight duration from the tracking devices allowed us to estimate total energy expenditure across their entire migrations and annual cycle. Two major patterns emerged. First, time and energy budgets during spring migration matched theoretical expectations for fast travel supported by intensive fuelling. Second, autumn budgets were roughly double, indicating a slower overall pace. A key driver behind these differences was daylength: it increases in spring and decreases in autumn. Longer days provide more time to refuel, which boosts migration speed and helps explain the late-spring migration sprint toward the breeding grounds.

In short, we have discovered that long-distance migration is a highly complex phenomenon composed of various context-dependent behaviours, influenced by the energy cost of flight. Due to the high cost of flight, migratory birds have to carefully allocate the energy and time budgets across the journey. We still however do not know how birds know how to adapt their migratory performance to match the required behavioural adaptations to succeed in their journeys.

Resumen divulgativo

Después de volar diez días sin detenerse, una aguja colipinta, con la energía casi agotada, llegó a su destino. Otro año más que consigue cruzar la extensión del Océano Pacífico, desde la costa de Alaska hasta Nueva Zelanda, unos 10 000 km. Mientras tanto, al otro lado del mundo, un ruiseñor ruso de apenas 30 gramos se encuentra parado al mediodía en medio del desierto del Sahara, esperando la caída de la noche para reanudar su viaje rumbo al sur. Estos son solo dos ejemplos de las excepcionales migraciones que las aves emprenden cada año y que les permite reproducirse en latitudes altas, donde solo hay recursos ciertas estaciones del año.

Las aves pueden completar sus largos viajes gracias a su capacidad de volar. Sin embargo, volar es costoso. Aletear de manera continua durante horas e incluso días sin parar consume una alta cantidad de energía a un ritmo elevado. Mi tesis intenta responder a la siguiente pregunta: ¿cómo gestionan las aves su energía de vuelo lo suficientemente bien como para volar tan largas distancias? Para intentar averiguar el cómo, he combinado dos enfoques complementarios: experimentos en un túnel de viento, donde se puede medir en condiciones controladas el coste energético del vuelo, y seguimiento individual de aves a lo largo de sus migraciones.

En el túnel de viento estudiamos la energética del vuelo del ruiseñor ruso *Luscinia luscinia* y la golondrina común *Hirundo rustica*. Como era de esperar, la potencia necesaria para volar sigue una curva en U con respecto a la veolcidad: volar tanto muy lento como muy rápido es costoso; volar a velocidades intermedias es más económico. También encontramos que la eficiencia de conversión energética, definido como la capacidad de transformar energía metabólica en energía mecánica para mover el aire al batir las alas, no es constante: alcanza su máximo a velocidades intermedias, las mismas que maximizan el uso de energía durante vuelos de larga duración. La razón del pico a velocidades intermedias es que la energía metabólica aumenta más rápidamente que la energía mecánica a velocidades altas y bajas

Adicionalmente encontramos que la conversión energética del vuelo difiere entre ambas especies estudiadas, lo que sugiere un compromiso entre especialización y flexibilidad en las velocidades con máxima eficiencia: una mayor eficiencia implica un rango menor de velocidades en las que se es eficiente, mientras que una mas baja eficiencia proporciona un mayor rango de velocidades de vuelo a las que las aves desempeñan bien. Este supuesto compromiso esta alineado con las características de vuelo de las dos especies estudiadas: los ruiseñores rusos (con una eficiencia mayor pero a velocidades más limitadas) pasan la mayor parte del año en el suelo y vuelan principalmente durante la migración, mientras que las golondrinas (con un mayor rango de velocidades en las que rinden bien, pero a una menor eficiencia) están adaptadas a un estilo de vida aéreo, aleteando gran parte del día. Nuestros resultados sugieren adaptaciones fisiológicas que optimizan el uso de la energía de vuelo a las velocidades más relevantes para la ecología de cada especie.

Debido a que las aves no llevan a cabo sus migraciones dentro túneles de viento sino en la naturaleza, también seguimos a ruiseñores rusos durante todo su viaje migratorio, marcándolos con pequeños dispositivos electrónicos. Con esta tecnología estudiamos sus rutas y comportamientos migratorios. Estas pequeñas aves realizan aproximadamente 18 000 km en un año y migran solo de noche, realizando varios grupos de vuelos nocturnos precedidos de periodos de acumulación de energía para poder sostener el alto coste de volar. Los patrones de migración observados se compararon con predicciones basadas en la optimización de la migración, que propone que las aves pueden priorizar su tiempo, su energía o su seguridad según el contexto. Nuestros resultados indican que los ruiseñores no siguen una única estrategia; cambian de estrategia conforme cambian las condiciones a lo largo de la migración. Las barreras ecológicas, como los desiertos, son especialmente influyentes en su comportamiento. Durante la migración de otoño, las aves cruzan el Sahara, volando de noche y parando de día en medio del desierto sin mostrar indicios de comer, mientras esperan hasta la siguiente noche, para continuar volando. Esto lo repitieron durante tres o cuatro días hasta que cruzaron por completo el Sahara, donde realizaron una parada de varias semanas. Nuestras observaciones indican que durante este tiempo las aves no minimizaron ni el tiempo ni la energía, pero mostraron un comportamiento alineado con maximizar su supervivencia al cruzar un entorno hostil y pobre en alimento. Sin embargo, en primavera mostraron otro comportamiento. Tras cruzar la Península Arábiga, donde tampoco comieron al parar de día, no realizaron una parada larga. Al contrario, continuaron migrado varias noches consecutivas (hasta 22 noches) hasta llegar a los lugares de reproducción. Nuestras observaciones indican que los ruiseñores se alimentaron de manera intensa durante cada día después de cruzar Arabia, lo que les permite almacenar suficiente energía para continuar volando cada noche. Esto sugiere que los ruiseñores rusos cambiaron su comportamiento haciendo un sprint, que les permite minimizar el tiempo de migración hacia las áreas de reproducción.

Adicionalmente, pudimos vincular las mediciones del coste energético en el túnel de viento con la duración de cada vuelo en la naturaleza, lo que nos permitió calcular el gasto energético total de la migración. Observamos dos patrones contrarios. Primero, en primavera el coste energético y de tiempo de la migración coincidieron con las expectativas teóricas para un viaje rápido sostenido por un reabastecimiento intenso. Segundo, en otoño los valores calculados fueron aproximadamente el doble de lo que se predice teóricamente, lo que indica un ritmo general más lento de migración. Un factor clave detrás de estas diferencias fue la duración del día (fotoperiodo): aumenta a lo largo de la migración de primavera y disminuye a lo largo de la migración de otoño. Debido a que los días más largos proporcionan más tiempo para reponer energía, esta diferencia en fotoperiodo es una causa probable que acelera la migración en primavera y no en otoño.

En resumen, hemos descubierto que el viaje migratorio de larga distancia que involucra cruzar barreras como océanos y desiertos es un fenómeno altamente complejo. Las aves muestran un comportamiento que depende de estas variaciones en el ambiente, donde, ayudadas por su capacidad de volar, deben ajustar su uso de la energía y el tiempo disponible para completar el viaje. Aun así, todavía quedan muchas preguntas por responder, como, por ejemplo, ¿cómo sabe un pájaro que debe ajustar su comportamiento para completar diferentes periodos migratorios que requieren diferentes costes energéticos? Adicionalmente, esta tesis muestra cómo el uso de metodologías complementarias proporciona una visión más completa de la ecología de la migración de las aves.

List of Papers

Paper I

Macías-Torres, P., Friman, S. I., Johansson, L. C., Hedenström, A. (2025) Energy conversion efficiency peaks at intermediate flight speed in a migratory songbird. Current Biology 35 (12), 2987–2993.e4. https://doi.org/10.1016/j.cub.2025.05.025

Paper II.

Macías-Torres, P., Friman, S. I., Johansson, L. C., Hedenström, A. (2025) Flight energetics of barn swallows across speeds: high aerodynamic efficiency, but low energy conversion efficiency. (manuscript)

Paper III.

Macías-Torres, P., Hedenström, A. (2025) Within-season flexibility in migratory strategies in a long-distance migratory songbird. (submitted)

Paper IV.

Macías-Torres, P., Hedenström, A. (2025) Time and energy budgets in a long-distance migratory songbird: The decisive role of daylength. (manuscript)

In addition, I have co-authored on the following Papers during my doctoral studies. These are not included in this thesis:

Macías-Torres, P., Alerstam, T., Andersson, A., Bäckman, J., Thorup, K., Tøttrup, A. P., & Sjöberg, S. (2022). Activity patterns throughout the annual cycle in a long-distance migratory songbird, the red-backed shrike Lanius collurio. *Movement Ecology*, *10*(1), 55. https://doi.org/10.1186/s40462-022-00355-0

Sjöberg, S., **Macías-Torres, P.**, Andersson, A., Bäckman, J., Thorup, K., Tøttrup, A. P., & Alerstam, T. (2025). The structure of the annual migratory flight activity in a songbird. Proc. R. Soc. B, 292. https://doi.org/10.1098/rspb.2025.0958

Author's contribution

Paper I

Conceptualization: **P.M.T**., S.I.F., L.C.J., and A.H.; Methodology and Data Collection: **P.M.T**., S.I.F., L.C.J., and A.H. Formal Analysis: **P.M.T.**; Visualization: **P.M.T**. and L.C.J. Writing-Original Draft: **P.M.T.**; Writing-Editing: **P.M.T**., S.I.F., L.C.J., and A.H.; Funding: A.H. and L.C.J.; all authors discussed the results and commented on the manuscript

Paper II

Conceptualization: **P.M.T.,** S.I.F., L.C.J., and A.H.; Methodology and Data Collection **P.M.T.**, S.I.F., L.C.J., and A.H. Formal Analysis: **P.M.T.**; Visualization: **P.M.T.** and L.C.J. Writing-Original Draft: **P.M.T.**; Writing -Editing: **P.M.T.**, S.I.F., L.C.J., and A.H.; Funding: A.H. and L.C.J. ; all authors discussed the results and commented on the manuscript.

Paper III

Conceptualization: **P.M.T.** and A.H.; Methodology and Data Collection: **P.M.T.** Formal Analysis: **P.M.T.**; Visualization: **P.M.T.** Writing-Original Draft: **P.M.T.**; Writing -Editing: **P.M.T.** and A.H.; Funding: A.H. ; all authors discussed the results and commented on the manuscript.

Paper IV

Conceptualization: **P.M.T.**; Methodology and Data Collection: **P.M.T.** Formal Analysis: **P.M.T.**; Visualization: **P.M.T.** Writing-Original Draft: **P.M.T.**; Writing -Editing: **P.M.T.** and A.H.; Funding: A.H. ; all authors discussed the results and commented on the manuscript.

Two barn swallows flying. Illustration by Ye Xiong

Introduction

Animal migration is a fascinating phenomenon that involves the seasonal movement of millions of individuals, often across continental scales (Alerstam & Bäckman, 2018; Hahn et al., 2009). Migration can be defined as the return journey between breeding and non-breeding areas, as an adaptation to fluctuating, seasonal resources (Dingle & Drake, 2007; Newton, 2023). Among vertebrates, birds stand out for their ability to perform long-distance journeys, with some species travelling thousands of kilometres each year (Bairlein et al., 2012; Gill et al., 2009). It is the ability to fly which has allowed birds (and other flying animals) to conquer the aerial environment (Hedenström, 2002; Nilsson et al., 2025). Flight, albeit energetically costly, allows birds to travel great distances in a short time, making it an effective mode of locomotion to travel across the globe. This has resulted in species like the Arctic tern *Sterna paradisaea*, which travels from its breeding grounds in the Arctic to its wintering grounds in Antarctica (Egevang et al., 2010), or the common swift *Apus apus*, which remains airborne for up to 10 months while migrating across continents (Hedenström et al., 2016).

To human eyes, long-distance bird migration appears extraordinary as they cross continents, oceans, deserts, and mountain ranges, while encountering vastly different conditions along their routes, and yet they still arrive at their destinations with remarkable timing and precision. Performing such journeys is a routine behaviour for many bird species, which have evolved the needed morphological, physiological and behavioural adaptations to perform such journeys (Åkesson & Hedenström, 2007; Bishop & Guglielmo, 2022; Piersma et al., 2022; Weber, 2009).

It is their long journeys, which they perform on their wings, what have inspired this thesis. Here, I tackle bird migration from a flight energetics perspective, with the aim to gain a deeper understanding of how birds execute their thousand-kilometre migrations across continents. To address this, I combine measurements of flight energetics in controlled wind tunnel experiments with individual-based tracking of wild birds using state-of-the-art bio-logging technology. Using this comparative framework, I contrast flight energetics with migration patterns, hoping to provide new insight into the costs and constraints that has shaped bird migration.

Bird flight in relation to bird migration

Why fly? Flight is undoubtedly a remarkable feat for humans, probably due to the fact that we cannot fly without engineering assistance. Flight itself is a very costly mode of locomotion. Just think of a hummingbird flapping its wings about 50 times per second (Bishop & Guglielmo, 2022). However, the main advantage of flight is its speed. Any flying animal can move rapidly through the environment compared to other forms of locomotion, like walking or swimming (Schmidt-Nielsen, 1972). Thus, despite its high energy requirement per unit of time, the greater speed of flight is the key, making it a highly energy-efficient mode of travel overall. It is the cost of transportation, defined as the energy required to move a unit mass over a unit distance, which is relatively low in flying animals, with swimming having the lowest cost of transportation (Johansson et al., 2014). More specifically, flight allows animals to cover greater distances per unit of fuel (similar to measuring a car's range in kilometres per litter of fuel). Because flight is then an energy-efficient mode of locomotion, it has facilitated the movement of birds between distant regions, eventually paving the way for the evolution of long-distance migration (Alerstam et al., 2003). Consequently, the longest migratory distances are found among animals that can fly (Alerstam & Bäckman, 2018).

How far can a bird fly with a given amount of energy? How long does it take to get there? Answering such questions requires accurate estimates of the flight energy consumption. Although sometimes obvious, in biology, energy is the capacity to do work, and it is captured, stored, and transformed by organisms mainly as chemical potential (e.g., ATP, glycogen, fat) and expended as mechanical work and heat (Clarke, 2017; Schmidt-Nielsen, 1997).

Quantifying the energy cost of flight allows us to examine how birds adaptively organize their energy expenditure to complete their migrations. For example, given the flight energy cost and total flight hours, it is possible to estimate the energy required to complete a migratory journey spanning thousands of kilometres across continents. Consequently, by knowing the energy required to fly it is also possible to estimate how much energy should be deposited before the actual flight and the time required to reach such energy levels. Thus, it is reasonable to expect that flight costs would influence the structure of flight and fuelling episodes along the annual cycle. Additionally, by knowing the energy required to complete the migratory journey within the scope of the annual cycle, it will improve our perspective of the energetic trade-offs of such behaviours (Buehler & Piersma, 2008; Marra et al., 2015; Shamoun-Baranes & Camphuysen, 2025).

This thesis is motivated by extensive theoretical and empirical research on bird flight energetics (e.g., Butler, 2016; Hedenström, 2025; Pennycuick, 2008; Tucker, 1970; Wikelski et al., 2003) and migration ecology (e.g., Alerstam & Lindström, 1990; Hedenström & Alerstam, 1997; Newton, 2023; Piersma et al., 2022).

Aims and outline of the thesis

Bird migration is, at its core, a movement challenge shaped by the ability to fly efficiently. However, we still know relatively little about the energetics required by migratory birds to complete their journeys. This thesis aims to elucidate how migratory birds perform their journeys from a flight energetic perspective. Because time and energy are limited resources, migratory birds must allocate these carefully in order to complete migration successfully, while also meeting the other energetic demands across the annual cycle (Bowlin et al., 2010; Marra et al., 2015). By answering how birds complete their long-distance migrations from an energetic perspective, it is also possible to infer selection pressures and ecological constraints that may have shaped the evolution of migratory strategies (Alerstam et al., 2003; Piersma, 2007). To address such question, I combined insights from two complementary approaches, hoping to provide a more complete picture of flight energetics and migration ecology in long-distance migrants (Pennycuick, 1998).

First, I quantified how efficiently birds are at flying by measuring energy use across a range of speeds. For that I used controlled wind tunnel experiments in two long-distance migratory songbird species, the thrush nightingale *Luscinia luscinia* and barn swallows *Hirundo rustica*. An introduction to the energetics of bird flight and the key findings from **Papers I and II** are presented in the section "Power Required to Fly". There I discuss the factors influencing flight energy use in migratory species and what have my results have revealed about flight efficiency.

Second, I aimed to understand how a long-distance migration is performed, how much energy is required and how migratory birds adjust their behaviour accordingly. For that, I have used tracking technology to study the migratory routes and behaviour of the thrush nightingale. These data reveal their migration patterns and the behaviours necessary to successfully complete the journey (**Paper III** and **IV)**. The section "Ecology of Bird Migration" provides the background to understand how a migratory flight is conducted in relation to the flight costs. I interpret the findings through complementary ecological and energetic lenses, using optimal migration theory to link behaviour, fuel use, and performance across seasons and landscapes.

Together, these works aim to provide a more comprehensive picture of flight energetics and migration ecology, with a focus on a long-distance migratory songbird.

Paper specific aims

Paper I: We investigate the flight energy costs at different speeds in migratory thrush nightingales. Moreover, we tested the hypothesis if flight efficiency is constant across flight speeds. By measuring both total energy consumption (metabolic power) and power generated by the flapping wings needed to stay airborne (mechanical power) across a range of speeds, we tested the power-speed relationship as well as the speeds at which whole-animal energy-conversion efficiency is maximum.

Paper II: With ultimate goal of understanding how flight energy costs and efficiency vary across species, we investigated the flight energetics of the barn swallow. Using the same methodology as in Paper I, we measured flight power and efficiency across a range of speeds. In addition, we assessed flight efficiency using the historical tilted wind tunnel method (partial efficiency), which was originally used to derive the first estimates of flight efficiency.

Paper III: We investigate the migration strategies used by thrush nightingales along their journey. Using individual-based tracking technology, we describe the migratory patterns and behaviours of this migratory songbird in detail. We investigated variation in diurnal activity, a proxy for fuelling intensity, during various phases of their migration. We confronted the observed behaviours and patterns with predictions from optimal migration theory to evaluate whether nightingales follow a consistent strategy or adjust their approach along the route, with a focus on the crossing of ecological barriers such as the Sahara Desert.

Paper IV: We aimed to study energy and time budgets of thrush nightingale's migration. By combining wind-tunnel flight energy measurements (Paper I) with individual-based tracking (Paper III) and thermoregulatory models, we estimate the total annual energy expenditure of this long-distance migrant. Additionally, we also compared the time allocation between flight and stopovers, testing predictions of time and energy allocation derived from optimal migration theory. We also explore the effect of daylength along the migratory journey as a factor explaining the variation in daily energy expenditure.

Methodology

The wind tunnel

Estimating the energy cost of flight can be challenging, and in most cases a wind tunnel is needed (but see Wikelski et al., 2003). A wind tunnel is analogous to a running treadmill, where a human being runs on a moving surface, but instead, in a wind tunnel it is the air that moves, accelerated by a fan. A wind tunnel allows researchers to fly animals under controlled conditions while adjusting key variables, such as flight speed.

Lund university has a state-of-the-art wind tunnel where the airspeed can be modified while keeping the turbulence at a minimum (Figure 1; Pennycuick et al., 1997). The tunnel has a close-circuit design, meaning the air circulates along the length of the tunnel (Figure 1). Here, animals are trained, usually for several weeks, until they adapt to the new flight environment inside the testing section (wide, high, length: 1.2 x 1.08 x 1.7 m). Training birds to fly inside the wind tunnel takes a big proportion of the experiments, as when working with wild birds, they are naturally wary of humans and the unfamiliar environment. A good flying bird in the wind tunnel is a gem, and its value is almost incalculable.

The wind tunnel at Lund University can be tilted to simulate climbing or descending flights, allowing researchers to study the energy costs and efficiency of these flight modes (Bernstein et al., 1973; Hudson & Bernstein, 1983; Tucker, 1972). However, the birds are restricted to fly at the wind tunnel’s fixed altitude and cannot be exposed to the high-altitude conditions they would encounter during migration in the wild. (Gauthreaux, 1972; Ivy & Williamson, 2024; Sjöberg et al., 2021).

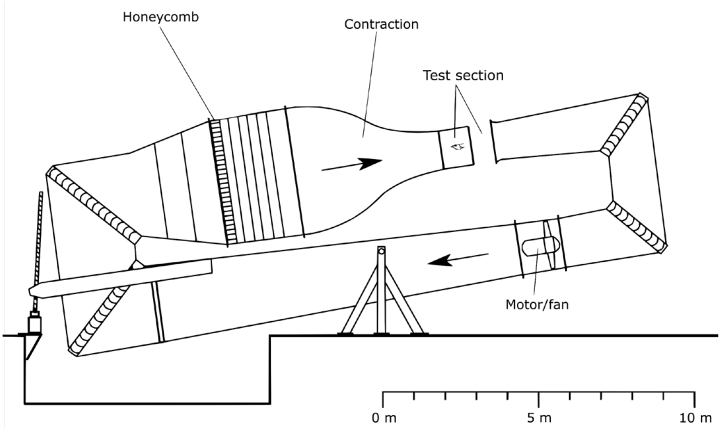

Figure 1. Lund University wind tunnel. The air flows in the direction of the arrows. Before the test section, where birds are flown, the honeycomb and contraction ensure a laminar flow. Adapted from Pennycuick et al. (1997).

Flow visualization

A flying bird flaps its wings, which accelerates the air around it to move, generating a turbulent air behind known as a wake (Spedding et al., 2003). A wake contains vorticity, spinning air, and could be seen as the bird's aerodynamic footprint, as it contains information about the forces produced by the bird to remain aloft and move forward (Figure 2). A visual form of a vortex wake is the condensed air that appears behind airplanes, known as wingtip vortices. By studying the bird's wake, researchers can estimate the magnitude of aerodynamic forces (lift, thrust, weight and drag) and the rate of kinetic energy added to air behind the animal, which reflects the power required to fly (Johansson et al., 2018; Rosén et al., 2004).

Air is transparent, making its visualization and quantification challenging. To visualize the flow and quantify the forces that a bird produces while flying we used particle image velocimetry (PIV). This methodology requires a set of high-speed cameras, a laser, and microscopic aerosol particles suspended in the air. A laser beam illuminates the particles, while the cameras capture pictures in a quick succession. The cameras take several hundred pictures per second (around 720 pictures per second in our set up), allowing us to compare the position of particles between successive frames. Then the airflow can be computationally reconstructed based on the air displacement, resulting in a vector field (like in Figure 2).

PIV measurements are restricted to a relatively small volume inside the test section of the wind tunnel (approximately a plane of dimensions 20 x 30 cm; just a little wider than the animal's wingspan). This is because the wake contains the information about the kinetic energy, and it is confined to a limited area. Thus, the birds were trained to fly in front of this plane.

The rate of kinetic energy added to the air by the bird's flapping wings was used to estimate mechanical power of flight in **Papers I and II**. The more air that is moved and the faster it moves, the more power is generated by a flapping bird.

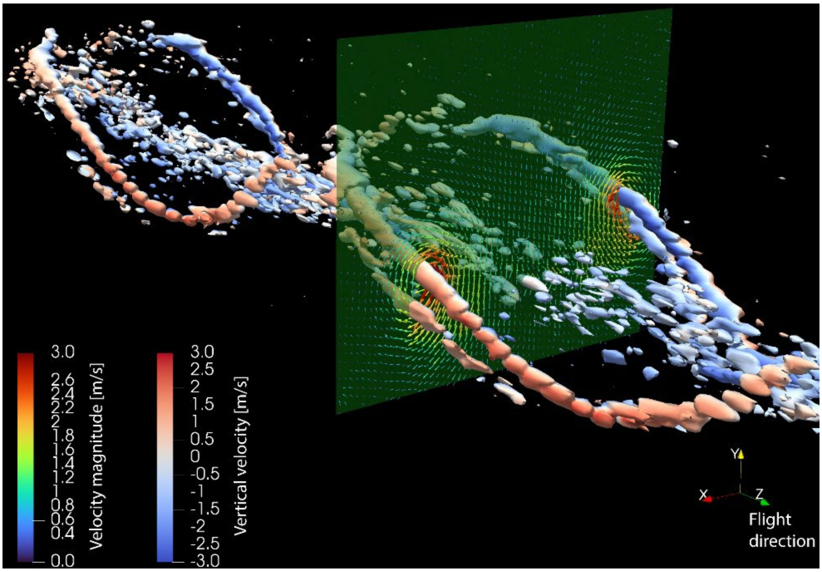

Figure 2. Vector field reconstruction using the PIV technique. A bird flying towards the left generated vortices in the air as it flapped its wings. Flow field reconstruction (green plane with vectors). Two complete wingbeat sequences can be observed. The mechanical power generated by a flying bird is the rate of kinetic energy added to the air by the flapping events, estimated from the vector fields. Adapted from Paper I.

Metabolic energy

Metabolic power is the rate at which a bird's tissues consume energy substrates to support work and maintenance. In practice, flight metabolic power is estimated indirectly from gas exchange, typically by assessing either oxygen consumption or carbon dioxide production, as continuous flapping flight is exclusively aerobic (Butler, 2016). This is because aerobic metabolism relies on oxygen to oxidize energy-rich molecules and generate energy, with carbon dioxide being released as a byproduct (Butler, 2016). Classic wind-tunnel studies measure $\dot{V}O_2$/ $\dot{V}CO_2$ with a face mask attached to the bird to quantify the metabolic cost of flight across speeds (e.g., Tucker, 1968). However, this mask will obviously cause extra costs when flying. Thus, limitations arise when the aim is to estimate metabolic power in un-instrumented flying birds, this is, without respiratory masks that will hinder their flight ability.

The ^{13}C-labelled sodium bicarbonate method ($NaH_2{}^{13}CO_2$; here referred as NaBi) allows to indirectly estimate the amount of CO_2 produced during any activity, such as flight, from which it is possible to infer the metabolic costs without any instruments attached to the bird. The NaBi method relies on ^{13}C, a stable isotope of carbon and works similarly as doubly labelled water methodology (Speakman, 1998). It assumes that the energy used during flight is obtained through oxidative metabolism, meaning that dioxide production reflects the metabolism rate of the flying bird (Hambly & Voigt, 2011). The biological half-life of the isotope is around 10-20 minutes. Thus, this methodology allows to measure energy expenditure over short periods of time.(McCue & Welch, 2016).

When a ^{13}C-enriched solution is administered to an animal, the stable isotope ^{13}C is incorporated into the body bicarbonate pool until equilibrium is reached. Then the heavy isotope is eliminated as CO_2 is expired in the form of $^{13}CO_2$. Thus, the elimination rate of ^{13}C reflects the amount of exhaled CO_2. If the elimination rate of ^{13}C is measured before and after an activity, the difference between the amount of ^{13}C present in the breath before and after the activity is directly related to CO_2 production and hence metabolic energy expenditure. The method has been used in several sized animals, including humans, birds and bats for measuring energy over short term activities (Currie et al., 2023; Hambly & Voigt, 2011; McCue & Welch, 2016). The NaBi method was used to measure the metabolic power of flight at various speeds in birds in **Paper I and II**. Additionally, the metabolic power estimates were used in **Paper IV** to calculate the total energy required to complete a migratory journey.

Tracking devices

It was only recently that technology has provided researches with small enough devices so that we can follow individual migratory birds as small as a 10 gram willow warbler *Phylloscopus trochilus* (Sokolovskis et al., 2018). Thus, great advances in bird migration have become available due to new miniaturized bio-logging technology that allows to fit small size bird with multiple sensors, shedding light into many new aspects of bird migration (Bäckman et al., 2017; Flack et al., 2022; Jetz et al., 2022; McKinnon & Love, 2018; Sjöberg et al., 2018).

In **Paper III and IV**, I used custom built multi-sensor data loggers (MDLs; Figure 3). These electronic devices record data from the onboard sensors at a given frequency and store it inside a memory. The data recorded by the MDLs is only available upon recapture of the bird, usually the year after deployment. With this type of technology it is possible to determine the precise timing of the migratory flights (Bäckman et al., 2017), position (Nussbaumer et al., 2023; Rakhimberdiev et al., 2016), flight altitude (Norevik et al., 2021; Sjöberg et al., 2021) and activity and resting patterns (Macías-Torres et al., 2022), providing a valuable method to study bird migration ecology (e.g., Hedenström & Hedh, 2024; Norevik et al., 2020).

Figure 3. Two multisensor data loggers retrieved from thrush nightingales after one year of deployment. These devices recorded detailed data on migratory behaviour throughout the annual cycle. Photo: the author.

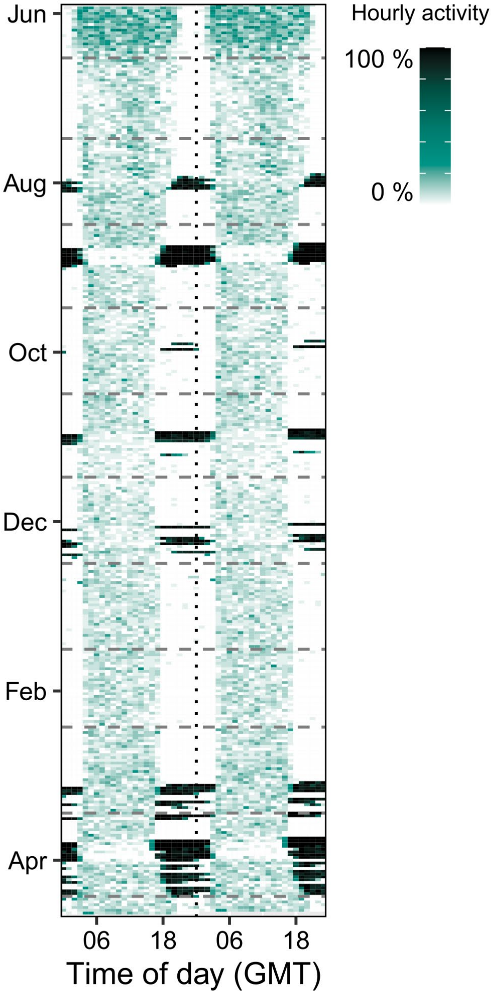

Figure 4. Typical actogram of a thrush nightingale derived from the accelerometer sensor. Two consecutive days are plotted in the X axis, with midnight in the middle (dotted line). The second day is repeated in the next row on the left. Colour denotes the activity level recorded by the accelerometer: white illusatrates inactivity, black maximum possible activity and green intermediate levels of activity. Maximum activity is achieved while on migratory flights, which only took place at night hours. Intermediate levels of activity are observed between sunrise and sunset approximately between 4 and 18h (GMT), indcating short flights, hops, or any other form of locomotion. Modified from Paper III.

In my thesis work I have used MDLs to track the migration journey and gain insights into the migratory behaviour of thrush nightingales breeding near Lund, Sweden. Briefly, one MDL incorporate the following sensors:

- *Accelerometer*: Acceleration is measured in one axis with a sample being recorded every 10 minutes in the vertical Z-axis, aimed to record the vertical acceleration of the bird’s wingbeats (Bäckman et al., 2017). With this sensor it is possible to infer migratory flights and its flight duration, as well as the intensity of other movements across the annual cycle. From acceleration data it is possible to build a visual interpretation of the activity of the bird over a year, an actogram (Figure 4).

- *Barometer*: A pressure value is recorded every hour, reflecting the atmospheric pressure at the bird's current location and time. The recorded pressure data can be used to infer the bird’s position at a given time by comparing the pressure fingerprint recorded by the logger with the ambient pressure data, as the natural temporal variation in pressure is unique to each location (Nussbaumer et al., 2023).
- *Thermometer*: along with the pressure value, a temperature value is recorded every hour. This temperature value is influenced by the ambient temperature as well as by the bird’s skin temperature, as the logger lays on the back of the bird (Sjöberg et al., 2023).
- *Light sensor*: Light intensity was recorded to register sunrise and sunset times, which has been used to infer the position of the bird based on sunrise and sunset times (Rakhimberdiev et al., 2016). Its use in this thesis is secondary, only assisting geolocation by pressure.

Combining wind tunnel and wild tracking

By using both laboratory-based (wind tunnel) experiments and individual-based tracking methods, I was able to investigate the energy costs of flight during migration from complementary perspectives. The wind tunnel experiments allowed to manipulate the variables under study, flight speed in this case, enabling precise flight power measurement (Hedenström & Lindström, 2017). In contrast, tracking data provided insights into the birds’ behaviour in their natural environment, which is an essential context for understanding their biology (Biewener & Wilson, 2025; Bowlin et al., 2010).

In this thesis, both approaches were used on **Paper III** to corroborate flight power estimates from previous studies and calculate fuel loads. Both approaches were directly integrated in **Paper IV**. There, I combined flight energy costs measured in the wind tunnel with migratory flight durations recorded by MDLs to estimate the total energy expenditure required to complete migration in thrush nightingales. Thus, in **Paper IV** I link flight performance and observed migratory patterns to gain insights about the time and energy allocation needed to conduct such long-distance migration.

Study species

In this thesis two long-distance migratory songbird species: the thrush nightingale and the barn swallow. The thrush nightingale was both flown in controlled conditions in the wind tunnel and tracked in the wild with MDLs, while barn swallows were only flown in the wind tunnel.

The thrush nightingale is a medium-sized passerine bird that breeds at northern latitudes and migrates through the Eurasian-African system, spending the non-breeding period in sub-Saharan Africa (Collar, 2020). There are several reasons that make this species an excellent model for studying flight energy costs and migratory behaviour.

First, it has been successfully flown in previous wind tunnel studies, which provided significant insights into their flight kinematics (Pennycuick et al., 1996; Rosén et al., 2004; Spedding et al., 2003) and power (Klaassen et al., 2000; Kvist et al., 1998). Building on previous flight power estimates, in the current thesis I have revisited the flight energetics using updated methodology, providing accurate estimates of both metabolic and mechanical power.

Second, the species' fuelling capacity in relation to migration has been previously studied (Fransson et al., 2001; Klaassen et al., 2000; Lindström & Kvist, 1995), offering solid estimates regarding maximum fuel deposition rate and insights into their physiological fuelling capacity to interpret energy use during long-distance migration.

Third, thrush nightingales have been previously tracked using light-level geolocators, providing initial information on their migratory routes and timing (Stach et al., 2012), indicating a high likelihood of success when tagging this species with MDLs. In this thesis, I used MDLs which provided high resolution data on migratory flights, allowing for precise estimates of time spent in migratory flights. Additionally, because MDLs record continuous activity (24/7), the bird's diurnal activity is captured. This is a useful proxy for fuelling intensity when assuming that higher daytime activity reflects higher foraging effort (Pokrovsky et al., 2021; Yu et al., 2024).

Barn swallows were studied in the wind tunnel to investigate flight energetics and efficiency. This species was selected due to its long-distance migratory behaviour and aerial ecology, spending most of the time on the wings foraging on flying insects (Brown & Brown, 2020). The extensive time spent on the wings, similar to other aerial insectivores (Hedenström et al., 2016), suggests evolutionary adaptations for energy-efficient flight (Guglielmo, 2018), making them a relevant study case for studying flight energetics.

Previous wind tunnel studies have examined the flight kinematics of barn swallows (Bruderer et al., 2001; Park et al., 2001; Pennycuick et al., 2000) and their flight energy costs (Schmidt-Wellenburg et al., 2007). However, direct measurements of flight energetics have remained limited. In this thesis I provide direct measurements of metabolic and mechanical power and provide first estimates of their flight conversion efficiency across speeds. The addition of this species into the thesis offers a comparative basis for evaluating flight power and efficiency across species with different flight ecologies.

Figure 5. Left, a thrush nightingale captured in the breeding grounds near Lund, Sweden. Right. Barn swallow flying in the wind tunnel during experiments performed for Paper II. Photo: the author.

Power required to fly

This thesis focuses on flapping flight; therefore, the flight power of gliding flight is not discussed. For a bird to fly forward, it must overcome two main forces, weight and drag, by generating two opposite forces: lift and thrust, respectively. Weight is generated by the gravity pulling the bird downwards, while drag is the resistance generated by moving through a fluid. Unlike aircrafts, birds lack fixed wings that produces lift and separate engines that produces thrust; therefore, both forces are generate by flapping the wings. Lift is generated by an air foil which deflects the airflow downwards, producing an upwards directed force that counteracts weight. Thrust, is produced by wing flapping by adjusting the wing's angle to direct the lift vector forward, which counteracts drag (Pennycuick, 2008; Tobalske, 2022). To generate the needed forces, the birds flap their wings by contracting the flight muscles. Doing so requires oxidizing fuel to power the flight muscles, the metabolic power. The flights muscles move the wing up and down, transforming this movement into work on the air to produce enough lift and thrust, the mechanical power.

Birds adjust their flapping kinematics to balance the production of the aerodynamic forces according to the needs: generating lift requires more power at low speeds and while drag is the main force to overcome at high speeds (Johansson, 2024; Pennycuick, 2008; Tobalske, 2022). According to aerodynamic theory, the mechanical power of a flying animal follows a U-shaped curve when plotted against airspeed, known as the power curve (Figure 6a; Box 1; Hedenström, 2025; Pennycuick, 1968). This means that flying at very low or very high speeds is more energetically costly than flying at intermediate speeds. Wind-tunnel measurements have confirmed the U-shaped power curve across species (Bernstein et al., 1973; Hedh et al., 2020; Kvist et al., 1998; Tucker, 1968, 1972; Ward et al., 2001; **Paper I and II)**, with each species having its own species-specific power curve depending on the birds morphology, wing kinematics and flight style (Bishop & Guglielmo, 2022; Tobalske et al., 2003, **Paper I and II**).

A power curve illustrates key ecologically relevant flight speeds: the minimum power speed, where energy cost is lowest, and maximum range speed, which maximizes distance per unit of fuel (i.e., minimum cost of transportation; Figure 6a). A power curve is a cornerstone in optimality, as it allows to predict the flight behaviour in animals (Alerstam & Lindström, 1990). If the power curve of a bird species is known, then it is possible to draw prediction about their flight speed over migration. For thrush nightingales, the metabolic flight power curve has been estimated on multiple times using the same wind tunnel but with different methodologies. Despite these methodological differences, the resulting power estimates consistently identify a minimum power speed of ~8 ms^{-1} (Klaassen et al., 2000; Kvist et al., 1998; **Paper I**), indicating the robustness of the power curve for this species.

The metabolic power during flapping flight is particularly energy-demanding because of the continuous muscular activity by the pectoralis and supracoracoideus muscles needed to flap the wings and generate both lift and thrust (Biewener, 2022). The flight muscles can represent about 20% of the bird's body mass (~0.5% in humans) and are almost entirely composed of oxidative muscle fibres specialized in sustained aerobic metabolism (Biewener, 2022; Butler, 2016). This constant muscular activity results in energy expenditures of 5–9 times the basal metabolic rate (Bishop & Guglielmo, 2022; Butler, 2016; **Paper I and II**). As an example, a thrush nightingale flying for 12 hours in a wind tunnel lost on average 3.8 g (13.7% of its starting body mass), while a bird sleeping for 12 hour without eating consumed 0.67 g (2.4% of the starting boy mass; Klaassen et al., 2000). Thus, flapping flight consumes energy at a rate highest than any other animal movement (Butler, 2016), but its high speed allows birds to cover a great distance for a given unit of energy (Schmidt-Nielsen, 1972). For migratory species covering thousands of kilometres, managing the costs of flight is central to successfully complete their journeys.

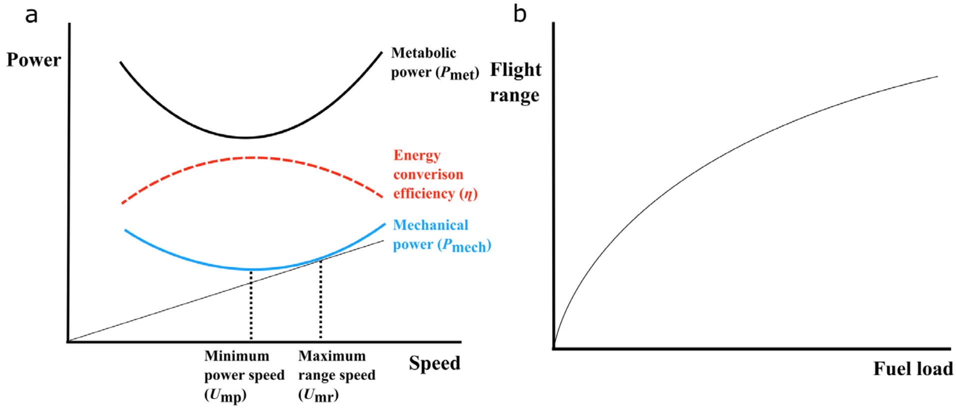

Figure 6. Two fundamental flight realtionship dervied from biomechanical principles. (a) General power-speed relationship. Metabolic power is indicated in black and mechanical power in blue. The ratio between the two is the energy conversion efficiency, in red, here exemplified with as a concave function with airspeed. From this power curve, two ecologically relevant speeds are inferred, minimum power speed (U_{mp}) and maximum range speed (U_{mr}). (b) Flight range in relation to fuel load for an animal using flapping flight. For visual purposes, the relationship between flight range and fuel load has been exaggerated. These two relationships derived from biomechanics are the baseline to infer flight migration strategies.

Box 1. Flight power and efficiency

Flight mechanical power: rate of work exerted by the animal on the surrounding air to propel itself through the air, so that it can stay aloft and move at a certain speed. The mechanical power is the result of overcoming the weight and drag of the bird, and has three main components: induced power (power required to generate lift by accelerating air downwards), profile power (power needed to overcome the drag generated by moving the wings through the air) and parasitic power (power needed to overcome the drag generated by the body). But why does power against airspeed have a U-shape? At low speeds, induced power is high, as birds must work harder to generate enough lift due to limited airflow. At high speeds, parasite power (the drag on the wings times flight velocity) increases, while profile power remains relatively constant across speeds. Together, these three components create a U-shaped relationship between power required and flight speed (Pennycuick, 2008).

Flight metabolic power: rate of work that a bird exerts in order to flap its wings by cycling muscle contractions as a result of substrate oxidation. When measured at the whole-animal level, it includes not only the energy used for moving the flight muscles but also the basal metabolic rate and additional costs associated with circulatory and respiratory function, thus covering all the energy demands of both flight and basic physiological maintenance. Metabolic power can be estimated by measuring rates of exchange in oxygen or carbon dioxide of the animal as they oxidize substrates to fly.

Flight energy conversion efficiency: proportion of mechanical power generated from a given amount of metabolic power. The amount of energy not converted into mechanical power nor used by any other physiological demanding activities is lost as heat. Efficiency can be estimated just for the flight muscles (muscle energy conversion efficiency) as well as for the whole animal (whole-animal energy conversion efficiency: including metabolic costs from basal metabolic rate, circulatory and respiratory physiological costs). Partial efficiency refers to the ratio of change in power output (mechanical power) to the change in power input (metabolic power) at different flight efforts, usually in ascent or descent flight conditions (Tucker, 1968). It is independent of the basal metabolism and other overhead costs that the bird has, assuming that these remain the same at any flight effort. Thus, partial efficiency relates to the flight engine efficiency only.

Flight energy conversion efficiency

Flight metabolic power is a more ecologically relevant property of flight costs than the mechanical power, as it directly determines how quickly a bird depletes its fuel reserves, ultimately shaping the flight decisions of a migratory bird. Metabolic power exceeds mechanical power because not all the energy from oxidized fuel is converted into useful work on the air, with the difference dissipated as heat; the ratio between the two defines the flight energy conversion efficiency (η; Box 1; Figure 6 and **Figure 7**).

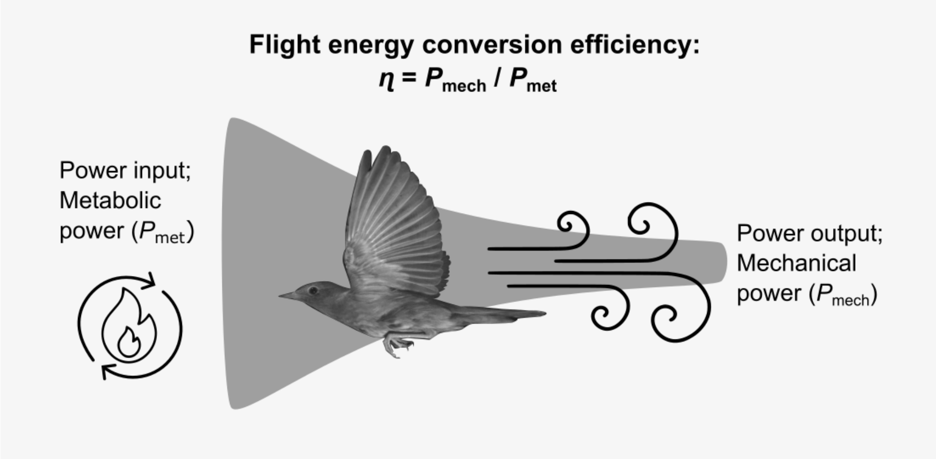

Figure 7. Flight power and energy conversion efficiency (η). Flight power can be measured in terms of metabolic power (P_{met}): the rate at which fuel is oxidized to supply the flight muscles with enough energy to flap the wings; or mechanical power (P_{mech}): the rate of energy transferred to the air. Metabolic power always exceeds mechanical power, with the extra energy lost as heat. The ratio between the two is the energy conversion efficiency and reflects how effectively a bird turns fuel into the aerodynamic power needed to remain aloft. Modified from Paper I.

In order to get a trustworthy estimate of the flight energy conversion efficiency, one must measure both mechanical and metabolic power. However, this is technically challenging, due to the intrinsic difficulty associated with flying birds at controlled airspeed, while measuring the critical variables. Consequently, energy conversion efficiency has been mostly estimated using indirect alternative approaches.

In a very elegant way, the change in metabolic power was measured in relation to the expected increase or decrease in mechanical power during climbing and descending flight in a budgerigar *Melopsittacus undulatus* by Tucker (1968) using a tiltable wind tunnel. This approach quantifies the ratio of *change* in external work to the *change* in metabolic energy expenditure, named as partial efficiency. In that study partial efficiency ranged from 0.19–0.28 (Tucker, 1968). This technique was repeated in other bird species with similar results (in fish crow, *Corvus ossifragus*, with a range in partial efficiency of 0.20–0.29, Bernstein et al., 1973; and in a laughing gall, *Larus atricilla*, , partial efficiency range: 0.19–0.29, Tucker, 1972).

Consequently, a constant value of 23% was assumed to be the reference value for the energy conversion efficiency in avian flapping flight, which has since then been used across species and airspeeds in aerodynamic theory (Pennycuick, 1975) and flight models (KleinHeerenbrink & Hedenström, 2023).

Aerodynamic models can predict how much mechanical power a bird needs to fly (KleinHeerenbrink & Hedenström, 2023; Pennycuick, 2008). If the energy conversion efficiency is known, this can be used to estimate the bird's metabolic power, which is a more ecologically relevant measure for birds. Thus, because conversion efficiency links the aerodynamic power to the metabolic expenditure, it plays a critical role in the understanding of the energy cost of flying birds. This is particularly important in migratory birds, as they spend prolonged periods in flight consuming substantial amounts of energy (Gill et al., 2009; Shamoun-Baranes & Camphuysen, 2025). In particular, a higher conversion efficiencies have been predicted for species that undertake non-stop migratory flights lasting several days, when maximizing energy use is critical (Piersma et al., 2022).

Given that flight is an adaptation that allows exploiting spatially and seasonally variable resources (Alerstam et al., 2003), physiological adaptations leading to the optimal utilization of flight energy should be under natural selection. Since ultimately it is the metabolic energy consumption that is under selection pressure, it is reasonable to expect physiological tunning of metabolic flight power at speeds most relevant to a species' ecology. This tuning would, in turn, influence the optimization of energy conversion efficiency at some speeds. Some studies have indicated that conversion efficiency can change with flight speed and body mass within a species (Kvist et al., 2001; Ward et al., 2001), which further supports the hypothesis of an adaptive response of conversion efficiency to meet ecologically important speeds (e.g., minimum power speed or maximum range speed Hedenström, 2025).

Advances in methodology have allowed researchers to estimate metabolic and mechanical power with improved accuracy without hindering the flying animal. Using isotopic carbon (^{13}C enriched sodium bicarbonate, $NaH^{13}CO_2$) to estimate metabolic power, and PIV (particle image velocimetry) to infer mechanical power, it was possible to measure whole-animal energy conversion efficiency the first time, without relying on flight models (Hedh et al., 2020). This resulted in whole-animal energy conversion efficiency of 14–22% in blackcaps *Sylvia atricapilla*, but it's relationship with speed remained to be empirically tested.

Using state-of-the-art techniques, we measured both metabolic and mechanical power and estimated whole-animal energy conversion efficiency in two long-distance migratory bird species, the thrush nightingale and the barn swallow (**Figure 8**; **Paper I and II**). Ideally, these measurements would be conducted simultaneously, but due to methodological difficulties these were performed on the same birds but at different times, which should still provide reliable insights

(Hedenström & Lindström, 2017). We showed that conversion efficiency was not constant across speeds, but varied with it, peaking at intermediate values that coincide with the ecologically relevant speeds in both studied species (Figure 6a; **Paper I and IV**). Thus, there is indication of a physiological tuning of flight toward speeds for efficient transportation, which is particularly relevant in migratory birds. The concave shape of conversion efficiency with speed was the results of the metabolic power curve being lower at intermediate speeds and steeper at low and high speeds. However, the specific physiological factors influencing variation in the metabolic power across different speeds, which results in an optimum in conversion efficiency remain unknown.

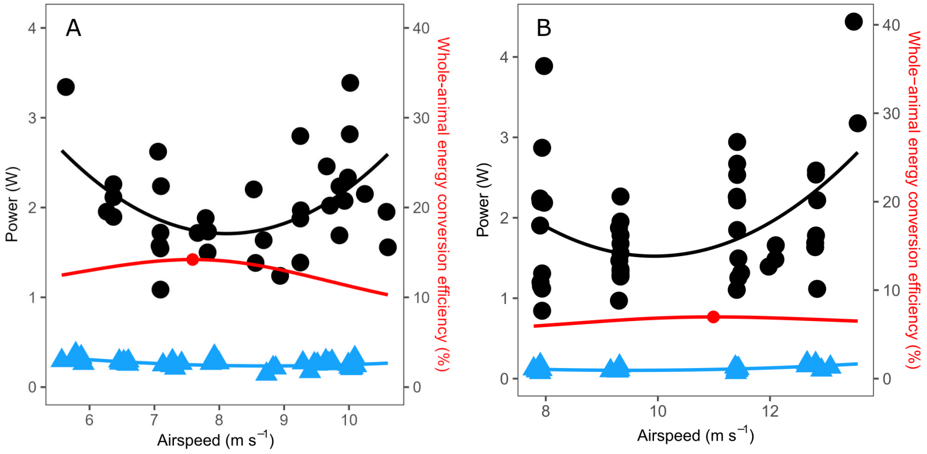

Figure 8. Whole-animal energy conversion efficiency across airspeeds in thrush nightingales (A) and barn swallows (B). Metabolic power is indicated in black and mechanical power in blue. The ratio between the two is the energy conversion efficiency, in red. Modified from Papers I and II.

Additionally, we observed that the maximum energy conversion efficiency was species-specific. Our measurements followed indications from Currie et al. (2023) that efficiency increases with body mass. Thrush nightingales (mean mass ~33 g) showed higher maximum conversion efficiency ($\eta_{\max} = 15\%$) than barn swallows (mean mass ~18 g, $\eta_{\max} = 7\%$), but the increase was larger than predicted by the scaling factor in Currie et al. (2023). However, it is worth noting that this mass scaling factor was derived from indirect estimates of conversion efficiency, which may not fully capture real patterns. Moreover, the peak in conversion efficiency in relation to speed also seemed to differ between species, being higher and sharper in thrush nightingales at flight speeds around ~7–8 m s^{-1}, but broader and shallower in barn swallows across ~8–13 m s^{-1} (**Paper II**).

Together, the results of **Paper I and II** suggest that energy-conversion efficiency varies with speed in two bird species, contrary to what was previously assumed (Hedenström, 2025; Pennycuick, 2008). Additionally, there is indication for a potential trade-off between specialization and flexibility: higher efficiency at a narrow speed range versus lower efficiency spread across a broader range.

Thrush nightingales spend most of the non-migratory period on the ground, only performing short flights and rely on sustained flapping flight during migration (**Paper III**). This species exhibited a sharp efficiency peak near their minimum power speed. In contrast, barn swallows, an aerial insectivore that regularly fly across a broad range of speeds while foraging (Bruderer et al., 2001; Turner, 1982), showed a lower but broader energy conversion efficiency peak. Thus, both studies point at flight efficiency being tuned to match each species' ecological demands.

The concave shape observed in the energy conversion efficiency curve across speeds arises from the fact that metabolic and mechanical power do not scale identically with flight speed. The metabolic power increases more steeply than mechanical power at both low and high speeds, resulting in lower efficiency at the extremes and a peak at intermediate speeds. One of the many underlying causes may be the nonlinear scaling of metabolic processes involved in sustaining flight. For example, when flying at suboptimal speeds, flight muscles may operate outside their most efficient regime; muscle fibres' shortening velocity or contraction frequency can be affected, which lead to an increase in oxygen consumption, raising the metabolic costs disproportionately (Biewener, 2022; Butler, 2016). Future research integrating muscle physiology, biomechanics, and aerodynamics will be essential to uncover the pattern behind the U-shape metabolic power curve and the concave function of conversion efficiency.

Fuelling the migratory flight

Because flight demands energy at a very high rate, migratory birds must accumulate substantial energy before the onset of migration. However, as a bird increases its mass, so does the flight costs per unit of distance travelled (Lindström & Alerstam, 1992), so energy must be stored in the most efficient way possible. Migratory birds rely on fat as their main energy source because it has the highest energy density, 7-9 times higher than other substrates (Guglielmo, 2018; Jenni & Jenni-Eiermann, 1998). In addition to fat, protein is also used as fuel during migratory flights, although at a lower percentage. Protein releases more water per unit as a byproduct of combustion than fat, being particularly important in long flight hauls (Butler, 2016; Elowe et al., 2023). Consequently, due to the high energy demands of flight, some bird species can double their body mass before the onset of the migratory journey by increasing their fat stores (Piersma & Gill, 1998).

The heavier a bird is, the higher the flight cost (Hedenström, 2025). The more fuel is stored the longer the flight range they can fly, but due to the increase in flight costs with increasing mass, flight range does not increase linearly with increasing fuel loads (Figure 6b). This relationship between mass and flight range is a pivotal concept in optimal migration theory (Alerstam & Lindström, 1990), predicting that the migratory performance is expected to be adjusted as body mass changes (Hedenström & Alerstam, 1995). However, the increase on flight costs due to a larger mass was not as high as previously thought, mainly due to an increase in the muscle energy conversion efficiency with mass (Kvist et al., 2001). Importantly, flight power scales with mass (*m*) within same species (e.g., $m^{0.58}$ in barn swallows; Schmidt-Wellenburg et al., 2007; $m^{0.35}$ in red knots *Calidrid canutus* (Kvist et al., 2001) at a lower rate than the scale factor across species ($m^{0.9}$; Hedenström, 2008). All this indicates that although an increase in mass translates to an increase in flight power, the increase may be moderate. If efficiency increases with body mass, it implies that migratory birds would make a better use per unit of fuel and the penalty of carrying fuel loads will thus be considerably smaller than previously thought.

Migratory birds are known to adapt their digestive system to increase their energy metabolizable capacity while fuelling for the migratory journey; shrinking the digestive organs when not in use during active migratory flights (Guglielmo, 2018; Lindström & Kvist, 1995; Piersma & Lindström, 1997). When fuelling, the energy intake increases linearly with available feeding time (Kvist & Lindström, 2000). However, fuelling intensity is not uniform along their migration, but it is trigger by environmental cues, like the magnetic field, triggering birds to fuel more rapidly in some areas than others (Fransson et al., 2001). Thus, when birds are fuelling intensively and food is plentiful, birds will approach their metabolizable energy intake ceiling (Lindström, 1991; Lindström & Kvist, 1995).

In **Paper III** we estimated the fuel loads required for a thrush nightingale to complete their migrations using the range equation (Figure 6b). Fuel loads estimates were based on the mass-loss rate per hour in a thrush nightingales that performed various 12-hour flight in a wind tunnel reported by Klaassen et al. (2000). The flight power estimate in that study overlapped with our flight power measurements form **Paper I** (1.9W at m s^{-1}), reflecting the robustness of the flight power estimate in this species.

From MDLs, we found that the thrush nightingales organised their migrations into several migratory periods (cluster of consecutive nocturnal flights; Figure 4), each with distinct flight duration and thus distinct fuel loads. While the total distance of each migratory period could be covered by carrying less than one lean body mass in additional fuel, two critical periods demanded substantially larger loads. To evaluate whether these predicted fuel loads were reflected by different fuelling behaviour, we compared period-specific fuel requirements with diurnal activity intensity—a proxy for fuelling intensity (Pokrovsky et al., 2021; Yu et al., 2024). We found a qualitative correspondence: migratory periods that required higher fuel loads tended to show higher diurnal activity (Figure 4 in **Paper III**), consistent with an increased fuelling effort, further supporting that fuelling does not occur evenly along the migration (Fransson et al., 2001).

Powering the migratory journey

To conclude this section, it's important to emphasize that while flight is a high energy-demanding mode of locomotion, it enables birds to travel vast distances quickly, thanks to high airspeeds. This translates in flight having a relatively low cost of transportation (J g^{-1} km^{-1}). However, the power required to fly is not fixed but changes between species and across flight speeds (U-shape flight power curve).

Crucially, the energy conversion efficiency links the mechanical power and the metabolic power in a flying animal and plays a key role in determining how much fuel is actually consumed during flight. Understanding how conversion efficiency changes with speed, bird species and mass is crucial in understanding flight migratory costs.

Moreover, migratory birds must deposit fuel before the onset of their migratory journeys. The increase in fuel translates into a heavier body mass, raising the flight cost, and thus, flight range does not scale linearly with fuel load. This is a fundamental principle, which explains why birds must not always store as much energy as possible, but carefully balance their fuel stores based on the flight needs ahead. Together, these insights illustrate the complex interplay in bird flight, between aerodynamics, physiology, which in turn allows birds to perform their remarkable migratory feats .

Ecology of bird migration: migration in relation to flight cost

Migration is a complex phenomenon that requires birds to integrate multiple factors across time and space (Åkesson & Hedenström, 2007). At the centre of this behaviour lies flight energetics: sustaining active flapping flight for hundreds of hours is highly costly and must be contemplated within the context of the annual cycle (Marra et al., 2015). This means that the time and energy invested in migration must be balanced against other critical events of the annual cycle such as breeding and moult (Hedenström, 2006). Consequently, the energy cost of flight is not just a physiological concern; it becomes a central factor shaping migration patterns and the annual cycle scheduling of a migrant (Shamoun-Baranes & Camphuysen, 2025).

The high energy costs of flapping flight requires the migratory journey to be structured into fuelling phases, when body reserves are accumulated, and flight periods, when the accumulated fuel is burnt and transformed into movement (Åkesson & Hedenström, 2007). The structure of fuelling and flight periods inside the migratory journey varies with species, ecology, and environmental opportunities (Evans & Bearhop, 2022). For example, some birds, such as waders, accumulate all energy needed to fly before the migratory journey begins, covering all or most of the migration distance with a single long non-stop flight lasting several days (Gill et al., 2009; Klaassen et al., 2011). In contrast, many passerines, divide the journey in several alternating phases of refuelling and flight (Delingat et al., 2006; Sjöberg et al., 2025). The observed migration patterns (i.e., when and where birds migrate), emerge from the interplay of external factors (e.g., spatial distributions of food and suitable stopover habitats; Briedis et al., 2020; Piersma et al., 1994; Thorup et al., 2017), and internal energetic constraints (e.g., flight energy consumption, maximum fuel loads and the fuel load-flight range relationship; Figure 6b; Alerstam et al., 2003; Hedenström & Alerstam, 1992). Thus, it is critical to understand how flight energetics and the environmental factors interact with each other and shape the migration patterns and strategies.

Migration pattern and strategies

Critically, migration patterns are not the same as migration strategies. Migration patterns are outcomes revealed by tracking devices: routes, timing, and stopovers sites; migration strategies are the underlying decision rules shaped by currencies such as time, energy, or risk (Alerstam & Lindström, 1990; Lindström, 2020; McKinnon et al., 2010). Migration patterns are the observable outcomes shaped by both migration strategies and the environmental constrains (Carneiro et al., 2019; Lindström, 2020). This is a crucial distinction because the tracking outcome may mislead if read directly as strategies, as mixing both concepts is common in the literature (Clements et al., 2025). As an example, a bird "aiming" to minimize its energy during autumn migration, could still show a faster autumn than spring migration if winds support or fuelling conditions are better then (Lindström, 2020).

Using MDLs, in **Paper III** we describe the migration pattern of thrush nightingales in detail. The tracking data revealed the location and precise duration of each migratory flight and stopover, as well as other behavioural features (**Figure 9**). The observed migratory route in this thesis overlaps with that previously reported by light level geolocators (Stach et al., 2012; Thorup et al., 2017). Additionally, we report that nightingales conduct series of consecutive nocturnal flights aggregated in migratory period with prolonged stopovers in between, a pattern consistent in other long-distance migratory passerines (Adamík et al., 2023; Sjöberg et al., 2025). Interestingly, they avoided diurnal flights and only performed nocturnal migratory flights with the exception of flights over sea crossings (see section "Ecological barriers").

How to migrate optimally – the thrush nightingale

Although there is a genetic basis for migratory behaviour in songbirds (Berthold et al., 1992; Caballero-Lopez & Bensch, 2024; Sokolovskis et al., 2023), each migratory bird still makes numerous decisions during its journey, such as where to stop, when to depart, how fast to fly or how much fuel load to carry. Each decision has energetic and temporal consequences (Alves et al., 2013; Bontekoe et al., 2023; Flack et al., 2016), with the ultimate consequence being the risk of dying. Thus, we can expect birds to make their decision based on some kind of optimality criteria.

During migration several currencies should be balanced. It is expected that migratory birds may be in a rush to arrive early at the breeding grounds compared to its conspecifics, as this may translate to acquiring the best territories and mates, which may increase the breeding success (Bell et al., 2024; Kokko, 1999). Conversely, the resources landscape is heterogeneous and seasonal (Thorup et al., 2017), meaning that fuelling opportunities are sometimes unpredictable, when migrating at the lowest cost may be the best alternative. Lastly, predation can be high along the route, with birds adapting their behaviours to reduce their exposure (McKinnon et al., 2010). Therefore, migratory birds are expected to optimize three criteria: time, energy or safety (Alerstam & Lindström, 1990).

Optimal migration theory (OMT) is a toolbox that helps analysing and understanding adaptive behaviours in bird migration. It predicts what a bird would do under ideal conditions when optimizing one of the alternative currencies: time, energy, or safety (Alerstam & Hedenström, 1998; Alerstam & Lindström, 1990). OMT is based on two main cornerstones, the previously introduced power curve and flight range (Figure 6). In order to infer strategies, we require predictions that separate currencies and allow to confront tracking data with those predictions. Expected behaviours can be derived based on alternative optimization criteria, such as optimal stopover duration (Hedh & Hedenström, 2023), optimal fuel load at departure (Lindström & Alerstam, 1992), as well as optimal flight speeds (Nilsson et al., 2013).

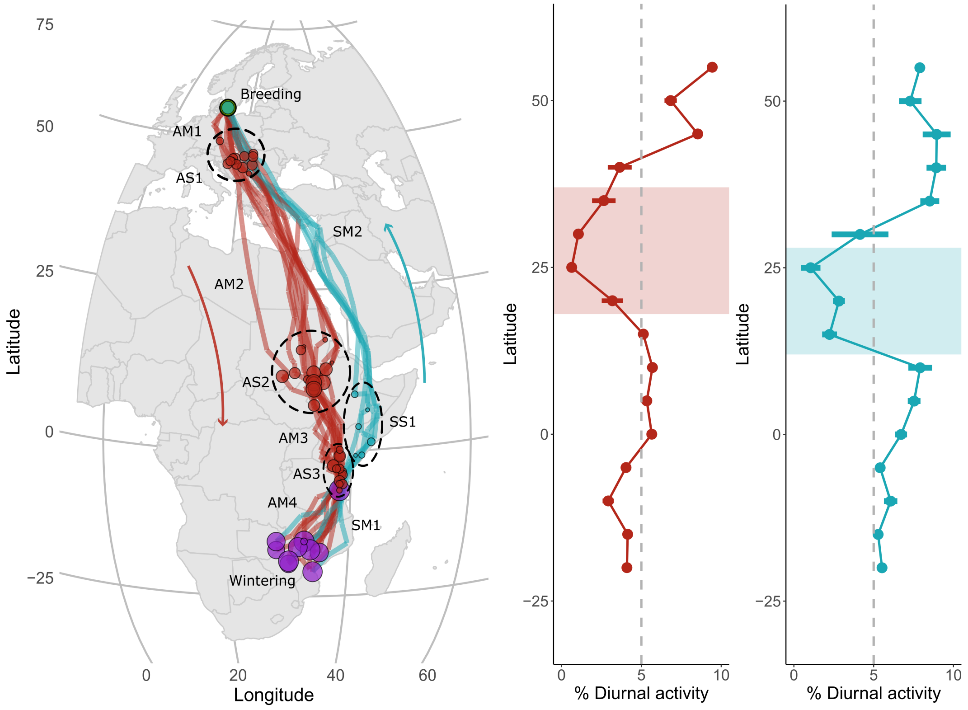

Figure 9. (left) Most likely migratory routes of 11 thrush nightingales caught near Lund, Sweden. Red = autumn migration, blue = spring migration, green = breeding grounds, and purple = wintering grounds. Circles mark stationary periods lasting more than five days. The annual cycle was divided into major migratory and stopover periods: autumn migration (AM1–AM4), autumn stopovers (AS1–AS3), spring migration (SM1–SM2), and spring stopover (SS1). (right) Diurnal activity per 5 degrees latitude (%; mean and SE) for autumn, in blue, and spring migration, in red. Coloured areas illustrate ecological barriers: Mediterranean Sea and Sahara Desert in red. The Arabian Peninsula in blue. Diurnal activity is considered a proxy for fuelling intensity along the migration. Adapted from Paper III.

Of course, migrating birds do not mathematically derive their optimal flight and migration speeds[1], nor the optimal fuel load. Instead, natural selection has favoured behaviours that have yielded into successful migration outcomes (Alerstam & Lindström, 1990). Consequently, the effective "currency" guiding decisions may align more with perceived effort linked to metabolic energy. Such perception is likely informed by physiological cues indicating when for example fuel is low or "good enough" to continue migrating. Behaviour is also strongly context-dependent, and birds are expected to adapt to winds, predation risk, and food availability, shifting the speed and fuelling choices that are advantageous at a given moment. Thus, while predicted optima are useful benchmarks, real decisions arise from the interplay of internal state and external conditions, making the realised behaviour a context-dependent approximation rather than a fixed optimum.

In **Paper III** we explored the migration strategies used by thrush nightingales along their transcontinental migrations. We explore the structure and location of migratory flights and stopover periods within autumn and spring migrations (Figure 9). A big limitation when testing OMT predictions is that fuelling rate of a migratory bird is usually unknown. However, here we considered diurnal activity as a proxy for fuelling rate (Figure 9; Pokrovsky et al., 2021; Yu et al., 2024), which in combination with the length and duration of each migratory period we could qualitatively evaluate which currency birds optimize along their journey (Figure 10).

Under an energy minimization strategy, the bird's departure fuel loads are largely insensitive to local fuel deposition rate. Birds following this strategy would leave with just enough to reach the next site, set by step distance and search/settling costs. In theory, if suitable stopovers are evenly distributed along the migration, with other factors being equal, a bird should perform roughly equal migratory step lengths. By contrast, under time minimization, since the total speed of migration is almost directly proportional to the fuel deposition rate, birds should adjust departure fuel loads to local fuel deposition rate, resulting in increasing fuel loads with increasing fuel deposition rate (Alerstam & Lindström, 1990; Lindström & Alerstam, 1992).

We found that diurnal activity was heterogeneous along the migration journey, varying both across route and within migratory periods (clusters of consecutive migratory days without extensive stopover time in between; Figure 10). The variation in diurnal activity resembles that observed in other long-distance migratory species (Macías-Torres et al., 2022) and it is supported by birds fuelling at different rates based on environmental cues (Fransson et al., 2001). By combining this proxy with the migration performance (i.e., the location and number of flights and the total flight duration), we inferred the underlying strategies used along the

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[1] Migration speed: the total migration distance divided by total elapsed time, including both flight and stopovers for refuelling.

journey. We detected that nightingales were flexible in the migration strategy used: some migratory periods were consistent with a time minimization approach, others with energy minimization, whereas ecological barrier-crossing segments varied in the strategy used depending on the season (**Paper III**).

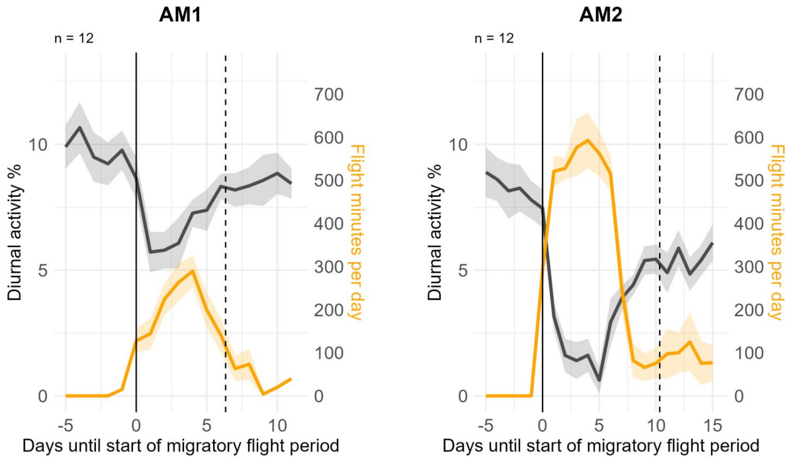

Figure 10. Diurnal activity and flight duration relative to the start of a migratory period (AM1 and AM2, matching migratory periods in figure 9). "AM2" corresponds to the crossing of me Mediterranean Sea and Sahara Desert. The x-axis shows days relative to the first day of the period (solid vertical line = start; dashed line = mean end day across individuals with data for that period, n). Black lines show mean diurnal activity (%), considered a proxy for feeding intensity. Orange lines show mean daily flight duration (minutes per day). Shaded areas represent the standard error of the mean. Adapted from Paper III.

Ecological barriers

In a utopic world with evenly distributed resources would results in migratory birds using the shortest (orthodromic) route between breeding and non-breeding areas fuelling at even rates throughout the journey. However, ecological barriers, such as oceans, deserts and mountain ranges, present migratory birds with extra challenges on their journeys that birds must respond adaptively to (Alerstam et al., 2003).

From the range curve, it is possible to infer that energy-minimizers may even prefer to use longer routes than crossing a barrier if it can be split into legs with smaller fuel loads, i.e., detouring avoiding the high costs of flying heavy (Alerstam, 2001). In relation to this, many bird species perform what is called loop migrations, taking different routes in spring and autumn (e.g. Pedersen et al., 2020; Willemoes et al., 2014). The causes behind loop migration may be the result of different selection pressures at different times of the year, prevailing wind conditions (Norevik et al., 2020) as well as a response to spatiotemporal resource distribution (Thorup et al., 2017).

Birds can also perform a single non-stop flight that extends in time to complete the crossing of a barrier. Birds doing this will require extra energy fuel and time due to accumulate the needed fuel loads (Figure 6b). When performing such non-stop flights over barriers, birds do not simply perform a straight flight, but they show complexity in the vertical space, as they often climb to higher altitudes when the flights extends into daytime (max altitude ~6000 m in passerines; Lindström et al., 2021; Sjöberg et al., 2021). At high altitude, the air is thinner and has lower density than at ground level. Because of different air properties, a bird flying at high altitude should modify its flight kinematics, resulting in a faster flight to maintain lift and thrust, shifting predicted optimal flight speeds (Pennycuick, 2008). Consistent with this, montane bird species show morphological adaptations as a response to less dense air, having larger wings and wing area (Yang et al., 2025).

Autumn migration

In **Paper III** we showed that thrush nightingales generally avoid prolonging flights into daytime, except on very few occasions when flying over water, hinting at additional costs or risks of daytime flight for this species (Sjöberg et al., 2023). Instead, when crossing the Sahara Desert, the birds migrated at night while resting by day. There are various migratory behaviours in songbirds crossing ecological barriers, from single non-stop flights (Sjöberg et al., 2021) to multiple nocturnal flights interrupted by daytime stops (Biebach, 1990; Jiguet et al., 2025) as in thrush nightingales. The causes of this variation in barrier crossing may be many, but in relation to the flight energy costs it has been pointed out that the plumage colouration may influence, as a lighter colour in migrants may indicate selection pressure on the prolongation of flight duration into daytime, to avoid extra thermoregulation costs (Delhey et al., 2021).

When crossing the Sahara Desert, the thrush nightingales took about 3 to 4 nocturnal flights while performing diurnal stopovers. During diurnal stopovers, the birds showed no indication of any fuelling opportunities as revealed by birds being quiescent during daytime (**Paper III**; "AM2" in Figure 10). By remaining inactive during daytime, waiting for the next night to resume migration, the nightingales wasted both time and energy. Time because the birds could have performed a continuous non-stop flight to cover the barrier; extra energy was used because the birds remained quiescent consuming at least basal metabolism during the daytime hours without refuelling until next night. While the main function of stopover is to refuel (Lindström, 2003) here we showed that birds also stop their flights without having apparent refuelling opportunities in the middle of the desert (Linscott & Senner, 2021).

Therefore, there is indication that thrush nightingales crossing the Sahara Desert do not minimize time nor energy but probably maximize survival. I speculate that time and energy may become secondary to safety during this part of the year, when mortality risk is elevated (Klaassen et al., 2014; Lok et al., 2015), and birds operate near their physiological limits.

There has been high emphasis on testing the contrasting time and energy minimization strategies in the literature with little attention to the risks (e.g., Hedenström & Hedh, 2024; Hedh & Hedenström, 2023; Norevik et al., 2017). This is probably a consequence of the limitations in the methodology employed, as MDLs used in many studies have to be recaptured and thus, we only know about the fate of those birds that survive. The pattern observed in **Paper III**, when birds crossing the Sahara Dessert do not minimize either time or energy but probably maximize survival is likely to occur in other bird species when subdue to their limits. Further research using technology that does not require to be recapture, will allow to explore the consequences of different behaviours on the survival of the birds on migration.

Spring migration

As supported by other studies, spring migration appears to be tightly scheduled (Alerstam, 2006; Briedis et al., 2018). We found that during the final segments, the thrush nightingales fly on almost every night over a period of about 20 days (see actogram; Figure 4). Diurnal activity indicates that they first cross the Arabian Peninsula using previously stored fuel in the last stopover in the Horn of Africa. Diurnal activity (%) shows a switching the approach after crossing the Arabian Peninsula. The birds increased diurnal activity to the highest levels recorded outside of the breeding grounds (when they feed the fledglings and show the highest diurnal activity; Figure 4). Thus, the birds switched into a forage by day, migrate by night until reaching the breeding grounds (**Paper III**). This matches a sprint time-minimization pattern (Alerstam, 2006; Briedis et al., 2018), in which birds undertake consecutive flights while replenishing fuel on a daily basis if the fuelling conditions are beneficial to migrate as fast as possible.

The migration pattern that we observed during the spring migration will require thrush nightingales to refuel enough every single day to power the next nocturnal migratory flight. From wind tunnel studies it was estimated that flying thrush nightingales consume about 1% of their body mass per hour (Klaassen et al., 2000). Similarly, under controlled conditions, nightingales can deposit more than 10% their body mass per day, when provided food ad libitum during long days (Klaassen et al., 1997; Kvist & Lindström, 2000), suggesting that a single day of intensive fuelling might be enough to fuel about 10 hours of flight might be enough. This would suggest that the nightingales are accumulating energy close to their maximum metabolizable energy rate (Kirkwood, 1983; Kvist & Lindström, 2000). As a numerical example, a thrush nightingale flying for 12 hours in a wind tunnel lost on average 3.8 g (13.7% of its starting body mass); birds can increase their mass about 3 to 4 g in one day of fuelling under controlled conditions (Lindström et al., 1999).

Thus, it seems possible from a flight energetic perspective that fuelling during just one day under ideal fuelling conditions is sufficient to gather enough energy to perform one nocturnal flight. The intensive feeding is facilitated by the birds flying into longer daylengths as they progress in their migration, which provides them with longer feeding time windows (**Paper IV**). In fact, one of the reasons to migrate at night is the possibility of reserving the daytime hours for feeding (Alerstam, 2009). In order to complete the last migratory segment in spring, thrush nightingales require long days to refuel quickly, turn food into progress, and keep the sequence of night flights going (**Paper III and IV**).

However, this strategy seems risky, as they rely on finding good fuelling conditions along the route (Thorup et al., 2017), with bad weather conditions negatively affecting their migration performance (Tøttrup et al., 2012). This raises the question why thrush nightingales do not depart earlier from the wintering grounds, as this would be the best solution to arrive earlier at the breeding grounds if they are in a rush to arrive at their destination (Morbey & Hedenström, 2020). This is especially relevant given that the ultimate goal for a migratory bird is to maximise its chances of successfully reproducing, and for that arrival time is highly important. Other species like the great reed warbler *Acrocephalus arundinaceus* wintering in East Africa perform a two-month stopover during spring migration half-way to their breeding grounds (Bensch et al., 2025).

Time and energy allocated for migration

Because migration takes place is the context of the annual cycle (Marra et al., 2015; Shamoun-Baranes & Camphuysen, 2025), birds must carefully allocate the limited time and energy to various life cycle stages, balancing the migration-related costs with those associated with the reproduction or self-maintenance (Brown et al., 2023; Buehler & Piersma, 2008; Pontzer, 2025; Shamoun-Baranes & Camphuysen, 2025).

The total time and energy spent on migration can be estimated within the framework of OMT (Box 2). Although flight is the main characteristic of bird migration, it cannot be done without fuelling prior to the actual flight, which happens on the ground [except for species that can fly and forage (Strandberg & Alerstam, 2007)]. A migratory flight consumes energy at a high rate; energy is deposited at rates limited mainly by the digestive capacity and the feeding time available (Lindström, 2003). Consequently, the time spend on the ground is longer than the time spend on migratory flights, with a predicted ratio of 7:1 between stopover and flight (Hedenström & Alerstam, 1997). Therefore, the fuelling rate has a greater influence on overall migration speed than time aloft (Lindström et al., 2019), which is why many bird species migrate at night, minimizing the time spent on migration by maximizing time available for energy deposition (Alerstam, 2009). Similarly, stopovers should use twice as much energy as the total flight, based on estimates of fuel deposition rate against metabolism at stopover (2:1 Hedenström & Alerstam, 1997).

Box 2. Time and energy needed to complete the migratory journey

According to Hedenström & Alerstam (1997), if a migratory journey is sub-divided into periods of movement and stopovers (when fuelling takes place), the total energy spent on migration (E) is the energy spent during migratory flights (on the left side of the sum), plus the energy spent at stopovers (on the right of the sum):

$$E = \left(\frac{PD}{V} + \frac{PDx}{VP_{dep}}\right)$$

Where P is the flight metabolic power , D is the distance, V is the flight speed, x is the field metabolic rate at stopovers (the metabolic energy required to sustain life and deposit energy for the coming flights) and P_{dep} is the energy deposition rate at stopovers.

Similarly, the overall migration speed is determined by three variables: speed of locomotion, the rate of energy consumption during locomotion and the rate of energy deposition. Thus, the total time required to complete the migratory journey can be quantified as:

$$T = \left(\frac{D}{V} + \frac{DP}{VP_{dep}}\right)$$

Where T is the time spent on migration and the other variables are as above. Here the left side of the sum is the speed of the migratory flight, while the right side is the speed of the stopover at deposition the required energy.

Importantly, in this thesis T is known from the accelerometer sensor on the bird, from the first migratory flight on each season, separating between stopover and active migratory flights.

The total energy required to complete migration (E) was the sum of (i) flight metabolic power (P) times the total migratory flight time from accelerometer (T_{flight}); and (ii) energy spend while on the ground: estimated metabolic thermoregulation power (P_{therm}) for the time spent on the ground (T_{stop}) and the power of extra locomotion (P_{loc}; activity not identified as migratory flights) times the locomotion time (T_{loc}):

$$E = \left(PT_{flight} + (P_{therm}T_{stop} + P_{loc}T_{loc})\right)$$

Where (P) is the direct measurement of metabolic flight power (P) from **Paper I**, T_{flight} T_{stop} and T_{loc} are derived from the accelerometer sensor on the bird, P_{therm} is calculated from an endothermic model, including BMR and P_{loc} is assumed to be a proportion of the metabolic flight power (P). This approach is used in **Paper IV**.

Understanding how time and energy budgets are used in the migratory journey is of great importance to elucidate the tradeoffs that a migratory behaviour imply (Linek et al., 2024). Thus, estimating the total energetic cost of a migratory lifestyle requires integrating flight and non-flight behaviours over the entire annual cycle (Shamoun-Baranes & Camphuysen, 2025).

In **Paper IV**, we tested the predicted amount of time and energy budgets between flight and stopover during the migratory journey based on OMT (7:1 and 2:1 respectively; Hedenström & Alerstam, 1997) in thrush nightingales. We used the flight power measurements from **Paper I** to calculate the total energy consumed by each migratory flight based its duration measured from MDLs. Additionally, we estimated the energy expenditure at stopovers based on the ambient temperature and any other locomotion activity indicated by the MDLs (Box 2). With this, it was possible to estimate the total and daily energy consumption for each period of the annual cycle (Figure 11).

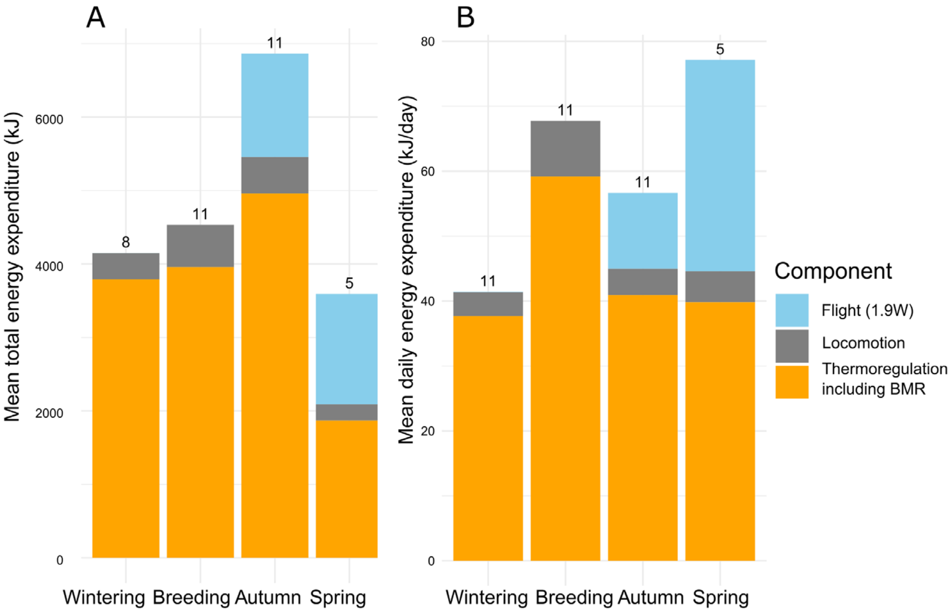

Figure 11. (A) Mean total energy costs (kJ) across seasons of the annual cycle in thrush nightingales. (B) Mean daily energy cost (kJ day^{-1}) per season. Bars show stacked components: migratory flight (blue), locomotion (grey), and thermoregulation (orange). Numbers above bars indicate the number of individuals contributing to each seasonal estimate. Three birds had incomplete wintering seasons and were excluded from the total energy costs but considered when computing the mean daily costs. Flight expenditure plotted assumed a flight power of 1.9W measured in Paper I. Modified from Paper IV.

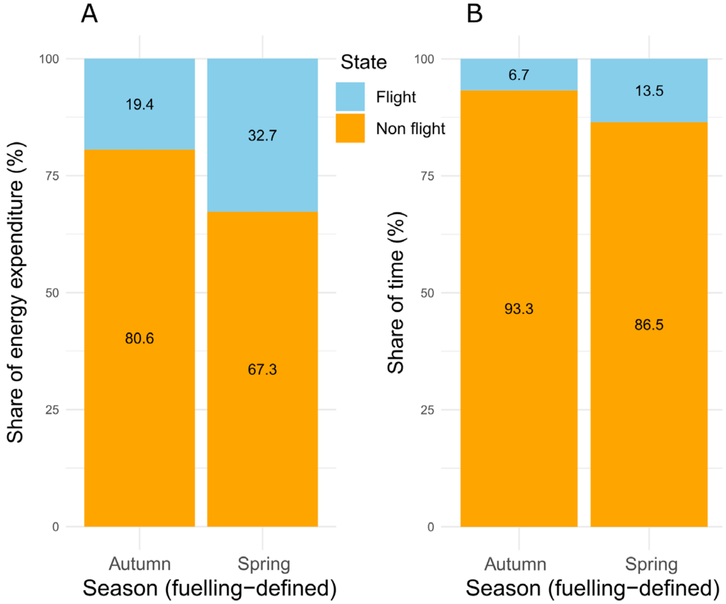

Figure 12. Energy (A) and time (B) allocations for each migratory season between migratory flights (blue) and non-migratory flights (orange) considering the first migratory fuelling period derived from a change in activity intensity before the first migratory flight. Flight energy expenditure was calculated using measurements from Paper I. Numbers on the bars illustrate the mean percentage of the total time and energy budget for each component across individuals. From Paper IV.

When accounting for the first fuelling period for each migratory season, ours values overlapped with the predicted ratio of 2:1 of energy spent at stopovers vs flight during spring migration, while it was doubled during the autumn migration (Figure 12). Similarly, we found that the predicted 7:1 ratio matched our calculation for spring migration, while for autumn migration the ratio was about twice as high (Figure 12). Both ratios were theoretically predicted under fuel ratios close to maximum (Hedenström & Alerstam, 1997). Thus, from our estimates it is possible to infer that migratory thrush nightingales were fuelling at rates close to the maximum predicted during spring migration but not during autumn migration. The predicted ratio also matched migration energy ratios in free-migrating *Catharus* thrushes during spring migration (Wikelski et al., 2003) and that of European nightjars during both migratory seasons (Norevik et al., 2017).

Additionally, we identified that daily energy expenditure increases significantly with daylength during both migratory seasons, indicating that longer photoperiods enable higher energetic throughput (Figure 13). Thus, energy allocation was constrained by seasonal daylight availability. As previously conjectured, daylength plays a central role in the way migration is structured (Bauchinger & Klaassen, 2005) and may act as a selective agent shaping long-distance latitudinal migration (daylight availability hypothesis; Sockman & Hurlbert, 2020). Seasonal differences in daylength gradients likely underpin the contrasting energy budgets and migratory patterns observed between autumn and spring. Thus, longer days allow for more time fuel, increasing the energy deposition rate per day, making the migration speed faster in spring than autumn (Bauchinger & Klaassen, 2005; Lindström et al., 2019). Longer daylength together with an gradient in resources during spring migration (Hedenström & Hedh, 2024; Thorup et al., 2017) are probably the major drivers for the observed differences in migration patterns between both.

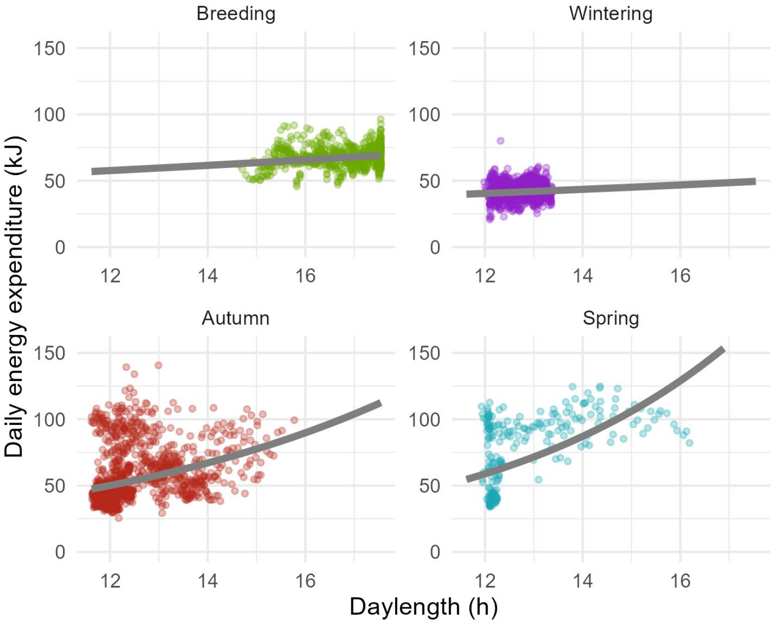

Figure 13. Relationship between daylength and total daily energy cost across seasons. Each point is a daily estimate for an individual bird. The grey line shows the season-specific prediction from a linear mixed-effects model fit to log-transformed daily energy expenditure [log(kJ)] and then back-transformed to the original scale. From Paper IV.

Conclusions and future work

Migratory birds spend hundreds of hours on their wings each season as they traverse the globe, making it quite important to understand the energy costs of flight, as flight energy costs will ultimately shape the ability of a bird to exploit its environment. In this thesis, wind-tunnel measurements and individual tracking across full migrations provided a more complete view of their migration flight energetics. I integrated these two complementary approaches to gain a better understanding of the energy expenditure in long-distance migratory birds. This thesis tackled questions about the energy needed to fly at different speeds and across bird species, as well as the migration patterns and strategies in a long-distance migratory songbird.

Papers I and II provided flight power measurements and whole-animal energy-conversion efficiency across a range of speeds in two long-distance migrants, thrush nightingale and barn swallows. Power–speed relationships follow the canonical U-shape, providing a quantitative basis for estimating in-flight energy use and identifying energetically critical speeds in both species. From direct measurements in flight power, energy conversion efficiency was estimated across speeds, revealing that it varied with speed and between species. Speed-conversion efficiency relationship indicates that birds perform best at intermediate speeds, aligned with ecologically relevant speeds for efficient sustained flights. Additionally, species-specific shape in conversion efficiency suggests a specialization–flexibility trade-off consistent with each species' flight ecology. However, this pattern will have to be confirmed by studying flight efficiency in more bird species.

Importantly, energy-conversion efficiency appears to scale with body mass (Kvist et al., 2001), which is specially relevant in migratory species as they increase their mass prior to prior to a migratory flight, which will in turn increase the flight costs. To disentangle key aspects in bird flight energetics in relation to migration, future work should compare flight physiology between migratory and non-migratory states within the same species and across a broad range of body masses (Guglielmo, 2018; Kvist et al., 2001; Lewicki et al., 2025).

Wind-tunnel studies have allow researchers to examine the physical and physiological properties of bird flight (Hedenström & Lindström, 2017), providing it is a great tool for testing flight energetics over long flight periods (Elowe et al., 2023; Klaassen et al., 2000). However, wind tunnels do not come flawless, but a critical view is whether flight in wind tunnels accurately reflects free flight in birds.

While the physics of flight remain the same, the confined space of wind tunnel section does not look any like the natural aerospace. There seems to be some discrepancy between flight energy costs and flight speeds in wind tunnel versus that observed in the wild (Masman & Klaassen, 1987; Pennycuick et al., 2013). Encouragingly, our barn swallow results (**Paper II**) overlap with previous studies measuring field-based flight energetics (Lyuleeva, 1970; Turner, 1982). Taken together, our wind tunnel studies provide valuable insights about key flight energy aspects in two migratory species. That said, careful selection and training of birds is essential, so that their performance closely matches free flight in the wild; otherwise, wind-tunnel data may misrepresent the flight energetics birds use.

Because migration expose birds to a range of challenges, tracking studies are crucial to reveal how birds adjust their behaviour across the journey. Coupling migratory patterns in thrush nightingales with diurnal activity (a proxy for fuelling), allowed us to infer the migration strategies used by these birds under the predictions from optimal migration theory (**Paper III**). Our results suggest that long-distance migration in this species is shaped by a context-dependent mix of currencies (time, energy, and safety) rather than a single, fixed strategy. Ecological barriers (the Sahara Dessert and Arabian Peninsula) modulate their migratory behaviours differently across seasons, underscoring flexible decision-making tuned to local fuelling opportunities and energetic demands. Methodologically, coupling tracking with a diurnal activity as a proxy for fuelling (**Paper III**), provides a comparative framework that can be applied across species to assess how environmental constraints shape migratory behaviour (Shamoun-Baranes & Camphuysen, 2025). By using this perspective, it provided evidence on the variation in fuelling intensity along the journey (Fransson et al., 2001) and a detailed view of barrier-crossing behaviour by this passerine species, adding to our knowledge of ecological barrier crossing behaviours (Bensch et al., 2025; Biebach, 1990; Sjöberg et al., 2021).

A compelling next step will be to examine how birds know how handle the challenges associated with crossing ecological barriers. Importantly, future work should delve into the ontogeny of behavioural variation along the migratory journey. I find particular interest to study whether migration strategies are learned as songbirds undertake their first journey or whether a genetic component to migratory behaviour enables juveniles to switch strategy in combination with external cues (Caballero-Lopez & Bensch, 2024; Fransson et al., 2001). I speculate that the variation in the migratory behaviour is probably regulated by an interplay between extrinsic and intrinsic factors, similar to the structure of the migratory periods (Sjöberg et al., 2025), with some learning improving the migratory decisions (Aikens et al., 2024).

However, an important caveat in tracking studies with loggers is the survivorship bias. We only know about the fate of birds that return successfully to their breeding grounds. We lack data about the whereabouts of songbirds that fail to succeed in their migrations. Most importantly, we lack information about the reasons why they fail to do so, which could teach us a lot about the selection pressures in bird migration. Further research using technology that does not require to recapture the birds will allow to explore the consequences of different behaviours on the survival of the birds on migration (Flack et al., 2022).

Combining wind-tunnel flight energetics from **Paper I** with individual-based tracking data in the same species allows to derive energy requirements during migratory flights (In **Paper IV**). This yielded in precise in-flight vs. stopover energy and time budgets during migration, which aligned with theoretical predictions during spring migration under rapid fuelling rates, but were about double during autumn migration. Importantly, daylength modulates the amount of daily energy expenditure, as longer days allow for higher fuelling rates, helping to explain the spring–autumn contrasting migration patterns. Together, these results suggest that spring migration operates under tighter time and energy budgets than autumn. This tightness may become more severe under the effect of climate change (Linssen et al., 2025) if migratory birds do not adapt quick enough (Both et al., 2010; Lamers et al., 2023).

Placing the time and energy budgets findings (**Paper IV**) in the annual-cycle context underscores the value of assessing migratory flight energetic trade-offs among life-history stages (Pontzer, 2025; Shamoun-Baranes & Camphuysen, 2025). If migration is an adaptation to track seasonal resources (Alerstam et al., 2003), its costs must be offset, for example by savings in thermoregulation (Linek et al., 2024). Although we do not test migration evolutionary origins, our time and energy ratios provide quantitative values to assess the energy costs of performing long-distance migration, which can help identify potential trade-offs and bottlenecks across species and migration patterns (Buehler & Piersma, 2008).

In this thesis, all flight energy measurements (**Papers I and II**) and estimates (**Papers III and IV**) were assumed to be carried out at ground level, same as the wind-tunnel measurements. In reality, birds migrate at higher altitudes, where the air density, oxygen availability, temperature and humidity are different (Ivy & Williamson, 2024; Nilsson et al., 2025). Therefore, extrapolating our wind tunnel measurements to free flight requires caution, are there is likely to be a shift in the cost of transport and the location of energetically relevant speeds when flying at high altitudes (Hedenström & Alerstam, 1995). Hypobaric wind-tunnel experiments (Ivy et al., 2025) and altimetry bio-logging (Bishop et al., 2015; Sjöberg et al., 2023) will provide valuable insights into the altitudinal effect on bird flight energetics. In relation to this, understanding why some species extend flights into daytime while climbing (e.g., Sjöberg et al., 2021), whereas others remain strictly nocturnal, deserves further attention. Finally, it remains unknown whether airspeed varies throughout migration, either in relation to body mass or environmental conditions (Hedenström & Alerstam, 1996), a factor that would directly influence flight energy costs (**paper I and II**) and, by extension, the overall migration energy budget (**paper IV**).

While the benefits of wind-tunnel studies are important on their own (Hedenström & Lindström, 2017), as well as the new insights into bird migration from miniaturized multisensor loggers (Bäckman, et al., 2017; McKinnon & Love, 2018), their combination is truly synergistic to understand the topic of bird migration. In my view, such integrative work is essential: the biological complexity is so great that only multiple, complementary methods can provide a full perspective. Looking ahead, the future of bird migration is exciting as new tracking technology advances quickly, providing researchers with increasingly powerful tools to better understand this fascinating phenomenon.

Acknowledgments

This text readability has been improved substantially by comments from Anders Hedenstrom, Christoffer Johansson, Linus Hedh, Jesper Brodersen and Blanca Alejo. Thank you so much for your valuable input. This project has received founding from. The project was funded through grants from the Swedish Research Council to AH (2020-03707) and the Knut and Alice Wallenberg Foundation (KAW 2020.0096).

Thank you!

Here I am on the final day before submission, reflecting on how quickly these 4+ years have flown by. I feel the reason for time passing by so fast is largely because of the people who made this journey far better than I ever imagined. This section is for you. I will try to my best to mention each of you.

Foremost I have to thank my supervisor, **Anders**, for your trust in me. I am amazed by your knowledge in so many diverse topics. I find amazing that studies from the past century always seem ready to pop right out of your brain, it is a superpower. I appreciate your smooth assistance throughout this process, allowing me to explore my own ideas with both the wind tunnel and with the loggers. Thank you so much for always having the door open for discussion. It has been incredibly fun to be part of this project and to share time with you in conferences and fieldwork trips.

Christoffer, you have been a great co-supervisor. Without you this thesis wouldn't be possible. You have assisted in every single brainstorming and provided great support whenever I asked you. I am amazed by your ability to always improve whatever text I send you.

Eric, thank you for being a great departmental representative. You carefully oversight all meetings and deadlines. I have particularly fond memories of ISP meetings that ran late due to our scientific discussion of flying animals. Thank you, **Natalie** for being a good scientific advisor. I enjoyed our casual chats and the pizza! **Jessica**, thank you for your impressive efficiency with any paperwork that I have asked you.

Sissel, you have been like a co-supervisor, but not just over the last 4 years, but more so over the last 7 years, since you accepted me as a master student when I first arrived in Copenhagen. You introduce me to Lund and have advised me in many aspects of my life. I am pretty sure I wouldn't be writing this if it wasn't for your assistance. Thank you for so much.

Thank you, **Thomas**, for being a great halftime opponent, always providing great feedback on any of my projects. **Åke**, your sense of humour is hilarious. Thank you for the all the fun discussions about bird migration, hopefully one day I can join you in the mountains.

Linus. I should have listened to you and started writing sooner as you advised me; however, I did listen to you and took good care of the wind tunnel ;-). Anyways, your help over these years has been of enormous value to me. Thanks for all the great moments in the department, at the pub and in the field. More importantly, thank you for the knife that has provided me with so many loggers back.

Vio. Thank you for everything. You rock. You are able of making everyone's day much better by chatting with you and making them laugh. Thank you for showing me how to first put a logger on a small chiffchaff. Thank you for letting me crash in your sofa whenever I needed. Keep your energetic spirit. nHub ;-)

Jesper, thank you for being such a wonderful office mate. I will never forget our first trip together to Poland, not because of the meeting, but because of the hilarious moment at the beginning of the trip. We should also go again to Tarifa. **Elsie**, thank you for being so caring, the wonderful barn swallow paint and for your friendship. **Kat**, thank you for so much fun on pub-quiz and for letting me tease you about how bad Danish food is, which is actually true. **A-K**, thank you for helping me catching the barn swallows and fighting the wild boars. **Tamara**, I admire your honesty; thank you for the best pottery coffee cup ever. **David**, thanks for all the great moments and chats about life. Good luck travelling around the world. You also taught me that I should be grateful to myself for finishing the thesis, so thank you and thank me ;-). **Javier A** thank you for the best lizard pic that I own (and the only one) and for being such a good person. Whenever I get stress, I remember your advice that I should go out and watch birds and seals more often. No one cares about the Papers in reality.

All the flight lab has contributed to many discussions about one or another project of this thesis, thank you to all the current and old members of the lab: **Anders, Christoffer, Victor, Linus, Eric, Daniele, Frida, Sonja, Erica, Per, Chuyu, Gabriel**. Most of the hours spent in the darkness of the wind tunnel were not alone, but with people who made it much more enjoyable: **Sonja, Anders, and Christoffer**. Thank you, **Gabriel**, for so many chats about migratory birds and for showing me how to catch the first ever thrush nightingale of my thesis.

Big shout out to all **the birds** that either in the wind tunnel or by carrying a backpack to Africa and back, have contributed to write the story in this thesis. Doing fieldwork is a lot of fun, because of the birds, of course, but more so because of the people that joined and helped me catching nightingales at forbidden hours in the morning and evening, with a clear lack of sleep. Thank you to all the people that joined me in the field **Linus, Lydia, Vio, Harald, Moreno, Jesper and more**.

The devices used during fieldwork were developed by **Arne A.** and **Johan**. Thank you for your work and discussions about the loggers. I know we share a big frustration whenever a retrieved logger did not work at all, luckily some did work. The tracking analysis were done with great support from **Raphaël**, thank you for replying to my hundreds of emails.

It is usually said how important it is to work in a sound workplace. Well, I have been the luckiest person because I have the best workplace, a department full of great people with whom I have shared many fun talks and Friday pubs. Thanks to the current and past fellow PhD students: **Kalle, Zach, Elsie, Hongkai, Qinyang, Kristaps, Linus, Pedro, Robin, Simon, Sofie, Tianhao, Twinkle, Violeta, Yun-Ting, Agnes, Jesper, Ximena, David, Elin, Iain, Erica, Rae, Jamie, Katie, Susana, Samatha, Frida, Sara, Agnieszka, Ruben, Jöran, and more.** Also, thank you to the people from the biology building that eventually dared to cross the bridge and have fun at the ecology building: **Elin, Valentin, Andre.**

These are many other wonderful people around the department that made my time much more enjoyable: **Cecilia, Angela**, **Ernö, Carolina, Javier P., Javier A., Moritz, Quentin, Amparo, Nicholas, Finja, Colin, Juancho, Zsófia, Yedra.** There department is also full of researchers that are available for any casual chat, contributing to an inspiring workplace. Thank you, **Dennis, Bengt, Maja, Caroline, Jan-Åke, Staffan, Charlie, Emily, Michi, Anders B., Sussane, Guiseppe, Arne H., Hannah, Johan N., Juan Diego and Olivia.** Thank you, **Per L**., for sharing your philosophical perspective in every scientific aspect. Also, thank for you classical music, often drifting through the corridor.

During my PhD time, I had the incredible opportunity of visiting the wind tunnel in London Ontario, Canada. I'm really grateful to **Chris**, who made it possible. I am truly sad that our work could not make it into this thesis. However, I will make sure that it sees the light rather sooner than later. I still can't believe we made it into the NYT! Likewise, I am grateful to all the other people that made my stay in Canada so enjoyable: **Catie, Jess, Mel, Marina, Francis, Michela, Gabby, Andrew, Kevin, Yolanda.**

Also, big thank you to **Stephen** and **Daniel**, I have so many good birding memories with you!

On the other side of the bridge, when not working, I was lucky to have great friends, with whom we have spent so many great moments and great food! **Alessandro, Giorgia, Henrique, Thais**, and of course thank to the little ones, **Cecilia and Theresa**. Similarly, thank you to the ringing gang of CES Vestamager: **Amanda, Jesper J., Kasper, Rie, and more.**

Living abroad is sometimes not easy. Many of my friends live thousands of kilometres aways, still, they made me fill like time did not pass whenever I visited back. Thank you, **Carlos, Calle, Alberto, Alvarito, Carra, Cori, Chete, Jose, Julian, Julio, Luisma, Manu, Kini, Pablo, Pepe y Juancho.**

Thank you to my family for being so supportive in the distance. A mis **padres**, gracias por educarme y enseñarme los valores que hoy tengo. Se que nos echamos de menos, pero me apoyáis en todas las decisiones que tomo, aunque eso implique estar lejos. Gracias por tanto. **Olga, Ana,** gracias por ser mi familia, os quiero.

Víctor, gracias por enseñarme tanto, te aprecio mucho. También gracias a mis tías **Pepi y Angelita** por vuestros mensajes, os quiero.

Lastly, big thank you, **Blanca**. I'd need several pages to list everything I am grateful for. You are the most caring person I know. You have showed me I could do so much more, pushing my personal and academic limits. This thesis would simply not have been possible without you.

Picture 1. Sunrise over Blanks Mosse on a misty morning in May. This is where most thrush nightingales in this thesis were caught.

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