Charles University, Faculty of Science, Department of Ecology

Study program: Ecology

Vojtěch Brlík

Ecological consequences of seasonal bird migration

Ekologické důsledky sezónní migrace ptáků

Dissertation

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Contents

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Abstract

Environmental seasonality, and associated fluctuation in resource abundance, affects organisms throughout their life cycles. Periods of resource scarcity can be avoided by seasonal migration, strategy common in animals, including birds. However, the long journeys of migratory birds separate the stages of their annual cycles in space and time, and present them with a variety of challenges. Environmental conditions that migrants experience may have local effects, or may carry over across seasons, and have delayed impacts on individuals and populations. To better understand the interactions between migratory animals and their environment, we integrated individual tracking, environmental measures, and population data within a full annual cycle perspective. We contributed to the understanding that environmental conditions can affect migratory populations both en route and during stationary non-breeding periods, and that their effects can be observed on a continental scale. We also showed, across species and migratory flyways, that stages of the annual cycle are tightly linked during migration, but that these links weaken during prolonged non-breeding stationarity, with implications for individual success and future prospects under ongoing environmental change. To enhance the ability to trace animal movements, we also developed a stable sulfur isotopic map for sub-Saharan Africa, revealing a longitudinal gradient across this biodiversity-rich region with promising applications in wildlife conservation and ecological studies. Overall, large-scale tracking datasets integrated with data on long-term population changes can provide valuable insights into environment–animal interactions, serve as a reference for studies of their temporal dynamics, and can guide targeted conservation efforts.

Abstrakt

Sezónnost prostředí, doprovázená kolísající dostupností potravy, ovlivňuje organismy v průběhu celého života. Obdobím nedostatku zdrojů se lze vyhnout sezónní migrací, která je u živočichů včetně ptáků běžná. Dlouhé cesty však staví tažné ptáky před řadu problémů, protože jednotlivá období ročního cyklu jsou od sebe oddělena v prostoru i čase. Podmínky prostředí, které tažní ptáci využívají, mohou na ptáky působit lokálně, ale jejich vliv se může projevit i napříč sezónami. Abychom lépe porozuměli interakcím mezi tažnými ptáky a prostředím, propojili jsme data ze sledování migrace s daty o podmínkách prostředí a populačních změnách v rámci celého ročního cyklu. Přispěli jsme tak k poznání, že podmínky prostředí mohou ovlivňovat migrující populace jak během zimování, tak v průběhu tahových zastávek, a že tyto dopady lze pozorovat i v kontinentálním měřítku. Ukázali jsme také, že napříč druhy a tahovými cestami jsou fáze ročního cyklu během migrace úzce provázány, ale že tyto vazby slábnou v průběhu dlouhých období zimování, což má důsledky pro úspěšnost jedinců a pro predikci budoucích scénářů ve světle globálních změn. Vytvořili jsme také mapu stabilních izotopů síry pro subsaharskou Afriku, na které je patrný longitudinální gradient napříč tímto druhově bohatým regionem a která nabízí aplikace v ochraně volně žijících živočichů a v celé řadě ekologických studií. V této disertační práci ukazuji, že rozsáhlé soubory migračních dat integrované s daty o dlouhodobých populačních změnách poskytují cenné poznatky o interakcích mezi prostředím a zvířaty, slouží jako reference pro výzkum jejich časové dynamiky a mohou pomoci lépe zacílit ochranářská opatření.

Declaration of originality

I declare that this thesis, publications and unpublished manuscripts has not been submitted for the purpose of obtaining the same or any other academic degree earlier or at another institution. My involvement in the research presented in this thesis is expressed in the Author's contribution statement and is also included in the publications and unpublished manuscripts. All literature sources have been cited and acknowledged.

Prague, June 2023 Vojtěch Brlík

Open data statement

Data and metadata are publicly available for each publication from the Zenodo data repository (https://zenodo.org/) and AviSample Network (https://avisample.net/).

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List of chapters and author's contribution

This thesis contains both published and unpublished manuscripts that emerged from a collaborative effort involving numerous researchers. My personal contributions to each of the publications and unpublished manuscripts are outlined below, following the guidelines of CRediT (Contributor Roles Taxonomy).

Chapter 1

Brlík, V.*, Pakanen, V. M.*, Jaakkonen, T., Arppe, H., Jokinen, J., Lakka, J., Blomqvist, D., Hahn, S., Valkama, J. and Koivula, K. 2022. Survival fluctuation is linked to precipitation variation during staging in a migratory shorebird. – Scientific Reports 12: 19830. https://doi.org/10.1038/s41598-022-24141-5

**Contributed equally*

Contribution: Conceptualization (equal), Data curation (equal), Formal analysis (equal), Investigation (equal), Methodology (equal), Project administration (equal), Writing – original draft (equal) and Writing – review & editing (equal)

Chapter 2

Brlík, V., Procházka, P., Hansson, B., Stricker, C. A., Yohannes, E., Powell, R. L.* and Wunder, M. B.* 2022. Animal tracing with sulfur isotopes: Spatial segregation and climate variability in Africa likely contribute to population trends of a migratory songbird. – Journal of Animal Ecology *in press*. https://doi.org/10.1111/1365-2656.13848

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Contribution: Conceptualization (lead), Data curation (lead), Formal analysis (lead), Investigation (lead), Methodology (equal), Project administration (lead), Writing – original draft (lead) and Writing – review & editing (lead)

Chapter 3

Brlík, V., Malmiga, G., Dimitrov, D., Emmenegger, T., Gavrilov, A., Hasselquist, D., Peev, S., Willemoes, M., Yohannes, E., Hahn, S., Hansson, B. and Procházka, P. 2020. Population-specific assessment of carry-over effects across the range of a migratory songbird. - Behavioral Ecology and Sociobiology 74: 143. https://doi.org/10.1007/s00265-020-02929-7

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Chapter 4

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Barger, C., Rushing, C., Nathan, C., Victor, C., Irwin, D., Cikovic, D., Arlt, D., Hasselquist, D., Parejo Mora, D., de Zwaan, D., Rubolini, D., Tuero, D., Kishkinev, D., Bridge, E., Gow, E., Liechti, F., Bairlein, F., Bell, F., Jiguet, F., Norevik, G., Baudrin, G., Kramer, G., Justen, H., Schmaljohann, H., van der Jeugd, H., Streby, H., Tieleman, I., Ouwehand, J., Hill, J., Ross, J., Partecke, J., Avilés, J., Costa, J., Burant, J., Alves, J., Hagelin, J., Thorup, K., Snell, K., Hobson, K., Fraser, K., Kardynal, K., Savides, K., Delmore, K., Witte, K., Sokolovskis, K., Smith, L., Halupka, L., Remisiewicz, M., Burgess, M., Sander, M., Buchmann, M., Flade, M., Briedis, M., Hallworth, M., Krist, M., Liedvogel, M., Perlut, N., Tomášek, O., Cimprich, P., Adamik, P., Marra, P., Klvaňa, P., Bernardy, P., English, P., Matyjasiak, P., Cormier, R., Patchett, R., Ambrosini, R., Renfrew, R., Bani Assadi, S., Barisic, S., Fisher, S., Bensch, S., Emmenegger, T., Curk, T., Pärt, T., Albrecht, T., Laaksonen, T., Salewski, V., Heim, W., Cresswell, W., DeLuca, W. V., Rime, Y., Yamaura, Y., Hahn, S., Procházka, P., Norris, D. R. Consistent time dependencies across the annual cycle in small migratory birds: tight links during migration, non-breeding reset and compensation for delays. – Unpublished manuscript.

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Chapter 5

Brlík, V., Norris, D. R., Porkert, J., Trnka, A., Mikula, P., Vondrovicová, L., Trubač, J. and Procházka, P. Extensive individual variation in environmental space use between seasons in migratory birds. – Unpublished manuscript.

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Chapter 6

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Martí, D., Massimino, D., Moshøj, C., Nellis, R., Noble, D., Paquet, A., Paquet, J.-Y., Portolou, D., Ramírez, I., Redel, C., Reif, J., Ridzoň, J., Schmid, H., Seaman, B., Silva, L., Spasov, S., Staneva, A., Szép, T., Tellini Florenzano, G., Teufelbauer, N., Trautmann, S., van der Meij, T., van Turnhout, C., Vermeersch, G., Vermouzek, Z., Vikstrøm, T., Voříšek, P., Weiserbs, A. and Klvaňová, A. 2021. Long-term and large-scale multispecies dataset tracking population changes of common European breeding birds. – Scientific Data 8: 21. https://doi.org/10.1038/s41597-021-00804-2

Contribution: Conceptualization (supporting), Data curation (supporting), Methodology (supporting), Project administration (equal), Writing – original draft (lead) and Writing – review & editing (lead)

Chapter 8

Brlík, V., Pipek, P., Brandis, K., Chernetsov, N., Herrera M., L. G., Kiat, Y., Lanctot, R. B., Marra, P. P., Norris, D. R., Nwaogu, C. J., Quillfeldt, P., Saalfeld, S. T., Stricker, C. A., Thomson, R. L., Zhao, T. and Procházka, P. 2022. The reuse of avian samples: opportunities, pitfalls, and a solution. - Ibis 164: 343–349. https://doi.org/10.1111/ibi.12997

Contribution: Conceptualization (lead), Data curation (equal), Investigation (lead), Project administration (lead), Software (supporting), Writing – original draft (lead) and Writing – review & editing (lead)

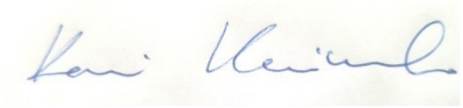
Letter of consent

To the members of the dissertation committee

This is to confirm that Vojtěch Brlík has made a significant contribution to the publications, which I led as the senior author. I concur with the Author's contribution statement.

Sincerely,

Alena Klvaňová, Ph.D.



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Rebecca L. Powell, Ph.D.

Petr Procházka, Ph.D.

Michael B. Wunder, Ph.D.

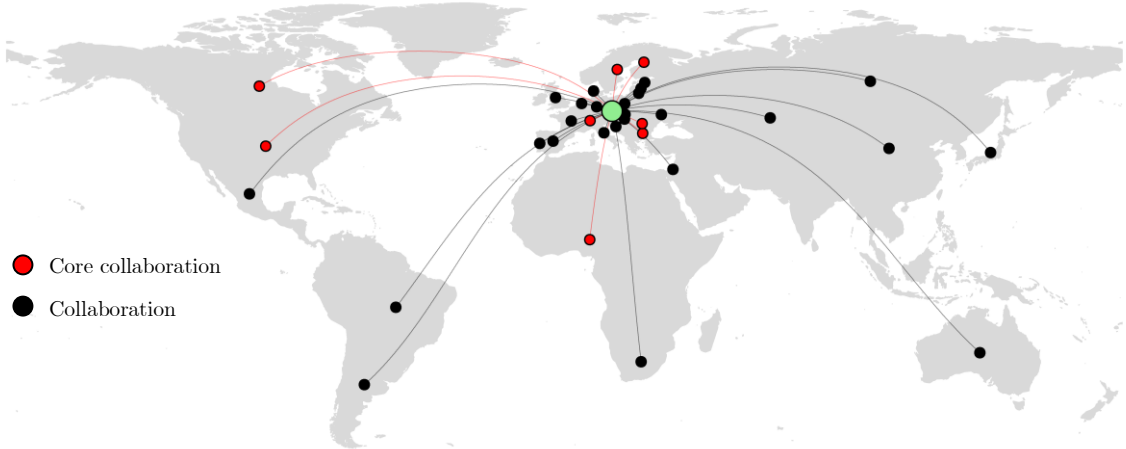
Genesis

This dissertation began to take shape during my graduate program at the Department of Ecology, Charles University. It was during this time that I started to develop ideas about seasonally migrating birds, their interactions with the environment and the implications of these relationships for individual success and demographic parameters throughout the annual cycle.

Initially, my goal was to combine multiple approaches to track the movements of small migratory birds, use remote sensing of the environment, various intrinsic markers, and measures of individual success and demographic parameters. I also aimed to expand my network of collaborators from the field of movement ecology, which I had started to build during my undergraduate thesis on the effects of light-level geolocators.

Unfortunately, the COVID-19 pandemic disrupted my initial project plans. It cut short my six-month stay in Denver, USA, and forced me to alter, postpone, or even cancel many of fieldwork plans. The pandemic had a negative impact on the trajectory of my postgraduate project but it also forced me to adjust plans flexibly, albeit with more time and effort than anticipated. I kindly ask the reader to consider this aspect while reading this thesis.

Due to the global pandemic, this thesis does not include results from multiple projects that involved extensive and exhausting field data collection. Obtaining permits for sampling at 120 locations scattered across Czechia, planning travels to distant locations across Nigeria, and supervising a three-month expedition along the European latitudinal gradient required a significant amount of time. Although these projects yielded valuable experiences and data, their results are absent from this thesis due to pandemic-related delays. Despite the delays and complications, I spent a total of 14 months as an intern outside of Czechia and over 10 months in the field collecting samples from approximately 5000 birds. Finally, this postgraduate project allowed me to establish a strong global network of collaborators, which I hope to continue expanding in my future research endeavors.



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Introduction

Environmental seasonality is a fundamental factor that impacts lives of organisms across the globe and throughout their life cycles[1,2]. These fluctuations often lead to short periods of abundant resources, which are crucial for reproduction, followed by extended periods of resource scarcity, during which organisms primarily focus on survival[2]. Consequently, the seasonal availability of resources forces animals to precisely time transitions between life stages, life cycle events, reproduction, or movements between locations[3].

Animals have adopted two widespread strategies to cope with the environmental fluctuations. The first strategy involves endurance of long periods with low resource availability resulting in year-round residency. In contrast, many animals migrate to avoid periods of resource scarcity[4–6]. Migratory species temporarily leave their breeding sites when environmental conditions become unfavorable, and subsequently, either the same individuals or future generations return when the resources improve in the following years[7]. Seasonal migration is a widespread phenomenon observed across various taxa[5,8–10], including birds. Every year, thousands of species[11] and billions of migratory birds undertake remarkable journeys along flyways[12,13], establishing connections between different ecosystems (Fig 1). Through their migration, birds contribute to the transfer of nutrients, dispersal of organisms and cause seasonal redistribution of species richness, thereby playing a crucial role in shaping ecosystems on a global scale[11,14–16].

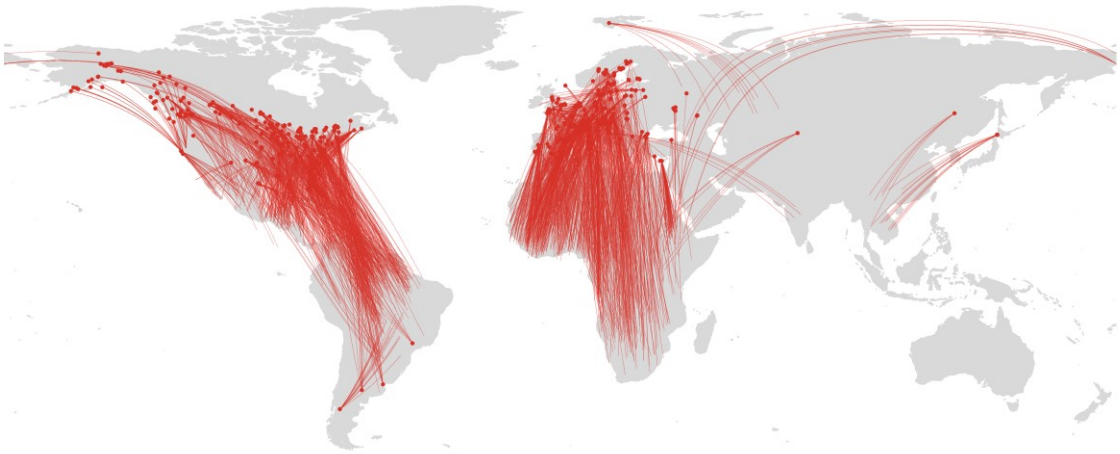

Figure 1. Migratory connections between breeding and non-breeding grounds of over 2700 small migratory birds (Chapter 4).

The extensive journeys of migratory birds[17,18] present them with a multitude of challenges, as their annual cycle events are separated in space and time. These challenges include adverse weather conditions[19], increased risks of predation and parasitism[20], and the potential disruptions caused by human activities[21]. While these challenges may have immediate impacts on animals, they can also carry over to subsequent annual cycle stages[22], causing delayed effects on reproductive performance[23], individual fitness and can translate to population dynamics of migratory birds[24]. The rapid global environmental change, caused by shifts and decreased stability of climatic patterns, further complicates lives of migratory

birds[25] that are essential for maintaining global ecological links but experience widespread and rapid declines[26–31].

To address a **fundamental question in animal ecology of how environmental conditions affect organisms**, it is essential to adopt a full-annual-cycle approach in the study of migratory birds[32]. Despite continuous advancements in tracking technologies, monitoring the movements of small migratory birds across continents still poses significant challenges and the scarcity of information from full annual cycles restricts our ability to understand general patterns of connections between the annual cycle stages and thus **ecological consequences of seasonal bird migration**.

This dissertation aims to contribute to the understanding of the **interactions between small migratory birds and their environment** throughout the annual cycle, with potential **implications for population trajectories** at broad spatial scales. At the individual level, the aim is to investigate the **connections between the annual cycle stages** and to uncover **general patterns across species** and geographic regions. In addition, we place emphasis on **advancing tracing techniques**, **addressing data limitations**, and **suggesting future research directions** arising from our findings.

Avian ecology throughout the annual cycle

Migratory behavior divides the annual cycle of birds into two main stationary periods: breeding and non-breeding and these periods differ in various aspects. During breeding, birds establish territories centered around their nests, while during the non-breeding period, they have much more flexibility in the use of the species-rich non-breeding regions[11,33]. While breeding periods are relatively well-studied, non-breeding periods have received considerably less attention[32,34], despite the fact that most of the long-distance migrants spend significant parts of their annual cycles within their non-breeding ranges (Fig 2). Fortunately, the past decade, described as the golden era of tracking[35], has generated a plethora of novel data on the year-round movement of migratory birds, providing unique insights into how individuals in a range of species manage time and use space throughout the year.

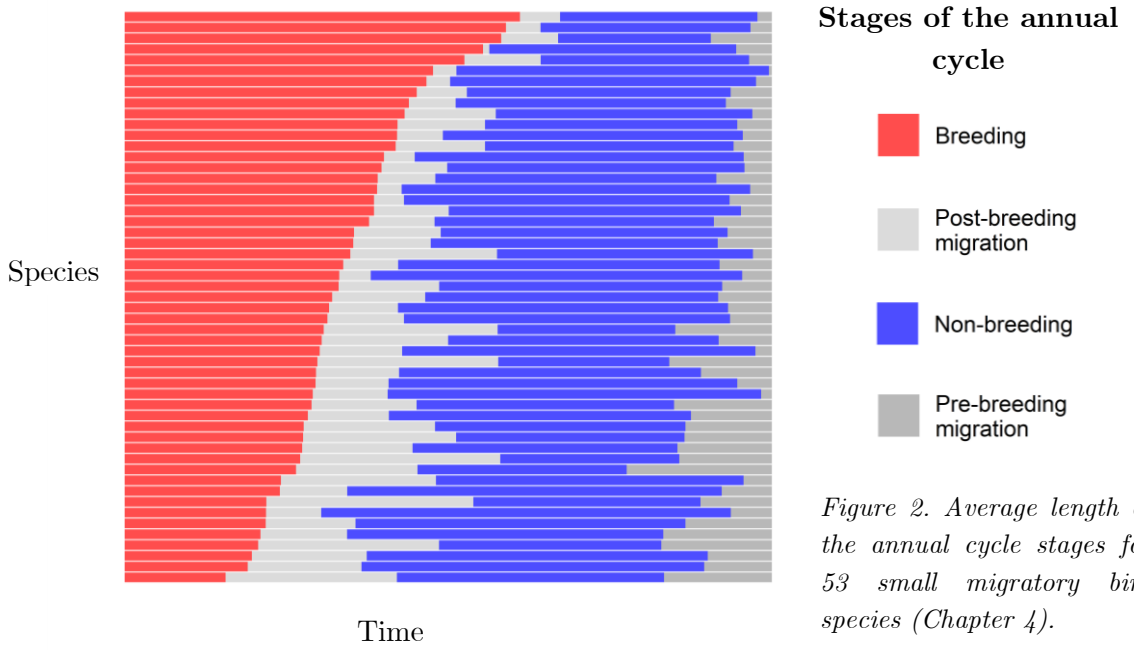

Figure 2. Average length of the annual cycle stages for 53 small migratory bird species (Chapter 4).

Seasonal interactions

Migratory birds encounter various environmental conditions as they travel across continents. Adverse weather conditions[36] or low availability of resources may have detrimental effects on survival[19] that can be detected across seasons[37]. These seasonal interactions have been observed in many long-distance migratory birds[37–39] and were suggested to drive their population dynamics on a continental scale[40], making the comprehensive understanding of these interactions even more crucial in the face of environmental change. Within the Afro-Palearctic migratory system, these seasonal interactions have been frequently linked to the amount of precipitation in the Sahel region[41], located south of the Sahara Desert and hosting many Afro-Palearctic migrants[11]. However, many of the early studies lacked detailed information on individual or population-specific non-breeding grounds[39,41] and thus environmental conditions, preventing precise estimates of the strength of these interactions between the environment and populations.

To this end, we integrated detailed population-specific tracking data with weather conditions to explain the extensive variation in apparent survival observed over 19 years in a northern European population of a small shorebird, the Little Ringed Plover (*Charadrius dubius*)[42]. We revealed that most of the tracked individuals followed the Indo-European migratory flyway, previously reported in only one individual tracked from Sweden[43], to their final non-breeding sites in India. We showed that 47% of between-year variation in apparent survival was explained by the amount of precipitation in the staging region during post-breeding migration located along the Indus River, indicating the migratory period as a bottleneck for this migratory population. Climatic models suggest increase in the amount of precipitation in this region[44] and the survival of long-distance migrants like the Little Ringed Plover could be thus positively affected in the future. However, climatic changes are usually associated with increased between-year variation that could lead to increased survival fluctuation, with negative impacts on population growth rates and ultimately result in population decline[45]. In this study, we demonstrated the importance of staging regions within the annual cycle as a population bottleneck in a migratory bird and also showed the potential of multi-source data integration. We believe such an approach is the key to identify where, when and how are populations limited, to forecast future changes, and for efficient evidence-based conservation (Chapter 1).

On a continental scale, some species exhibit significant variation in migratory patterns between populations[46–48]. Populations with distinct migratory patterns can overlap in migratory divide zones, which often occur when populations recolonize distribution ranges from glacial refugia, particularly in Central Europe[49]. The Eurasian Reed Warbler (*Acrocephalus scirpaceus*), a small migratory passerine, is an example of such a species with a migratory divide, and its migratory pattern was recently described using light-level geolocators[50]. Not only do these populations differ in their initial migration direction and routes, but the tracking data also suggested a large-scale spatial segregation within their non-breeding range in Africa. Based on these findings, we developed an isotopic marker using a novel stable sulfur isotopic map for sub-Saharan Africa (see *Stable isotopes in movement ecology*) allowing us to identify individual's non-breeding region. Migratory phenotypes of Eurasian Reed Warblers indeed segregated into non-overlapping regions within sub-Saharan Africa and these regions exhibited notable differences in climatic stability, which likely contributed to the long-term population changes observed in Europe. While further investigation is needed, this study provides one of the few examples that the relationship between migratory behavior and environmental conditions may affect population changes on a continental scale (Chapter 2)[51].

In conclusion, our results demonstrate the vital role of tracking and tracing in understanding the seasonal interactions between bird populations and environmental conditions throughout their annual cycle. It also emphasizes that these seasonal interactions can have a significant impact on populations, even during staging periods, and can affect populations on a continental scale.

Carry-over effects

Twenty-five years ago, it has been discovered that the environmental conditions in non-breeding grounds have local effects, and can carry over in time to influence the arrival of individual migrants at breeding sites[52]. This pivotal study highlighted the non-lethal nature of these seasonal interactions at an individual level, and subsequent research over the past two decades has further emphasized the significance of these seasonal links, known as carry-over effects, mainly between non-breeding and breeding periods in understanding the individual variation in breeding performance of migratory species[22,53].

Recent advances in direct tracking of migration have provided means to trace and uncover the intricate nature of seasonal interconnections within the complete annual cycle of migratory birds. Early studies examining the full annual cycle have suggested a strong domino effect[54] between consecutive events, particularly during migratory periods, while prolonged stationary non-breeding periods were shown to prevent the accumulation of carry-over effects within the annual cycle[55–59].

To deepen our understanding of these carry-over effects throughout the annual cycle, we focused on the Great Reed Warbler (*Acrocephalus arundinaceus*). This passerine species serves as a model for investigating movement ecology within the Afro-Palearctic migratory system, providing valuable insights into aspects such as intra-tropical migration[60], prolonged high-altitude flights over the Sahara Desert[61,62], or extensive spread within the non-breeding range[63]. By using individual tracking data from a significant proportion of its breeding range, our primary objective was to examine the time dependencies between consecutive annual cycle events, such as arrivals and departures. Although timing itself does not directly reflect individual success, it serves as a reasonable proxy for fitness components and can be measured remotely throughout the annual cycle.

In our study, we not only confirmed the domino effect between consecutive events and the buffering capacity of prolonged stationary non-breeding periods, but we also discovered that northern population exhibit weaker links between events compared to southern populations. This difference likely arises from the longer migratory routes undertaken by the northern population, increasing their exposure to unfavorable weather conditions[36] and reducing the influence of preceding events. In contrast to many previous studies, we did not find strong relationships between the environmental conditions of the non-breeding sites and pre-breeding migration, despite incorporating various metrics using NDVI (Normalized Difference Vegetation Index)[64,65] and stable carbon isotopes as remote proxies for environmental conditions at their non-breeding sites (Chapter 3).

In conclusion, these findings, along with a brief review of the literature, demonstrated significant variation in the strength of time dependencies and carry-over effects among populations. Additionally, there is some degree of variation observed between species, sexes[66], study years, and the metrics used to measure the strength of these connections between stages of the annual cycle. Collectively, drawing generalized conclusions about time dependencies within the annual cycle and their implications for individual success and population dynamics is challenging.

The ecological importance but inherent variability of time dependencies formed the basis for a global initiative with the aim to consolidate tracking data to uncover general patterns of time dependencies in small migratory birds. Within an extensive network of movement ecologists, we have built a global tracking database from over 2700 individuals, 130 sites, and 62 species, spanning three major migratory flyways (Fig 1-3). Our findings indicate that, across species and migratory flyways, stages of the annual cycle are tightly connected during migration but these temporal links weaken during prolonged stationary non-breeding periods. The non-breeding period thus prevents the accumulation of carry-over effects between migratory and breeding periods. Importantly, we have also observed that individuals can compensate for their delayed departures by shortening their migratory periods. This pattern, previously reported in only a few species[67,68], has now been found to be consistent across species and flyways.

The results of this collaborative research effort have provided the first temporal patterns within the annual cycle that appear to be applicable across populations, species, and flyways. They offer insights into the links between seasons, with implications for individual variation in breeding performance, and further advocate for the importance of comprehensive full-annual-cycle approaches[32,69] in understanding the ecology of migratory birds and provide a basis for further investigation using this largest database of tracking data from small migratory birds (Chapter 4).

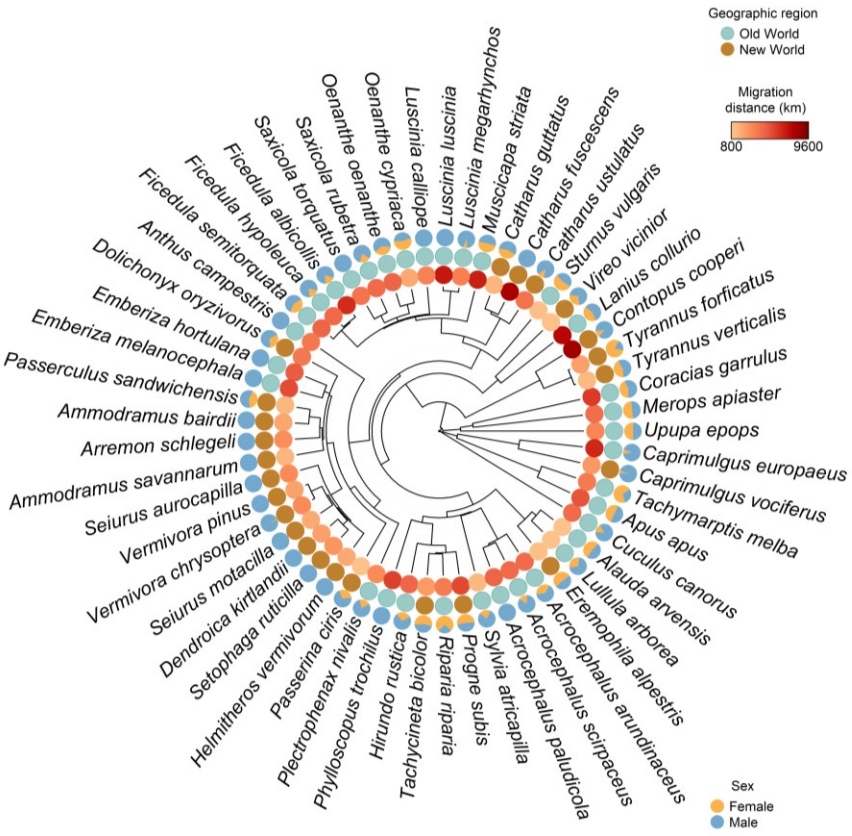

Figure 3. Phylogenetic relationships between 53 species represented in the analysis of time dependencies along with average migration distance, geographic region, and sex ratio (Chapter 4).

Seasonal changes in niche positions

Widespread declines of many migratory birds[26–30] had led to large-scale efforts to track migration routes in order to understand how species will respond to ongoing environmental change[70]. One of the key results to arise from the tracking of migration is that many species show substantial individual variation in migratory routes[71], suggesting that migratory birds may be somewhat resilient to anthropogenic-induced changes in the environment that occur at specific locations in their annual cycle. However, tracking technologies rarely provide more detailed information on the niche used by individuals at different stages of the year. Similar to tracking geographic space use across the annual cycle, information on how individual migratory birds use niches would be valuable for understanding the capability of migratory birds to respond to factors, such as climate change and habitat loss, that could influence their long-term abundance.

To explore the seasonal changes in niche positions between the breeding and non-breeding seasons, we employed isotopic niche[72] using the isotopic compositions of two tissues sampled from individual migratory birds. Stable isotopic compositions in tissues can provide insights into both environmental conditions and dietary patterns during the time of tissue formation[73]. Stable carbon isotopes (δ^{13}C) are typically used to indicate habitat use along a dry-wet gradient[74,75], while stable nitrogen isotopes (δ^{15}N) are employed to infer trophic positions[76,77]. The selection of tissues and timing of sampling were carefully designed to ensure that blood plasma samples originated from the breeding grounds[78], while claw tips were formed at stationary non-breeding grounds[79,80]. By examining changes in individual niche positions across seasons, we demonstrated a substantial variation on the individual level.

The substantial individual variation in the niche differences across seasons suggests that some migratory birds may be resilient to the environmental change. Furthermore, we found significant individual variation across all studied species, despite their diverse habitat preferences (from open to dense vegetation), foraging strategies (from insectivory to frugivory using gleaning, snatching or flycatching), and non-breeding ranges, indicating a wide range of individual strategies, including both niche tracking and switching[81]. These findings imply that migratory species may have the capacity to mitigate the adverse impacts of environmental change through individual variation.

Although our findings highlight the potential capacity of migratory species for flexible adaptation, further research is needed to investigate the plasticity and geographic patterns of individual strategies across populations and migratory flyways, as well as the heritability and broader ecological and evolutionary implications of individual changes in niche positions across seasons (Chapter 5).

Stable isotopes in movement ecology

Stable isotopes are ubiquitous and are integrated into ecosystem components through food webs[73]. Environmental isotopic compositions can vary between habitats, indicate trophic positions or geographic origin of animal tissues, and their analysis have thus emerged as a valuable tool in ecology[82].

Geographic variations in isotopic compositions of animal tissues are influenced by various biogeochemical processes. These variations create geographic distribution patterns and their predictions, so called 'isoscapes', have proven to be highly valuable in movement ecology and can be used to study altitudinal migration, quantify migratory connectivity, or trace geographic origins used to inform demographic models and guide conservation efforts[46].

Currently, continental or global isoscapes are available for hydrogen (δ^{2}H), carbon (δ^{13}C), nitrogen (δ^{15}N), oxygen (δ^{18}O), and strontium isotopes ($^{87}Sr/^{86}Sr$)[82–84]. However, they are mostly applied in regions with distinct isotopic gradients or areas with unique isotopic signatures. Some isoscapes exhibit systematic spatial patterns, while others show weaker spatial structures. Improving the precision of geographic assignments can be achieved through optimized sampling strategies[85] or by combining predictions from multiple isoscapes with different spatial structures[86,87]. Developing novel isotopic maps thus remains vital for advancing the stable isotope ecology with significant implications in animal ecology, wildlife conservation and forensics.

Sulfur isotopes (δ^{34}S) are less explored isotopic marker but have the potential to contribute to the development of regional and continental isoscapes. Sulfur is widely present in animal diets[88–90], and its isotopic compositions can be influenced by various factors such as marine aerosol transport[91,92], air concentrations of combustion gases[93], and bedrock geochemistry[94]. Sulfur isotopes also show negligible discrimination, isotopic offset between organisms in a food web[88–90,95], that allows a single δ^{34}S isoscape to be applied to a wide range of taxa.

Previous attempts to map the geographic distribution of δ^{34}S on a continental scale have shown promising results[96,97]. In the contiguous USA, the δ^{34}S isoscape exhibited a spatial pattern similar to that of δ^{2}H, indicating the influence of coastal-to-inland transport of marine aerosols on δ^{34}S distribution[96]. The coastal-inland pattern was also observed within Europe, using archaeological and historical samples collected in terrestrial environments[97]. However, our European δ^{34}S isoscape modelled from samples collected in wetland habitats showed less distinct gradient, likely due to the complex redox state of wetland soils. In contrast, our δ^{34}S isoscape for sub-Saharan Africa displayed a large-scale gradient mainly driven by the distance to the coastline, creating isotopically distinct regions between longitudinal zones, lacking in the previously available isoscapes in this region[82,83]. The first application of the sub-Saharan δ^{34}S isoscape to trace non-breeding origins of the migratory Eurasian Reed Warbler provided evidence for large-scale spatial segregation of populations within their non-breeding grounds, with distinct climatic conditions that likely translate into large-scale population trends detected in their breeding grounds (Chapter 2).

In summary, both the African and European δ^{34}S isoscapes demonstrate the potential of stable sulfur isotopes as a valuable tool for tracing geographic origins of tissues and animals. These isoscapes thus expand the existing isotopic toolbox and could be widely applied in ecology, conservation biology, and forensics. In particular, the multi-species geographic tracing tool will be highly beneficial in sub-Saharan Africa, a biodiversity hotspot that hosts not only resident and migratory birds but also a wide range of other animals[98]. This region currently faces threats stemming from a rapidly growing human population, resulting in changes in land use[99,100] and a rise in wildlife trafficking[101]. The newly derived δ^{34}S isoscape could be employed to identify regions with species congregations, and thus counter wildlife trafficking, or in ecological studies to trace space use of animals (Chapters 2 and 6).

Finally, it is worth highlighting the potential of stable isotope analysis[102,103]. This cost-effective method allows tracing many individuals from many populations and many species. It also provides an opportunity for retrospective investigations using extensive sample collections[104] (described in *Big data in animal ecology*). Moreover, the multi-tissue approach allows us to infer environmental conditions across multiple annual cycle periods, offering valuable insights into individual strategies in seasonal niche use that might potentially mitigate the negative impacts of environmental change on birds[105] (see *Avian ecology throughout the annual cycle*).

Big data in animal ecology

Data are the backbone of ecology, playing a crucial role in examining hypotheses, uncovering connections among components of ecosystems, and validating deterministic theoretical models. To uncover both generalities and exceptions in taxonomic, geographic and temporal patterns, it is essential to use data that cover such variations[106]. However, this may pose significant challenges in animal ecology.

Population changes

Datasets that track long term population changes across species and distribution ranges are crucial to capture mechanisms behind recent biodiversity loss and to enable precise targeting of conservation actions[107,108]. However, collecting long-term and large-scale information on population changes across many species is challenging for various reasons. In particular, there are limited financial resources to support such efforts and limited human resources with adequate skills and training in the identification of species and systematic data collection[109] but broad interest in birds worldwide showed potential to overcome some of these challenges[110]. Amateur birdwatchers are often well-trained in bird identification and many of them are willing to participate in community and citizen science[111] projects aiming to better understand diverse natural processes[109,112–114].

The Pan-European Common Bird Monitoring Scheme (PECBMS)[115] currently uses data from 28 national bird monitoring schemes in Europe to annually produce a continental dataset on relative changes in breeding bird population sizes of 170 species[115–117]. These data have manifold applications and have been used for the evaluation of conservation efforts[118], investigation of various research questions[119–128], and for manifold policy purposes. We made this dataset publicly available along with the comprehensive description of the methodology, with a brief overview of the past applications and suggested future prospects. The PECBMS dataset now also contains country-level estimates of population changes that may be crucial for applications on finer scale and may further enhance the potential of this long-term and large-scale dataset in research, conservation and policy (Chapter 7).

Tracking of individuals

Individuals form the base of the ecological hierarchy. The knowledge of their occurrence in space and time, relationships with the environment, and their implications for individual success is essential for understanding the complex system of links between breeding and non-breeding areas. By tracking individuals, we can establish foundations for studying these complex links[129,130] but to comprehend general movement patterns across space and time, it is imperative to integrate movement data within a global community of movement ecologists[131,132]. Only this approach will let us answer fundamental questions of how the environment and its seasonality influence animals – where, when, and how.

MoveBank database already provides deep insight into lives of thousands of tracked individuals and set basis for a wide network of researchers collecting this type of data[70,133]. Importantly, this network of (near)real-time observations about occurrence of individuals have already demonstrated tremendous implications far beyond the field of movement

ecology – spanning environment awareness to early warning systems for natural disasters[129,130].

However, when it comes to tracking small animals, especially highly mobile small migratory birds, the available technology is limited to miniaturized tags[134] that store the information on board without the capability to transmit the data to a receiver[135]. Consequently, researchers often receive tracking data with a delay, typically after recapturing the tracked animal and the raw data usually require preprocessing to reconstruct migratory routes and schedules[136]. Currently, the primary tracking methods for following the movements of small individuals during their intercontinental migrations are light-level geolocators and GPS tags[35,137,138]. We thus targeted the community of researchers using these tags and aimed to integrate findings they collated over the past 15 years since the technological advancements enabled the tracking of small migrants (body mass <100 g)[135]. We would like to emphasize the inclusive aspect of this project and the natural need to credit contributing researchers. Only in this inclusive way, we can advance discoveries and long-term projects essential for uncovering more about the hidden world of movement ecology of small migratory birds, connecting continents and ecosystems. Our community-wide network now connects over 100 movement ecologists who have collected tracking information from over 2700 individuals at 130 sites from 62 species of small migratory birds across four migratory flyways (Fig 1-3). The overarching objective of this network is to uncover the general cross-species patterns in movement ecology of small migratory birds (Chapter 4).

Animal tissue samples

Millions of avian tissue samples have already been collected for various scientific projects worldwide. However, these samples have a potential to answer a wide range of questions[139] if they could be located, made available and reused for other purposes. Extensive reuse of such samples could yield large datasets, and facilitate interdisciplinary collaborations bringing new ideas[140]. Besides, the reuse of already collected samples could save financial and human resources needed for sampling, help overcome geographic sampling bias[34], bridge researchers from underrepresented groups and regions, or help studies on endangered species with ethical limitations preventing novel sample collections.

As an example, the samples of known spatiotemporal origin can be used for modelling of isotopic maps that have immense implications for ecology, conservation and forensics (see *Stable isotopes in movement ecology*). The δ^{34}S isotopic maps for sub-Saharan Africa and Europe, presented in this dissertation, were partly modelled from feather samples that were initially collected with a different purpose[141] and only reused for the development of isotopic maps (Chapters 2 and 6). Alternatively, the large sample collections could be used retrospectively[104,142] to trace environmental space use between seasons and unveil the mechanism behind this process. However, despite a growing number of data repositories[143] and their benefits[144], looking for samples of interest is challenging. A lack of search tools specifying sample details and enormous number of published papers[145] largely limited such efforts until very recently, not to speak of samples from unpublished projects. Consequently, the absence of a searchable sample metadata repository hampers effective searches for the already collected samples and significantly restricts their broad scale reuse.

Therefore, we introduced the first metadata repository – AviSample Network (https://avisample.net/) – that is publicly available and designed for storing basic sample metadata from a wide range of research fields. The main aims are to store and advertise information about collected bird tissues, and to help researchers find and contact owners of relevant samples. The database now contains metadata on over 33 000 samples, from over 400 species, from all continents with first samples dating back to 1847. This metadata collection promises to facilitate global connections between researchers, increase interdisciplinarity[140] and hopefully, inspire sample reuse across research fields and disciplines (Chapter 8).

Conclusion

Environmental conditions impact all animals and in migratory birds, these effects may transfer across stages of the annual cycle that are separated in space and time. Our research findings contribute to the understanding that not only environmental conditions during stationary non-breeding periods but also staging periods during migration can act as bottlenecks for migratory populations. Moreover, we demonstrated that variation in environment–animal interactions among populations may contribute to the observed differences in population trends on a continental scale.

Stages of the annual cycle in migratory birds are connected, particularly during migratory periods. However, these connections weaken during prolonged non-breeding periods, limiting the carry-over effects between migratory periods and consecutive breeding seasons. While the strength of these connections may vary among some populations or species, we demonstrate that the overall pattern of interconnections between the annual cycle stages is consistent across species and migratory flyways. These results have important implications for understanding sources of variation in individual success, will allow to predict impacts of environmental change, and further advocate full-annual-cycle approach to study ecology of migratory birds.

The newly developed stable sulfur isotopic map for sub-Saharan Africa expands the isotopic toolbox in the region and promises more precise geographic assignments using stable isotopes in this biodiversity-rich region currently facing numerous threats such as climate change, change in land use, and wildlife trafficking.

Finally, integration of long-term population data with tracking information enables a more comprehensive understanding of the connections between seasons and environment–animal interactions throughout the annual cycle. The continuous expansion and maintenance of these databases will solidify their status as invaluable references for comprehending the temporal dynamics of environmental–animal interactions and targeting conservation efforts.

Future directions

In research, it is common for new discoveries to raise numerous questions and open new avenues for further investigation. Here, I outline several future directions that I believe could provide valuable insights with ecological implications that would be of interest to a broader research community.

General patterns of migration in small birds

Through our research, we have discovered links between events of the annual cycle of small migratory species using a novel world-wide movement database (Chapter 4). We will continuously expand this unique database and further collate information on individual success within a community-wide network of movement ecologists. This database will help us understand the use of environmental space throughout the annual cycle, pinpoint drivers of timing, and identify how these components affect individual success essential to understand the complex of ecological links between the environment and migratory birds.

Seasonal changes in niche positions

Our research has demonstrated significant individual variation in seasonal changes of isotopic niche positions, consistent across species (Chapter 5). Although our findings highlight the potential capacity of migratory species for flexible adaptations, further research is needed to explore the individual plasticity of this trait, geographic patterns among populations and flyways, heritability of these strategies, and, most importantly, the eco-evolutionary implications of individual changes in niche positions between seasons.

Sulfur isotopic maps

The newly developed δ^{34}S isotopic map for sub-Saharan Africa has the potential to serve as an effective tracing technique (Chapter 6). This map could be used in conservation to identify regions where individuals and species congregate or where threatened species occur[82,146]. It could also be applied in ecology to track the origins of birds and insects, as well as in ecological forensics in this perishing biodiversity hotspot. As an extension of this study, we intend to create a δ^{34}S isotopic map for the entire African continent using plant tissues. This extension would greatly enhance the applications of this tool in the species-rich, under-explored but over-exploited part of the world.

Enhancing the isotopic niche

The concept of ecological niche, which refers to the conditions necessary for a species to exist, is challenging to measure in natural environments, especially for highly mobile migratory birds throughout the annual cycle[147]. While the natural isotopic composition of tissues is used to reflect both environmental conditions and dietary habits of individuals[72], the links with environmental variables that affect body condition and fitness of terrestrial animals are not very well understood. In the future, we aim to investigate these relationships by examining tissues from both temperate and tropical regions, and multiple species formed in known and diverse environmental conditions, with an objective to improve the interpretation of isotopic signatures in animal tissues.

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