

Multi-Scale Radar Demonstration of Coastal Light Pollution Effects on Bird Migration

Dissertation

zur

**Erlangung der naturwissenschaftlichen Doktorwürde
(Dr. sc. nat.)**

vorgelegt der

Mathematisch-naturwissenschaftlichen Fakultät

der

Universität Zürich

von

Simon Jonathan Hirschhofer

von

Schlossrued (AG)

Promotionskommission

Prof. Dr. Robert Weibel (Vorsitz und Leitung)

Dr. Baptiste Schmid (Leitung der Dissertation)

Dr. Peter Ranacher

Prof. Dr. Barbara Helm

Prof. Dr. Patrick Laube

Zürich, 2026

Abstract

Migratory birds undertake some of the most demanding journeys in the animal kingdom. Each year, billions of individuals travel across continents and hostile ecological barriers, guided by an interplay of endogenous rhythms, environmental cues and landscape features. These movements connect ecosystems at a hemispheric scale and provide important ecological services. In a world increasingly shaped by humans, migration has become a riskier endeavour. Habitat degradation and fragmentation pose major threats to biodiversity. Artificial light at night has emerged as a global pollutant that alters the nocturnal environment and disrupts the orientation of nocturnal migrants. Artificial illumination can divert broad-front migration, reduce navigational accuracy and increase collision risk with illuminated infrastructure. Sublethal effects from confusion and diversion may accumulate and influence population dynamics. Despite growing research interest, important questions remain unresolved, particularly with respect to low illumination levels and geographic context. Little is known about how dim, patchy light affects migrants that have just crossed an ecological barrier with little or no artificial light. This situation characterises parts of southern Europe where birds arriving from crossing the Mediterranean Sea approach the coast. This dissertation investigates the effect of relatively dim artificial light at night in the coastal landscape of the Croatian Adriatic.

The work combines data from BirdScan MR1 ornithological radar and C-band weather surveillance radar across two regions, Istria and Dalmatia. This dual-system approach captures behaviour from the scale of individual targets to the distribution of aerial biomass across the wider landscape. The dissertation comprises three studies that together describe the spatiotemporal structure of migration, quantify fine-scale behavioural responses to dim illumination under different atmospheric conditions and evaluate the impact of coastal illumination on the regional distribution of migrants.

The first study establishes an ecological framework by describing the nocturnal migration of spring migrants along the eastern Adriatic coast. Migrants follow two main directional gradients. One group crosses the Adriatic from Italy, arriving from the southwest. A second group follows the coastline from the southeast. These routes exhibit distinct patterns that vary through the season and within nights. In early spring, the flow of birds arriving from the sea dominates, whereas coastal movement intensifies in April, producing a clear bimodality of directions within the same night. Although both groups initiate flight soon after sunset, migrants crossing the sea reach the radar sites two to three hours later than coastal migrants. Based on existing literature, it can be inferred that coastal migrants rely on different navigational cues than sea-crossing migrants and are thus affected differently by light pollution. Consequently, the co-occurrence of these two migratory routes, coupled with their partial temporal separation, creates a unique opportunity for a real-life experiment.

The second study used a pair of BirdScan MR1 ornithological radars in the small city of Rovinj and the nearby Palud Ornithological Reserve to quantify behavioural reactions to light on a local scale. The contrast between the dimly illuminated town and the relatively dark rural site enabled subtle responses to be detected at illumination levels far below those considered in previous studies. Distinguishing between the two directional groups revealed that sea-crossing migrants were consistently more affected by artificial light. At the illuminated site, they flew at lower airspeeds and at lower flight altitudes than at the dark site, suggesting confusion and vertical attraction. These effects were amplified by cloud cover, especially the

reduction in flight altitudes. Coastal migrants showed weaker but similar signs of disorientation. Although a spatial redistribution of birds could be inferred, light did not significantly alter overall migration intensity. These results suggest that even dim illumination can influence the behaviour of sea-crossing migrants, particularly in visually challenging conditions.

The third study uses weather surveillance radar in northern Dalmatia to evaluate the spatial redistribution of broad-front migration on a regional scale. The radar is positioned between the city of Zadar and the darker landscape of the Vransko Lake Nature Park. On nights dominated by sea-crossing migration, bird densities were consistently higher above an illuminated urban area than above a darker area. The difference reached thirty per cent, indicating substantial redistribution. Two periods of stronger attraction emerged. The first occurred early in the night, when many birds had likely departed from small offshore islands and were sensitive to visual cues during post-departure reorientation. The second period occurred several hours after sunset, aligning with the arrival of birds that had completed the crossing from Italy. These results provide robust evidence that moderate coastal illumination shapes the spatial organisation of avian migrants on a regional scale.

Together, the three studies demonstrate that artificial illumination influences migratory behaviour across spatial and temporal scales. Even dim coastal illumination can trigger measurable responses, ranging from reduced airspeeds and critically lowered flight altitudes to large-scale redistribution towards illuminated areas. Cloud cover intensifies these reactions locally. Coasts that receive frequent sea-crossing migrants appear to be especially sensitive, because the abrupt shift from a dark seascape to an illuminated coastline introduces an additional sensory stressor. Offshore archipelagos may further increase this risk, as reorientation during departure could enhance attraction to light.

Beyond its scientific contribution, this dissertation demonstrates that artificial illumination can be problematic even at relatively low brightness levels. Because the cumulative sublethal effects of disorientation and diversion caused by artificial illumination remain unclear, as does the link between spatial redistribution, lower flight altitudes, and collision mortality, this dissertation supports avoiding artificial illumination wherever and whenever possible. In other words, we should recognise that any reaction by sensitive animals to an artificial sensory stimulus could be harmful, effectively turning artificial illumination into light pollution. Unlike other anthropogenic ecological crises, light pollution is ridiculously easy to deal with. There are straightforward, practical guidelines on how to mitigate light pollution. It is up to all of us to implement them.

Acknowledgements

I was fortunate to be co-supervised by two institutions: the Department of Geography at the University of Zurich, which provided the educational foundation for my PhD and a phenomenal workspace, as well as valuable methodological and academic support and a fabulous collegial environment. My PhD was also hosted by the Bird Migration Unit of the Swiss Ornithological Institute, where my four-year research project was embedded in the “Migration in an illuminated world” project. The Swiss Ornithological Institute also provided the four BirdScan MR1 ornithological radar devices that were fundamental to this work. Most importantly, they provided great advice regarding the ecological background of the work and the meaningful interpretation of the results. They also set up contacts with many different researchers and field assistants who were crucial for conducting the fieldwork. Pursuing a PhD has not only been an intellectual challenge, but also a great opportunity for personal and interpersonal development. Looking back, I can hardly believe the progress I have made. This would not have been possible without the support of the many wonderful people I have met on this journey, with whom I have shared memories and experiences through fieldwork, after-conference dinners, meetings, excursions, retreats, seminars, and over uncountable cups of coffee. I would like to extend special thanks to some of them...

Thank you, *Baptiste Schmid*, for the countless hours spent brainstorming ideas, conceptualising research, improving analyses and manuscripts, interpreting and learning from complex results, and maintaining a positive atmosphere during coffee breaks, nature walks and replacing flat tyres. You have been an inspiring and supportive supervisor, and I am grateful to have learned so much from your expertise in radar and quantitative bird migration research, as well as in life in general.

Peter Ranacher, thank you for your constant support in improving the language of my writing and identifying the common thread. You have always listened to my struggles and been an immensely good advisor and colleague. I especially value your time during the last year of this journey, when your working obligations changed, and Mathilda opened a new chapter in your life.

I would like to thank *Robert Weibel* for being my mentor ever since I took my first Geographic Information Science course, GEO 113, all the way back in my first semester as a bachelor's student. You have provided me with the best possible working environment. Not only have you dealt with all my autistic flaws, but you have also helped me to overcome some of them. Over the years, I have been impressed by your dedication to your students and by how you balanced professionalism with humanity.

Barbara Helm, thank you for accepting me as a new PhD student so quickly, especially since you were preparing for your new position as head of the bird migration research unit. I have especially enjoyed your positive and inclusive personality. I'll never forget how joyfully you celebrated the first results of this research or how enthusiastically you introduced me to your favourite bird when we observed the European stonechat family we discovered in Aber Falls.

Thank you, *Patrick Laube*, for agreeing to be an external member of my PhD committee and for being a mentor when I needed one.

Thank you, *Ross Purves*, for welcoming me into your group after Röbi's official retirement, and for your dedication as a thoughtful, empathetic and committed Head of the Graduate School, and later of the Department of Geography.

Many thanks to *Sanja Barišić, Maja Bjelić-Laušić, Davor Ćiković* and *Louie Taylor* for their local expertise in identifying suitable locations for the BirdScan MR1 radars, interpreting the results in the context of Croatian ornithology and assisting with the installation and maintenance of the radars.

Special thanks go to *Dieter Peter* and *Thomas Steuri* for their technical expertise with the radars and for helping to transport and install them. Special thanks go to Thomas Steuri for repairing the radars out of season and for his consistently prompt response and willingness to carry out repairs in the field. This would not have been possible without your dedication.

Thank you to *Felix Liechti* for sparking my fascination with radar-based ornithology.

I would like to thank the *Rogić, Taylor* and *Mofardin* families, as well as *OTP Bank* and the *staff of the Vransko Lake Nature Reserve*, for generously allowing us to operate radars on their properties.

Thanks go to my friends and colleagues at GIUZ and the university in general: Alexandra, Annina, Annika, Armand, Bingjie, Carlotta, Changyu, Cheng, Christiane, Corrado, Daniela, Dario, Diego, Donatella, Franziska, Guojian, Hoda, Inhye, Ismene, Jasmin, Jason, Jingi, Karin, Katia, Khaoula, Lara, Leonie, Louis, Marcel, Mina, Nouri, Qi, Roya, Sarah, Sergio, Takuya, Tiia, Tumasch, Zhiyong. It has been a pleasure to work with such enthusiastic, creative, empathetic, inclusive and diverse people. I will really miss you.

I would also like to thank my colleagues from the Migration Unit at the Swiss Ornithological Institute: *Birgen, Crinan, Elli, Janine, Joanna, Martins, Neringa, Pablo, Raphaël, and Yann*.

I would like to thank my family and friends for their fundamental and compassionate support throughout. I am grateful for their constant reminders to take time off work, and for their inspiration, motivation and laughter in the face of the sometimes chaotic nature of academic work. Special thanks go to *Elisabeth, Lukas, Salina, Marianna, Markus, Tobias, Alexandra, Eva, Maximilian, and Bart*. Special thanks also go to my dad, *Josef*, who sadly cannot read this anymore, for igniting and nurturing my fascination with all living things and nature, for always encouraging me, and for always making sure I knew you were proud of me and what I was doing. I wish I could share this milestone with you. Finally, *Bettina*, thank you for all your love, encouragement, motivation, empathy and support throughout all of this.

Table of contents

Abstract.....	2
Acknowledgements	4
1 Introduction	8
1.1 Motivation	8
1.1.1 The importance of birds	8
1.1.2 Birds under threat	8
1.2 Bird migration.....	9
1.2.1 The evolution of bird migration	9
1.2.2 Phenology	12
1.2.3 Navigation and orientation	16
1.3 Artificial light at night (ALAN) and light pollution	17
1.4 Tools for quantifying bird movement	20
1.4.1 Ringing	20
1.4.2 Biologging technologies.....	20
1.4.3 Radar.....	21
1.5 Research plan and study design.....	29
1.5.1 Project aim	29
1.5.2 Study area and radar monitoring	30
1.5.3 Research questions.....	38
1.5.4 Overarching research aim and structure of this thesis	40
2 Avian spring migration at the east Adriatic coast: coastal and sea-crossing dynamics of intensity, timing, and flight directions.....	41
2.1 Abstract.....	42
2.2 Introduction	43
2.3 Methods	46
2.3.1 Study area	46
2.3.2 Radar monitoring.....	47
2.3.3 Conceptualisation of nightly migration intensity profiles	48
2.3.4 Clustering intensity profiles	49
2.4 Results	50
2.4.1 Migration intensity	50
2.4.2 Flight directions.....	51
2.4.3 FPCA and clustering	52
2.5 Discussion.....	55
2.5.1 Migration intensity and flight directions in comparison	55
2.5.2 Nightly timing of migration	56
2.5.3 Limitations of the study	57
2.6 Conclusion	57
3 When nocturnally migrating birds encounter low-level light pollution patches: a case study from the Croatian coast	59
3.1 Abstract.....	59
3.2 Introduction	60
3.3 Methods	62
3.3.1 Study region and radar monitoring	62
3.3.2 Distinguishing between sea-crossing and coastal migration.....	64
3.3.3 Atmospheric data	64
3.3.4 Light pollution data.....	64

3.3.5 Modelling intensity and behaviour	65
3.4 Results	66
3.4.1 Effect of light pollution on mean nightly migration intensity (MTR)	66
3.4.2 Effect of light pollution on mean nightly airspeed	67
3.4.3 Effect of light pollution on mean nightly flight altitude	67
3.5 Discussion	68
3.5.1 The effect of light pollution on migration intensity (MTR) and flight behaviour	68
3.5.2 Conservation implications	70
3.6 Conclusion	71
4 Redistribution of sea-crossing bird migration in response to coastal artificial illumination.....	72
4.1 Abstract.....	72
4.2 Introduction	73
4.3 Methods	74
4.3.1 Study area and data.....	74
4.3.2 Weather radar data processing	75
4.3.3 Weather radar sampling areas	76
4.3.4 Filtering for sea-crossing nights.....	77
4.3.5 Weather radar bird density time series	77
4.3.6 Modelling bird densities	78
4.4 Results	78
4.5 Discussion	79
4.5.1 Discussion of the results	79
4.5.2 Limitations of this study	82
4.6 Conclusion	83
5 Synthesis.....	84
5.1 Conclusion	84
5.1.1 Answering the research questions	85
5.1.2 Methodological implications and limitations	92
5.1.3 ALAN vs. light pollution	94
5.1.4 Consequences for conservation	95
5.2 Outlook.....	97
Bibliography.....	102
Appendix A: Correction to Hirschhofer et al. (2025), “Avian spring migration at the east Adriatic coast: coastal and sea crossing dynamics of intensity, timing, and flight directions”.....	130
Appendix B: Supporting Information for the article “Avian spring migration at the East Adriatic coast: coastal and sea-crossing dynamics of intensity, timing, and flight directions.”.....	140
Appendix C: Supporting Information for the article “When nocturnally migrating birds encounter low-level patchy light pollution: a case study from the Croatian coast”....	145
Appendix D: Supporting Information for the article “Redistribution of sea-crossing bird migration in response to coastal artificial illumination”.....	153

1 Introduction

1.1 Motivation

1.1.1 The importance of birds

Birds are everywhere. They have populated every continent, from the ocean depths to the mountaintops, from the ice caps to the deserts, and from open grasslands to dense forests. They dive and swim; walk, hop and run; hover, soar and swoop. Their abundance and diversity make birds easy to love, and most people would agree that they are fascinating to observe and learn from, beautiful to look at and listen to, and definitely worth spending at least four years of a human lifespan studying them.

Birds are not only aesthetically and intrinsically important, but they are also immensely important for the functioning of ecosystems worldwide (Whelan, Şekercioğlu and Wenny, 2015). To mention a few, birds act as pollinators in sometimes unique relationships, feeding themselves and their offspring on otherwise detrimental herbivorous insects that are otherwise considered agricultural pests, and they act as seed dispersers, said to be capable of revegetating even deforested and fallow land (Whelan, Wenny and Marquis, 2008).

Migratory birds connect ecosystems separated by large geographic distances, providing ecosystem services across continents (Whelan, Wenny and Marquis, 2008). Being migratory means avoiding starvation in seasonally depleted habitats and following the abundance of resources across latitudes (Somveille, Rodrigues and Manica, 2015). Birds on the move thus feed on the otherwise excessive availability of nutrients, while avoiding competition over scarce resources (Somveille, Rodrigues and Manica, 2018).

The idea that birds keep gardens and farms free from insect pests is an old one. I came across an early publication that made me chuckle: “Man imagines himself to be the dominant power on the earth. He is nothing of the sort. The true lords of the universe are the insects” (Buckland, 1915, p. 701), followed by an ode to birds’ diverse usefulness to humanity. Meanwhile, scientists are increasingly recognising and quantifying the substantial economic value generated by birds through their predation of herbivorous insects in agricultural habitats. For instance, excluding birds from organically managed coffee plantations increased insect-caused damage by up to 40% (Johnson, Kellermann and Stercho, 2010), while nest boxes in apple orchards reduced damaged fruit by 50% (Mols and Visser, 2002).

Sadly, these ecosystem services, as well as the beauty and the song, are under threat.

1.1.2 Birds under threat

Bird numbers are declining globally (Petras and Vrezec, 2022; Rigal *et al.*, 2023). Compared to resident species, migratory birds have suffered specifically higher losses (Sanderson *et al.*, 2006). While a substantial part of population declines in resident species can be clearly attributed to agricultural intensification (Douglas *et al.*, 2023), the issue is much more complex in migratory species (Morrison *et al.*, 2013), as it is necessary to consider conditions throughout the whole annual cycle, from breeding range to the migrating stage to wintering habitats (Rushing, Ryder and Marra, 2016; Newton, 2024).

The mortality of migratory birds, especially during migration, stems from multiple sources. Ultimately, aside from extreme weather events (Newton, 2007), most of these factors go back

to our everyday lives (Kirby *et al.*, 2008). The top factors driving population declines include land-use changes such as agricultural intensification, deforestation and other forms of habitat degradation (Jetz, Wilcove and Dobson, 2007), as well as climate change. The latter can lead to an increasing mismatch between the timing of bird migration and the availability of food resources (Both *et al.*, 2006). The indirect effects of population declines, especially the longer-lasting negative effects that might lead to reduced fitness and increased susceptibility to other threats, are hard to quantify and still poorly understood (Nemes *et al.*, 2023).

Conversely, efforts have been made to quantify the direct lethality of birds caused by human activities (Loss, Will and Marra, 2012, 2015). Direct bird fatalities are primarily caused by collisions with human-made structures (Erickson, Johnson and Young Jr., 2005). As most birds migrate at night, there has been much debate about the extent to which they are affected by artificial light at night (ALAN), given that it impairs their sense of orientation (Gauthreaux, 1982; Van Doren *et al.*, 2017). In recent decades, ALAN has received significant attention from the scientific community due to its role in increasing direct mortality by attracting birds to light sources and thereby increasing collision rates with illuminated structures (Evans Ogden, 1996, 2002; Korner, von Maravic and Haupt, 2022). Furthermore, ALAN has been suggested to contribute indirectly to mortality by drawing birds towards suboptimal regions for rest and feeding during migration (McLaren *et al.*, 2018), and thus, leading to much more complex responses.

Globally, ALAN is increasing (Kyba *et al.*, 2017), and it is especially high within the most important migratory corridors of birds (Cabrera-Cruz, Smolinsky and Buler, 2018). At the same time, mounting evidence of the disadvantages of ALAN is fuelling initiatives to minimise it as much as possible (Saha, 2017; Burt *et al.*, 2023).

I used this as motivation to lay the groundwork for my doctoral dissertation. Here, I will examine the impact of ALAN on the behaviour of birds in-flight within a specific geographical setting, utilising contemporary quantitative ornithological tools. The study area is located in Croatia, a country that is already doing a lot to regulate ALAN, but which also offers unique advantages for quantitative ornithology in an illuminated nightscape. In the next three chapters, I will introduce the origins of bird migration, explain why, where and how birds migrate, and introduce the problems of ALAN and light pollution, before diving into the methods of quantitative ornithology. Finally, I will present the objectives and design of this doctoral project before moving on to the individual case studies.

1.2 Bird migration

1.2.1 The evolution of bird migration

Why do birds migrate? The answer to this question is deeply rooted in the evolution of birds and the origin of migration.

The question of whether migration evolved in birds of the southern tropics, which started moving away in search of new breeding habitats to exploit a surplus of resources and avoid competition, or in birds of northern, temperate regions, which were forced to move away from their breeding grounds to avoid seasonal depletion, has been debated for a long time (Salewski and Bruderer, 2007). These two concepts are known as the southern home theory and the northern home theory. The hypothesis currently accepted by scientists is based on

Palearctic-African biogeographical development over the last 60 million years (Bruderer and Salewski, 2008), and is closely linked to the origin and the evolution of birds.

Birds originated from and evolved alongside the dinosaurs around 160 million years ago during the Jurassic period. At that time, although birds were diverse in size and shape, their ecological diversity was rather limited (Brusatte, 2015). While molecular evidence suggests that some orders of modern birds have already been around in the late dinosaur era (Mourer-Chauviré, 1995; Cooper and Penny, 1997; Blondel and Mourer-Chauviré, 1998), most of the former bird diversity was lost during the cataclysmic events at the end of the Cretaceous, around 66 million years ago (Longrich, Tokaryk and Field, 2011). Mass extinctions created a unique dynamic in global biogeographic processes, which allowed for rapid diversification among survivors (Hull, 2015). Following the impact that led to the extinction of over 75% of species (Schulte *et al.*, 2010), birds were among the winning taxa that, on a geological timescale, quickly occupied various ecological niches and functions (Ericson *et al.*, 2006). In the early Cenozoic era, the Earth was much warmer than it is today. Lush tropical forests covered the entire planet (Latham and Ricklefs, 1993). This era of relative climatic stability lasted for around 15 million years. During this time, the Earth was dominated by a tropical to subtropical climate with little to no seasonality¹, and a very low temperature gradient from the equator to the polar circles (Blondel and Mourer-Chauviré, 1998; Bruderer and Salewski, 2008). These stable climatic conditions enabled angiosperm plants to spread quickly. This benefited birds and mammals, particularly birds, due to the increased diversity of plant seed sizes and shapes (Ericson, Irestedt and Johansson, 2003). In other words, the co-evolution between plants and birds created a multitude of new ecological niches and functions, which was the main driver behind the rapid spread (Ericson *et al.*, 2006; Brusatte, 2015).

From the mid-Eocene onwards, the Earth's climate gradually cooled, and the uniform tropical and subtropical conditions began to fragment into distinct climatic zones. Formerly continuous tropical or subtropical forests gave way to more open and heterogeneous landscapes in response to a cooling climate and increasing seasonality, especially at higher latitudes. These environmental changes profoundly altered the availability of food and breeding habitats, creating alternating periods of resource abundance and scarcity. The long-term cooling that began in the middle to late Eocene peaked in the transition to the Oligocene, around 34 million years ago, resulting in the first large-scale Cenozoic glaciation (Zachos *et al.*, 2001). Proxy records and modelling show a sustained drop in global temperatures and changes in ocean circulation due to declining atmospheric CO₂ levels and tectonically driven changes in geography (Bornemann *et al.*, 2016). This reorganised terrestrial climates and introduced stronger seasonality at higher latitudes (Hutchinson *et al.*, 2021).

An essential factor in the evolutionary process towards the modern migration systems was the profound climatic and geological reorganisation of the late Cenozoic. Around 30 million years ago, the global climate began cooling, finally ending the warm and stable conditions that had dominated the early Cenozoic. The uplift of the Alpine-Himalayan orogenic belt and the closure of the Tethys Sea transformed northern Africa and the Mediterranean region, promoting aridification and establishing a major biogeographic barrier between tropical and subtropical Africa and the increasingly seasonal Palearctic (Bruderer and Salewski, 2008;

¹ Of course, the inclination of the Earth's axis has created seasonal differences in the availability of solar energy on the ground, but temperatures were relatively stable. See Blondel and Mourer-Chauviré (1998).

Zhang *et al.*, 2014). This climatic differentiation created distinct ecological zones separated by relatively inhospitable deserts.

During the Quaternary period, beginning about 2.6 million years ago, cyclic glacial and interglacial phases repeatedly reshaped Eurasia's vegetation and habitats (Hewitt, 2000; Bruderer and Salewski, 2008). With glacial advances, temperate biomes shifted southward, while interglacial retreats reopened northern breeding areas. Concurrently, episodes of intensified monsoon rainfall periodically transformed the Sahara into a vegetated landscape, temporarily reconnecting African and Eurasian ecosystems (Claussen, 2003). These alternating conditions repeatedly promoted northward dispersal and subsequent southward retreat, reinforcing migratory behaviour as an adaptive response to shifting environments (P. Bell, 2000; Bruderer and Salewski, 2008).

The question of whether birds migrate to escape harsh winters or to take advantage of a seasonal surge in food and breeding opportunities is contentious. According to Salewski and Bruderer (2007), the real question is whether birds began migrating from old to new breeding grounds, or from breeding to non-breeding areas, in order to enhance their fitness and boost their chances of survival. Both perspectives might be true, depending on the evolutionary and ecological context, which means that migration likely arose from dispersal movements away from old breeding grounds to avoid competition, but then gradually became cyclic through natural selection by the enhanced fitness of migrants.

The initial step in the evolution of migration was most likely dispersal as an expansion movement of once sedentary populations (Cox, 1968; Alerstam, Hedenström and Åkesson, 2003). Such dispersal offered obvious benefits in terms of fitness: individuals that colonised new areas were able to exploit unoccupied ecological niches, experience less competition and access new nesting sites (Rappole and Jones, 2002). When these newly colonised regions offered stable conditions with little seasonality and especially with enough resources year-round, birds could remain sedentary. Expanding into regions with higher seasonal variation in temperature and resource availability was, however, linked to strong selective pressure to retreat during periods of scarcity (Somveille, Rodrigues and Manica, 2015). The most accessible direction of retreat was often along the same ecological corridors used during initial dispersal, typically back toward ancestral habitats where food remained available during the non-breeding season (Salewski and Bruderer, 2007). The evolution of this back-and-forth movement marked the beginning of cyclical, seasonal migration in birds. Over time, natural selection favoured traits that enhanced the capacity for sustained movement over longer distances, especially navigation and memory, physiological endurance, timing mechanisms, and energy storage, that underpin modern migratory systems (Cox, 1968; Gwinner, 1990; Rappole and Jones, 2002; Mettke-Hofmann and Gwinner, 2003).

Migration confers birds important reproductive and survival advantages, which come at the cost of increased energy expenditure and mortality during migration (Alerstam, Hedenström and Åkesson, 2003; Newton, 2006). The persistence of migration despite its risks indicates that, for many species, the fitness gains of exploiting seasonal productivity outweigh the costs that migration induces.

1.2.2 Phenology

When and where do birds migrate? Previously, I described why birds migrate, based on the biogeographical processes effective since the early Cenozoic era and the subsequent evolutionary development of birds. Here, we turn our attention to how bird migration looks today. What drives migration timing and routes in the modern world? How do birds synchronise their journeys with seasonal resource availability, especially for breeding? Finally, we transition to examining how recent anthropogenic activity affects these long-established dynamics.

As shown in the previous section, the origination of migration was a biogeographical process shaped by a transition from a globally warm climate to one with a comparatively narrow tropical belt and wide temperate latitudes marked by strong seasonality, resulting in a high variability in resource availability. Today, this climatic gradient continues to govern the timing, direction, and intensity of avian migratory movements across the globe (Kirby *et al.*, 2008; Dingle, 2014). Hahn, Bauer and Liechti (2009) estimated that an average of 2.1 billion passerine- and near-passerine birds cross the Saharan desert from north to south each autumn, in addition to those that winter in southern Europe. Most species migrate individually, on a broad front, and primarily at nighttime (Liechti *et al.*, 1996). This contrasts with the popular, iconic mental image of migration as coordinated formations of cranes, geese, or storks soaring on thermals on golden autumn days. The choice of day or night migration depends strongly on flight mode and ecology. Soaring birds are restricted to daytime when thermals form, whereas most smaller birds like passerines are nocturnal migrants, where they benefit from calmer, less turbulent air, celestial navigation, reduced risk of predation, and the possibility to forage in daylight (Alerstam, 2009). While most nocturnally migrating birds are otherwise active during the day, the switch to nocturnal activity happens abruptly on departure (Zúñiga *et al.*, 2016). While first-year migrants rely largely on inherited orientation programmes, adults increasingly use spatial memory and environmental cues to refine timing and routes (Åkesson and Helm, 2020).

The timing of migration is highly species-dependent, reflecting both food availability and the predictability of resources (Richardson, 1978; Jenni and Kéry, 2003; Gordo, 2007; Rubolini *et al.*, 2007; Végvári *et al.*, 2010; Haest *et al.*, 2019; Bauer, McNamara and Barta, 2020; Kanerva *et al.*, 2020). Generalists that feed on seeds and fruits can persist longer into autumn, while aerial insectivores, whose prey disappears early, are typically the first to depart (Haest *et al.*, 2019). Likewise, generalists can return to breeding grounds earlier in spring because they are less dependent on the precise timing of spring green-up (Végvári *et al.*, 2010).

In the Afro-Palearctic migration system, landbird migration follows three major flyways (Figure 1.1) that reflect broad ecological and geographical corridors connecting breeding and non-breeding regions (Gargallo *et al.*, 2011; Busse, Zaniwicz and Cofta, 2015), the western- (e.g., Nilsson *et al.*, 2019), central- (e.g., Monti *et al.*, 2024), and eastern flyway (e.g., Kralj *et al.*, 2020), which is sometimes referred to as the south-eastern flyway. The western flyway stretches from western Europe through the Iberian Peninsula and across the western Sahara into West Africa, while the eastern flyway extends from central and eastern Europe through the Middle East toward eastern Africa. Between them lies a central corridor that overlaps both pathways, but is particularly included in the Italian Peninsula, and leading more centrally across the Mediterranean basin (Newton, 2008; Hahn, Bauer and Liechti, 2009; Bairlein, 2016). Along these flyways, birds migrate on a broad front, shaped by winds, topography,

and the distribution of suitable stopover sites (Erni, Liechti and Bruderer, 2005; Hahn *et al.*, 2014; Shamoun-Baranes, Liechti and Vansteelant, 2017; Bruderer and Peter, 2022).

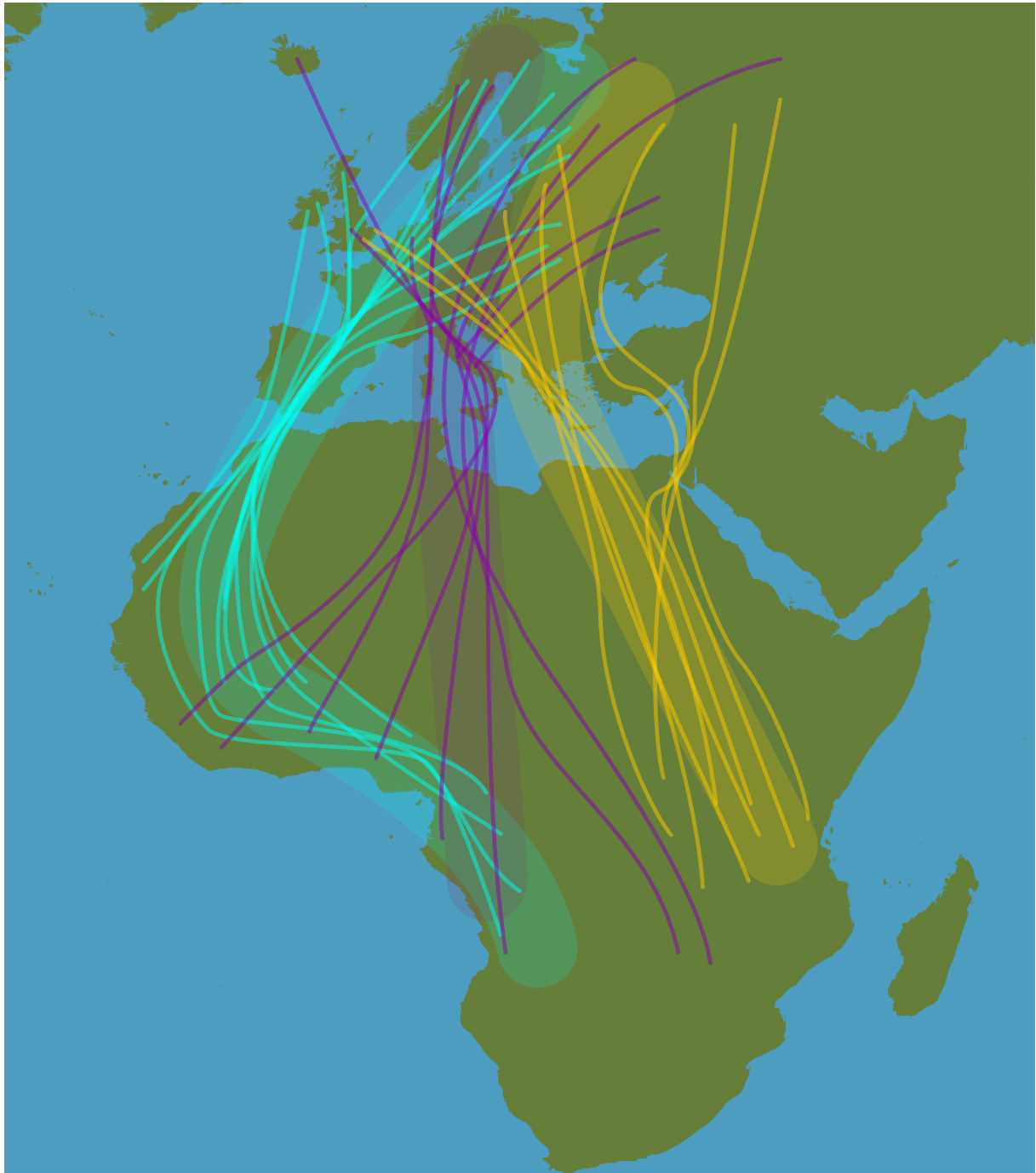


Figure 1.1. **Illustration of the Afro-Palearctic migration system.** Displayed are the three major flyways, the western (light-blue), central (purple), and eastern flyway (yellow). The illustration is a simplified concept, following (Busse, Zaniewicz and Cofta, 2015).

Flyway selection varies among populations, depending on the geography of their breeding and wintering ranges (Klein, Berthold and Gwinner, 1973; Helbig, 1992; Procházka *et al.*, 2018; Briedis *et al.*, 2020), while reflecting evolutionary history (Winger, Auteri, *et al.*, 2019), geographic constraints (Rössler and Schauer, 2014), and ongoing ecological processes such as drought intensification (La Sorte *et al.*, 2016).

In spring, the timing of Afro-Palearctic bird migration varies across Europe due to specific climatic and phenological gradients, as well as distinct differences between flyways (Briedis

et al., 2020). Birds migrating along the eastern flyway arrive at their breeding grounds 6 to 7 days later than those along the western flyway. This delay corresponds to the later spring greening and stronger continental climate in eastern Europe, where temperature seasonality is greater, and the development of vegetation lags behind that in the oceanic west (Briedis *et al.*, 2020).

The timing of birds during migration is closely related to the temperature and the local vegetation phenology at the wintering and stopover sites, supporting the idea that migrants fine-tune their arrival to match optimal resource availability at breeding sites (Hedenström *et al.*, 2007; Haest, Hüppop and Bairlein, 2018). This plasticity declines with total migration distance. Long-distance migrants mainly adapt their timing within the last 1000 to 3000 km of their migration (Schmaljohann and Both, 2017), while short- to medium-distance migrants show a much higher adaptability to environmental cues along the route (Haest, Hüppop and Bairlein, 2018; Lehikoinen *et al.*, 2019). Besides these population-level differences that depend on migration distance, weather, and partly on climate, birds also have an individual preference regarding the optimal timing of migration (Tøttrup *et al.*, 2012; Thorup *et al.*, 2013).

At a nightly temporal scale, the numbers of migrating birds can vary greatly. Whether to depart on a migratory flight or not, birds often decide based on the weather (Packmor *et al.*, 2020). Oftentimes, birds sit out heavy rain and strong headwinds (Erni *et al.*, 2002; Schaub, Liechti and Jenni, 2004), especially before barrier-crossing (Bradarić *et al.*, 2020; Manola *et al.*, 2020). Skilled flyers, however, are less dependent on specific wind situations (Saino *et al.*, 2010). This leads to a very typical pattern in the seasonal migration phenology, where during most nights only small numbers of birds migrate, while the largest proportion of the total migration volume focuses on a few nights within each season, so-called peak migration nights (Horton *et al.*, 2021; Hirschhofer *et al.*, 2024).

In addition to timing and routing, migration phenology encompasses variations in flight altitude and speed, which influence the way migratory movements unfold over time and space. While many nocturnal migrants typically fly at relatively low altitudes, often below 200 m above ground level (Bruderer and Liechti, 2004), flight altitudes are highly flexible and depend on atmospheric conditions and the landscape below (Bruderer, Underhill and Liechti, 1995; Bruderer, Peter and Korner-Nievergelt, 2018). Birds may ascend to much higher altitudes to exploit favourable wind conditions that reduce energetic costs and increase ground speed, particularly during long barrier crossings or under strong tailwinds (Dokter *et al.*, 2011, 2013; Kemp *et al.*, 2013). Similarly, elevated flight altitudes can be observed when migrants are forced to overcome major topographic obstacles, such as mountain ranges (Komenda-Zehnder *et al.*, 2001). Seasonal differences in flight speed have been observed, with migratory birds flying faster in spring than in autumn (Nilsson, Bäckman and Alerstam, 2014; Briedis *et al.*, 2020). This suggests that there is a selective pressure for rapid progress in spring. Additionally, significantly higher speeds were recorded when crossing ecological barriers, such as deserts and seas (Lopez-Ricaurte *et al.*, 2021).

During their migration, birds stop at suitable sites to rest, recover and refuel. In spring in particular, birds seem to migrate faster, mainly by refuelling more quickly, which requires high-quality stopover sites (Hahn *et al.*, 2014). Especially after barrier-crossing, when birds are exhausted and energy-depleted, or within otherwise suboptimal environments, high-quality stopover sites can become critical bottlenecks where birds compete over resources (Newton, 2006). Stopover sites of poor quality, characterised by low food quality and abundance,

predation, or high levels of competition, can subsequently affect migration, including reducing breeding success (Newton, 2004).

Stopovers have been aptly described as “interruptions of migratory endurance flight to minimise immediate and/or delayed fitness costs” (Schmaljohann, Eikenaar and Sapir, 2022, p. 1). During stopover, birds replenish their energy reserves (Schmaljohann and Eikenaar, 2017; Lindström, Alerstam and Hedenström, 2019), sleep, and recover physically from oxidative stress (Schwilch *et al.*, 2002; Skrip *et al.*, 2015), sit out adverse weather (Shamoun-Baranes *et al.*, 2010), and fine-tune their migration timing in response to environmental cues (Haest, Hüppop and Bairlein, 2018). It has also been suggested that they recalibrate their magnetic compass during a stopover (Cochran, Mouritsen and Wikelski, 2004). The factors influencing the decision to stop over, as well as to resume migration, can differ substantially between individuals depending on species, sex and migration strategy (Schmaljohann, Eikenaar and Sapir, 2022).

The spatial distribution and use of suitable stopover sites along the migration corridor are closely linked to the migration and survival strategies of bird species (Schaub and Jenni, 2000b, 2000a). Fierce competition over stopover site resources is often inherent in species that feed on evenly distributed but scarce food sources, resulting in generally slower migration speeds. Species that exploit unpredictable, but abundant food sources exhibit greater interannual variation in migration timing. Finally, generalist species that feed on widely and abundantly distributed food sources can maintain a fast and regular migration pace (Schaub and Jenni, 2000b).

In recent years, the role of stopover sites in adjusting migration timing in response to environmental change has received growing attention. Along their migration routes, birds can use stopovers as flexible buffers to fine-tune their progress in order to match the phenological development of vegetation, and thus the abundance of insects (Schmaljohann and Both, 2017). While it was thought that short- to medium-distance migrants in particular adjusted their timing based on phenological cues of vegetation, newer evidence suggests that long-distance migrants too adjust their timing based on conditions at stopover areas, but to a lesser degree (Haest, Hüppop and Bairlein, 2018). Of course, as the anthropogenic footprint on global ecosystems grows, including the atmosphere, these long-evolved dynamics are increasingly challenged (Halupka *et al.*, 2017; McLaren *et al.*, 2018).

Besides the optimal timing between peaking food resources and raising chicks, birds also need to optimise their timings in regard to being capable of occupying the best nesting territories. Competition over territories and mates is a powerful selective force shaping spring migration timing. In theory, individuals that arrive early at breeding sites gain access to higher-quality territories, nesting sites, and partners, leading to greater reproductive success (Kokko, 1999; Both and Visser, 2001; Smith and Moore, 2005). Early arrival can also allow more time for multiple broods within a season, particularly in temperate regions where breeding windows are relatively short (Møller, 1994). However, arriving early can come at the cost of spending less time during stopover, thus having fewer resources available when arriving at the breeding grounds (Alerstam, 2006), or which might involve a substantial risk of becoming victim to unfavourable weather (Newton, 2006, 2008). Thus, birds face a trade-off between the competitive advantage of early arrival and the energetic or survival costs of exhaustion and of encountering unpredictable conditions. This tension is especially pronounced in long-

distance migrants, whose ability to adjust timing to local conditions is limited compared with short-distance migrants (Both *et al.*, 2006; Schmaljohann and Both, 2017).

In essence, spring migration is governed by a trade-off between arriving early and thus securing prime territories, while maximising the number of offspring, and the risk of arriving too soon, when food might be scarce and weather conditions highly unfavourable (Richardson, 1978; Newton, 2006). Typically, the spring migration season stretches from mid-February to mid-May, while showing distinct differences between populations (Gargallo *et al.*, 2011).

1.2.3 Navigation and orientation

Migration confronts birds with quite specific navigational and orientation challenges. Migrating from breeding grounds to wintering grounds and back requires not only the optimisation of migration timing, but also precise spatial orientation and wayfinding across vast and often unfamiliar landscapes. In order to successfully navigate these journeys, migratory birds have evolved a variety of sensory adaptations that enable them to do so (Mouritsen, Heyers and Güntürkün, 2016; Tyagi and Bhardwaj, 2021). Evidence suggests that birds can integrate multiple environmental cues, such as magnetic inclination, celestial rotation and olfactory information, to estimate their geographic position relative to their destination (Åkesson and Helm, 2020). Some of these navigational abilities are inherited, forming part of an endogenous programme, while others are learned skills that improve with experience (Gauthreaux, 1982; Wiltschko and Wiltschko, 2012).

During migration, birds rely on a hierarchy of navigational cues that differ in scale and reliability depending on the migration phase and environmental context. Primarily, they use a combination of compass orientation to maintain a consistent migratory heading and true navigation, which is based on positional feedback beyond compass bearings, to reorient and fine-tune their heading towards a specific geographic destination (Thorup and Rabøl, 2001; Wiltschko, 2017). An example of true navigation in birds is the landmark orientation exhibited by homing pigeons, which, over the years, establish a topographic map of their home range (Wallraff, 2005). Roughly, the migratory journey can be separated into three phases. The first involves long-distance navigation based mainly on compass orientation using the magnetic field and celestial cues. Birds are also able to use true navigation to correct for displacement along the route (Thorup and Rabøl, 2001). During the second phase, known as the “narrowing-in” phase, birds approach their home range over the final 200 km while relying on finer-scale magnetic and learned visual cues, including geographic leading lines such as mountain ranges and rivers. Finally, over the last kilometre, birds pinpoint their exact destination, navigating on a local scale and relying on familiar landmarks (Mouritsen, 2018).

At a mechanistic level, orientation depends on multiple interacting sensory systems, some of which are dependent on light. It stands to reason that birds migrating at night would use the starry sky for orientation. Indeed, experiments on young birds have shown that they learn this compass system at an early age by observing and locating the centre of rotation of the night sky, which they then interpret as north (Michalik *et al.*, 2014). Obviously, celestial navigation by the stars requires clear skies without too high levels of light pollution, but there is more to it than that. A light-dependent magnetic compass appears to operate via radical-pair chemistry in ocular photopigments, providing a polarity-independent inclination cue for

directional sense (Rodgers and Hore, 2009). Birds recalibrate their magnetic compass daily using celestial cues at twilight, most likely polarised skylight near the horizon (Moore, 1982; Cochran, Mouritsen and Wikelski, 2004; Muheim, Moore and Phillips, 2006). Exposure to artificial light has been shown to cause birds to exhibit behaviour indicating reorientation and disorientation (Wiltschko and Wiltschko, 2001). Anthropogenic influence on the nocturnal lightscape has therefore the potential to disturb or disrupt migration at multiple levels.

1.3 Artificial light at night (ALAN) and light pollution

Throughout evolutionary history, the organisation of life on Earth has been structured by the alternation of light and dark and of its seasonal changes around the year. The rotation of the planet, the orbit around the sun, and the lunar orbit around the earth are the three most important cycles that create the daily and seasonal variation of natural illumination that structure ecological processes and internal biological rhythms. Birds have evolved under these stable light regimes. They have developed sensory organs which, for full functionality, depend on the natural interplay between day and night, synchronising their physiology and behaviour to natural photoperiods. Circadian and circannual clocks, driven by molecular clocks in the brain and peripheral organs, orchestrate daily rhythms in activity, metabolism, and hormone secretion. The pineal hormone melatonin, which is released primarily during darkness, acts as a key signal linking the external light-dark cycle with a bird's internal timing mechanisms (Gwinner and Brandstätter, 2001; Cassone, 2014). Experimental and field studies have shown that ALAN suppresses nocturnal melatonin secretion, one of the key drivers of the circadian system in birds (Dominoni *et al.*, 2013). This has disturbing effects on the regulation of a set of seasonally and daily recurring behaviours such as onset of song, gonadal growth, migration restlessness, and sleep (Dominoni, Quetting and Partecke, 2013a, 2013b; Dominoni *et al.*, 2014).

Over the past two centuries, humans have drastically transformed the aerosphere and the nighttime environment. ALAN was first limited to urban centres, but gradually expanded globally with industrialisation and electrification, replacing the natural darkness with a permanent twilight. The term “light pollution” is often used in an astronomical sense and refers to the degradation of the night sky by scattered ALAN. “Ecological light pollution” describes ALAN that alters natural light regimes in terrestrial and aquatic ecosystems (Longcore and Rich, 2004). For simplicity, I will refer here to ecological light pollution just as light pollution. Light pollution encompasses the chronic or periodic increase in nighttime illumination and skyglow, the term to address scattered light, produced by mostly urban, industrial, and other infrastructural illumination. It disrupts natural circadian rhythms, masks celestial cues and modifies the perceived intensity and spectral composition of nighttime light across ecosystems. Furthermore, when emitted light gets reflected at smooth surfaces, as they are often part of urban landscapes, the light can be polarised, which leads to a new kind of pollutant that has the ability to interfere with the magnetic compass system of birds (Horváth *et al.*, 2009). Today, ALAN is seen as a new, major pollutant and as such, as an environmental stressor that affects physiology, behaviour, and species interaction across taxa (Gaston *et al.*, 2013; Burt *et al.*, 2023).

Satellite observations reveal that in 2016, more than 23 % of the Earth's surface between 75°N and 60°S was experiencing light-polluted nights, while continuing to grow by around 2 % annually (Kyba *et al.*, 2017). Here in particular, the high intensity of light pollution across

the entire European continent and around the Mediterranean is leaving only limited refuges of true nocturnal darkness (Falchi *et al.*, 2016, 2019). The transition to energy-efficient LED technology has paradoxically accelerated this trend by lowering costs and extending the reach of illumination, while simultaneously shifting the spectral composition of nightscapes toward shorter, blue wavelengths that are particularly disruptive to biological systems (Gaston and de Miguel, 2022). Today, light pollution is highest in regions of frequent migratory passage around the globe (Cabrera-Cruz, Smolinsky and Buler, 2018), and it is also these regions where light pollution is still increasing the most (La Sorte *et al.*, 2022). Skyglow (the diffuse brightening of the night sky from artificial light scattered in the atmosphere) further extends the influence of ALAN, reaching hundreds of kilometres away from its sources, and even impacting areas that are otherwise under protection (Garrett, Donald and Gaston, 2020). Through skyglow, ALAN interacts with clouds and fog, increasing the perceived level of brightness up to tenfold (Kyba *et al.*, 2011). It is argued that for nocturnally migrating birds, light pollution presents a pollutant that reduces the functional connectivity of migratory corridors similar to habitat degradation on the ground (Korpach *et al.*, 2022).

From individuals to populations and communities, these effects have profound consequences for quantitative avian migration patterns. It is evident that during darkness, birds are lured toward bright light sources, a behaviour called phototaxis (Van Doren *et al.*, 2017). This has been demonstrated in countless case studies across different migratory systems. In New York City, for example, an extreme intensity light installation has attracted countless migrating birds from afar in such a way that the phenomenon was observable with a nearby weather radar (Van Doren *et al.*, 2017). Almost as if they had been captured by the light, birds reduced their flight speed and started flying in circles, showing clear signs of severe disorientation. Upon switching off the lights, the birds dispersed quickly, suggesting a clear link between the increased bird density and light (Van Doren *et al.*, 2017). Other research focused on quantifying the direct mortality resulting from light installations at buildings. Across these studies, the surface area of illuminated windows at a building was the strongest predictor of the number of fatal bird collisions with these buildings (Gelb and Delacretaz, 2009; Haupt, 2009; Parkins, Elbin and Barnes, 2015; Loss *et al.*, 2019; Lao *et al.*, 2020; Korner, von Maravic and Haupt, 2022). From almost 100 birds during a single night at a single building (Korner, von Maravic and Haupt, 2022) to around 234,000 birds for a whole city over a year (Parkins, Elbin and Barnes, 2015), the number of birds that collide with buildings and other infrastructure is immense. It was estimated that around 550 million birds are killed due to collisions with buildings each year across the US (Erickson, Johnson and Young Jr., 2005; Loss *et al.*, 2014). Most of these collisions happen during autumn migration, likely because it is the time when a lot of young birds depart on their migration for the first time (Loss *et al.*, 2019; Korner, von Maravic and Haupt, 2022). Within nights, it seems that most collisions happen during early morning hours, when birds seek a place to stop over, rest, and refuel (Gelb and Delacretaz, 2009).

The detrimental effect of light pollution on migrating birds might be dependent on the geographic context. Migrating birds often must cross wide ecological barriers such as deserts or seas. Not only do these lack the possibility for birds to land and rest, but often these barriers are comparatively dark due to the relative absence of human infrastructure. In contrast to terrestrial ALAN, illuminated infrastructure offshore, or along coastlines, has the additional factor of a high contrast from this relative darkness to the illuminated area. Evidence from such a context is scarce, but high numbers of dead birds found at an offshore

platform in the North Sea suggest that in this relative darkness, ALAN has a particularly strong effect in attracting birds from afar (Hüppop *et al.*, 2016). This effect is even stronger in weather situations with reduced visibility (Cochran and Graber, 1958; Hüppop *et al.*, 2016; Rebke *et al.*, 2019). Similarly, as shown by Van Doren *et al.* (2021), the numbers of dead birds at a lakeside building have been particularly high when parallel radar monitoring detected high densities of birds over the lake, and although the causality was not further investigated, it was assumed that birds over relatively dark waterbodies could experience stronger attraction to coastal ALAN, again with low visibility acting as an amplifier to collision numbers.

ALAN can act as an ecological trap, drawing birds toward cities or industrial zones, leading to detours and altering the spatial pattern of stopover densities. Besides the increased risk for deadly encounters with urban infrastructure, cars, or cats, flight tracks and stopover areas being altered by light pollution can also have more subtle, sublethal consequences (Nemes *et al.*, 2023). Light pollution can increase the migration distance (Korpach *et al.*, 2022) and has profound effects on the stopover density distribution of birds (Cabrera-Cruz *et al.*, 2020; Horton *et al.*, 2023). Even at critical stages of their migration, stopover densities seemed to be heavily affected by light pollution, providing further evidence that ALAN is drawing birds towards urban areas (Schekler *et al.*, 2022). Nonetheless, the relationship between ALAN and migratory bird behaviour still seems to be complex. Across spatial scales, another study argues that ALAN is only attracting birds on the macroscale, while locally, birds prefer darker areas (McLaren *et al.*, 2018). However, the attraction toward peri-urban environment at macroscales could be sufficient to act as an ecological trap (Horton *et al.*, 2023). Light pollution at stopover sites is often reported to be associated with lower stopover site quality, especially for insectivorous and omnivorous species (Morelli *et al.*, 2023). Arrival at the breeding sites needs to be timed precisely, especially during spring, to benefit from the best territories (Kokko, 1999). Timely arrival also enables migrants to exploit the peak in food availability during the spring green-up (Smith and Moore, 2005). Therefore, lower-quality stopover sites can have significant consequences for migration timing. Reduced food abundance at such sites can limit refuelling rates, delaying onward migration and arrival at the breeding grounds (Lindström, Alerstam and Hedenström, 2019). However, the cumulative, propagating effects that such sublethal consequences of attraction by ALAN have on individual birds and populations are not yet fully understood.

Not only scientists, but also legislative stakeholders have recognised the problematic consequences of light pollution on ecosystems and especially birds. Across the earth, national and international initiatives are increasingly focusing on reducing ALAN as much as possible to preserve and restore a more natural nightscape (Widmer, Marnane and Vounatsou, 2022; Convention on Migratory Species, 2024). In the US, the first attempts to reduce ALAN in large cities have been started (Evans Ogden, 2002; Saha, 2017). While the adoption of bird friendly solutions in urban planning and illumination regimes is a very positive development, and evidence suggests that reducing lights indeed reduces the number of bird fatalities (Korner, von Maravic and Haupt, 2022), there is evidence that even with relatively low-intensity, or even bird friendly illumination, behavioural responses can be found in birds (Cabrera-Cruz *et al.*, 2021; Osterhaus *et al.*, 2025).

1.4 Tools for quantifying bird movement

Quantitative research in ornithology has a long and diverse history that gradually increased the spatial and temporal scales and resolution at which avian migratory movement and behaviour can be studied. Early research relied primarily on direct, visual observation, which limited studies to a selection of rather large, conspicuous, diurnal migrants and to periods of favourable visibility (Papachristou, 2019). Today, most methods overcome these limitations. They allow ornithologists to quantitatively trace individuals across vast spatial extents or monitor avian movement constantly without the limitation of daylight and clear skies.

As this thesis exclusively uses terrestrial radar data, most of this section will be devoted to radar technology. However, to provide some context, I will begin with a brief overview of other relevant tracking technologies used in quantitative ornithology.

1.4.1 Ringing

One of the oldest and probably most well-known methods of quantitative ornithology is bird ringing. Birds are captured, fitted with small metal or plastic rings, while noting the time and place of the capture. If a bird is recaptured, the recovery data provide information on movement routes, migration distances, site fidelity, and, to a certain degree, survival rates. The first standardised ringing schemes were introduced in the early 20th century and soon developed into large international networks of ringing sites (Anderson and Green, 2009).

With more than a century's worth of data, the strength of ringing nowadays lies in the volume of data accumulated over such a long period of time and across continents, at a relatively low cost. The combined effort of bird ringing across nations has made it possible to reconstruct population-specific migration routes within migratory flyways alongside the annual migration phenology of migration (Stipčević, 1997; Pilastro *et al.*, 1998; Gargallo *et al.*, 2011; Kralj *et al.*, 2013). Nowadays, ringing aims to understand migratory connectivity between breeding and non-breeding areas at the population level, while developing statistical methods to account for observer effort and site detection probability (Clark, Thorup and Stroud, 2009; Korner-Nievergelt *et al.*, 2010; Thorup *et al.*, 2014).

Despite its historical and current importance, ringing is inherently limited by its dependence on re-encounters. Recovery rates are typically below 1 % for small birds, and obviously, the spatiotemporal resolution of these data is comparatively poor, and largely limited to the distribution of ringing and recapture sites². Yet, ringing remains highly important for long-term change detection (Anderson and Green, 2009).

1.4.2 Biologging technologies

Biologging involves equipping birds with miniaturised electronic loggers or transmitters to study their movement, behaviour, physiology, and environment by collecting their location, barometric pressure (altitude), acceleration, heart rate, external temperature, etc. (McKinnon and Love, 2018). Biologging methods in ornithology have revolutionised our understanding of avian behaviour (Bridge *et al.*, 2011). At first, tracking birds required following the target

² Many ring recordings are provided by birdwatchers or retrieved from dead birds following collisions or hunting.

physically, or focusing on local movement patterns such as stopover use (Gauthreaux, 1996). Triangular radio telemetry is still used to investigate the stopover ecology of staging birds. With very low costs per individual, the method allows the fine-scale following of birds within a limited geographic area (Mills *et al.*, 2011; Taylor *et al.*, 2011; Stach *et al.*, 2015).

Technological progress led to the development of small and lightweight biologgers, such as GPS and light-level geolocators, that allowed collecting or estimating positional data of birds automatically and independently over full migration cycles from breeding to wintering and back to breeding areas (McKinnon and Love, 2018; Werfeli, Ranacher and Liechti, 2022). Today, it is possible to track even small birds, which provides valuable insight into migration phenology, revealing precise timings of the onset of migration, stopover duration, and even the usage of the airspace in response to weather from barometric measurements (Rhyne *et al.*, 2024).

Small biologgers, such as light-level geolocators, weigh around 0.35 g and can be carried by small landbirds, such as passerines (McKinnon and Love, 2018). Light-level geolocators store data internally, meaning the device must be retrieved after the monitoring period to read the data. Thus, the application of geolocators is limited to the site fidelity of birds. Equipping birds with a low site fidelity with geolocators is therefore often of little value (McKinnon, Fraser and Stutchbury, 2013). Light-level geolocators indirectly determine the position of their carrier by measuring sunlight intensity at regular time intervals. The carrier's position must then be estimated by determining the times of sunrise and sunset. This method has limitations with regard to the positional accuracy and temporal resolution of the retrieved tracks (Bridge *et al.*, 2011).

Larger biologging devices, such as GPS units, partially overcome this issue by uploading data directly to a central database via either satellites or the mobile network (McKinnon and Love, 2018). As there is no need to recapture tracked birds to retrieve the data, it has become possible to track individual birds in near real time, enabling the study of movement patterns across whole lifespans (Tikkanen *et al.*, 2024). Modern GPS loggers weigh around 1 g. While GPS devices are becoming increasingly smaller, their application is currently still constrained by the body mass of the target species (Cami  n *et al.*, 2020). However, the major advantage is that, unlike light-level geolocators, GPS loggers can record flight tracks at high spatial resolution during the night (Bridge *et al.*, 2011).

Biologging devices can offer valuable insight into the effects of light pollution on birds. Depending on the size of the bird, and thus the type of the tracking device, the possibilities, however, differ. For smaller birds, whose body size limits the capability of tracking devices to rather coarse location tracking, or radiotelemetry can still provide valuable insight into how light pollution affects daily habits of birds and local habitat usage (Dominoni and Partecke, 2015). The spatiotemporal resolution of GPS instead is fine-grained and accurate enough to allow the detailed analysis of individual responses of birds to light pollution (Rodr  guez *et al.*, 2022).

1.4.3 Radar

Migrating birds can travel vast distances at high speeds, and during peak migration nights, millions of individuals may be on the move simultaneously (Horton *et al.*, 2021). Birds can move at high altitudes, and while it was reported that most would stay below 200 metres

above the ground (Bruderer and Liechti, 2004), migrating birds can reach extreme altitudes in response to favourable winds (Dokter *et al.*, 2011, 2013) or overcome topographic obstacles (Komenda-Zehnder *et al.*, 2001). Furthermore, most passerine birds migrate at night, making it hard to spot them visually. These dynamics make migration an inherently challenging phenomenon to study quantitatively over a continuous temporal window.

During the Second World War, radar technology was developed as an early warning system for incoming aircraft. One night, a radar researcher at the Air Defence Research and Development Establishment at Dover noticed strange echoes in a surveillance radar. He was able to assign them to gannets that were flying above the sea (Lack and Varley, 1945). Similar signals were observed by radar operators in different parts of the world. At first, it was believed that the signals originated from a meteorological phenomenon or were the result of some type of distortion or scattering. Visual control and the seasonal occurrence and directionality of these echoes, however, proved their origination from birds on their migration, prompting Harper (1958, p. 484) to state: “It is clear that radar can provide information of great value to the ornithologist”.

From the early discoveries of the 1940s and 1950s to the present, radar technology has undergone substantial development. Advances in computational infrastructure and the advent of big data methods in the 2010s enabled the creation of specialised sensors and software, establishing radar as the most powerful tool available to quantify the movements of organisms in the aerosphere (Shamoun-Baranes *et al.*, 2019). These developments led to the emergence of radar aeroecology, a distinct research field dedicated to studying aerial organisms and their interactions with the atmosphere (Kunz *et al.*, 2007).

Today, radar is widely used to quantify and monitor bird migration across wide spatial scales (Kelly *et al.*, 2012) and over long temporal scales (Deng *et al.*, 2023). Modern radar systems can continuously monitor biomass aloft and derive key variables from echoes, such as altitude distribution, groundspeed, and migration intensity.

Radar has also been the tool of choice in this dissertation. Two types of radar systems have been employed: a near-vertically scanning ornithological radar and volume-scanning weather surveillance radar. The following sections introduce these systems, discuss their main strengths and limitations, and explain their application in this research project.

The near-vertically scanning ornithological radar BirdScan MR1

The BirdScan MR1 (Figure 1.2), manufactured by Swiss Bird Radar Solutions AG, represents a compact and highly specialised radar system designed with an upward-pointing beam that continuously records the echoes of birds and insects passing overhead. The BirdScan MR1 is a modified X-band marine radar (Bridgemaster©, 25 kW, 9.4 GHz, wavelength ≈ 3.2 cm) equipped with a vertically oriented 20 dB horn antenna (17.5° nominal beam angle at -3 dB) rotating on a slightly nutated axis of 0.2° at 0.8 Hz. This configuration allows the extraction of flight direction from the modulation of echo intensity caused by the antenna’s nutation (Harman and Drake, 2004). The radar can operate in short-pulse (70 ns, range resolution 10 m, minimum detection range 40 m) or medium-pulse mode (290 ns, range resolution 35 m, minimum detection range 40 m). The maximum detection range depends on the pulse length and the radar cross section (RCS) of the target. For small songbirds (with an RCS of around 0.002 m^2), the maximum detection range is typically between 800 m (short pulse) and 1,100

m (medium pulse) above ground level. For larger birds, the maximum detection range extends to around 2,000 metres above ground level (Schmid *et al.*, 2019).



Figure 1.2. **BirdScan MR1** during installation at the Rovinj radar site, with the (freezing, but happy) author of this dissertation included for scale. Picture: Barbara Helm.

Echoes are detected and processed by a Kalman filter that tracks peaks in echo intensity in real time. The temporal variation of echoes during their passing through the radar beam is analysed using a trained random forest classifier that distinguishes birds from other biological and non-biological targets (Zaugg *et al.*, 2008). For bird echoes, the system additionally records wingbeat signatures, which enable further classification into subgroups (e.g., small intermittent-flapping songbirds or small continuous-flapping waders) based on RCS and wing flapping styles. Species-level identification, however, is not possible with the MR1 (Bruderer, 1997; Bruderer *et al.*, 2010).

The radar quantifies the migratory flux (the directed movement of avian biomass) overhead by computing the Migration Traffic Rate (MTR), a measure originally introduced by Lowery (1951). It represents the number of birds crossing a one-kilometre virtual transect per hour. Because the radar beam is conical, the sampled area increases with altitude, which introduces an altitude-dependent detection probability bias (Schmaljohann *et al.*, 2008; Schmid *et al.*, 2019). The calculation of the MTR, therefore, includes a geometric correction and ultimately allows comparing migration intensity between radar systems (Nilsson *et al.*, 2018).

During continuous operation, the BirdScan MR1 typically runs in hourly sequences comprising 20 minutes of medium-pulse mode and 40 minutes of short-pulse mode. The MTR is calculated separately for short- and medium-pulse recordings and then merged to exploit their complementary range resolutions: below 300 m short-pulse data only, between 300 and 800 m the mean of both, and above 800 m medium-pulse data only (Nilsson *et al.*, 2018).

Rain and other forms of precipitation can obstruct the correct detection of bird echoes. Therefore, the BirdScan MR1 automatically switches into blind mode during precipitation. This mechanism, however, doesn't always exclude all false echoes from precipitation, and a manual correction of blind times is necessary. For this purpose, the radar software creates 5-minute interval images of echo intensities over time and across altitudes (Figure 1.3).

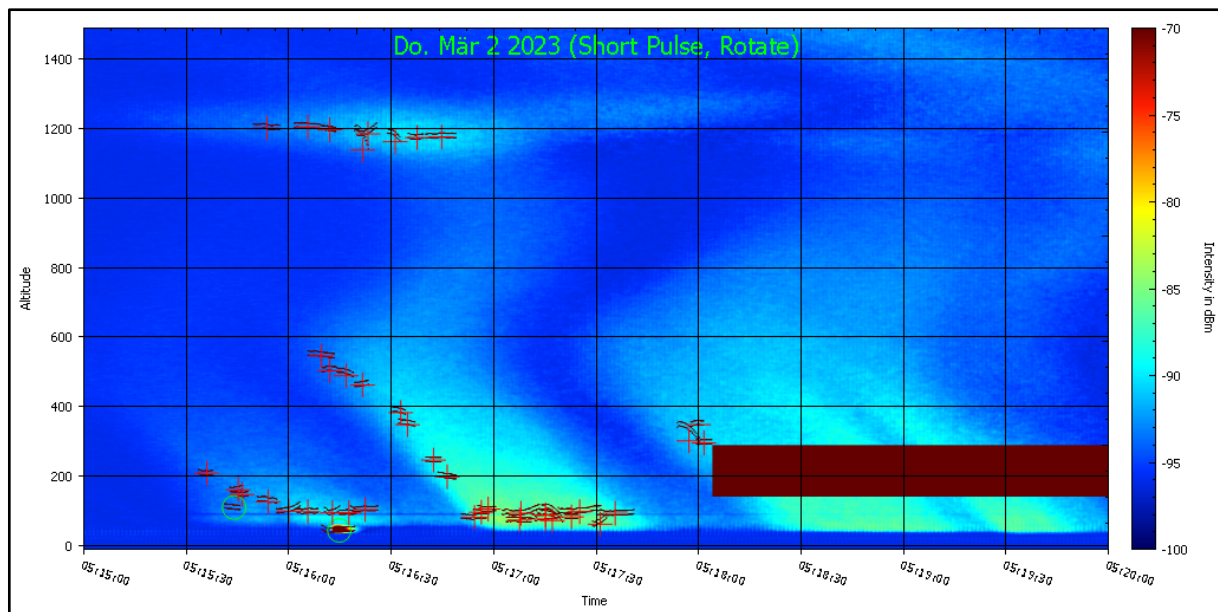


Figure 1.3. **Illustration of a rain-contaminated 5-minute monitoring interval of a BirdScan MR1.** The light blue, slanted areas represent rain, which falls over time. Red crosses can be seen in these rain events, objects that the radar has marked as non-birds, but also two green circles, objects that were incorrectly identified as birds. The red bar that begins halfway through the recording marks a period during which the radar was switched to blind mode.

Within a typical recording during a peak migration night, thousands of individual birds may fly through the radar beam (Figure 1.4).

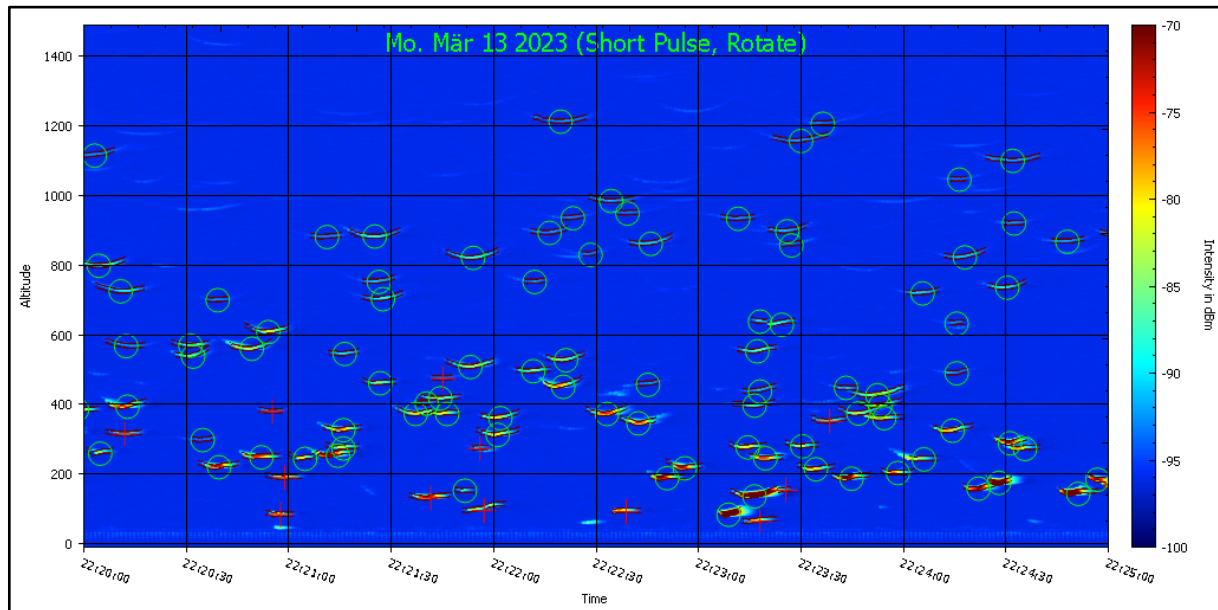


Figure 1.4. **Illustration of a 5-minute monitoring interval during a peak migration night of a BirdScan MR1.** Objects classified as birds are marked with a green circle. Each time a horizontally flying bird enters the radar beam and approaches the NADIR of the radar, its distance from the radar device decreases, and increases again as the bird leaves the beam. This results in concave shapes appearing in the image, with the lowest altitude of the continuously recorded echoes resembling the time when the bird is closest to the radar.

The BirdScan MR1 provides detailed information on individual flight behaviour of birds, allowing the analysis of fine-scale responses to atmospheric and anthropogenic predictors (Werber and Sapir, 2025). Furthermore, the BirdScan MR1 is a mobile radar station. The official version weighs around 100 kg and is thus applicable in the field, allowing the selection of specific sites for monitoring in response to specific research questions. On the other hand, the BirdScan MR1 is limited by its sampling volume. Given the relatively small opening angle, migration monitoring is restricted to a local spatial scale. To spatially expand these local observations to a regional scale, the coordinated deployment of multiple units is required (e.g., Tschanz *et al.*, 2019).

Weather surveillance radar

In contrast to the vertically directed ornithological radar BirdScan MR1, weather surveillance radar can survey much larger volumes of airspace. Weather radar scans the surrounding atmosphere in full 360° rotations at multiple elevation angles. Each rotation is called a scan (in the US, sweep), and the full set of scans at increasing elevation angles constitutes a polar volume (in the US, scan; Dokter *et al.*, 2019). Modern weather radar uses Doppler velocity to retrieve movement speed and direction of objects in the aerosphere and dual-polarised waves to collect information on their shape. Weather radar data can be classified into three stages, or “Levels” of processing (Hardegree *et al.*, 2008). Level I event data are the raw, analogue output from the scanning recordings, and are usually processed on site into Level II data products. Level II base data are reflectivity- and Doppler-derived products that are arranged on a polar grid, one for each elevation scan. Within each elevation scan, the altitude increases

with growing distance from the radar, depending on the elevation angle of the scan. Level III data products are generated from Level II base data and are, for example, vertical profiles of reflectivity, or the speed and direction of biological scatterers within the whole volume or a segment of the radar-surveyed volume. The temporal resolution of these products is limited by the time it takes to perform a full polar volume and is typically one every 10 to 15 minutes during clear sky conditions, or one every 5 minutes during rainfall.

In the United States, weather radar has been central to aeroecological research for several decades. Ornithologists have used data from the nationwide NEXRAD network, consisting of more than 150 S-band (10 cm wavelength) weather radars (Gauthreaux, Belser and van Blaricom, 2003). The mid-1990s upgrade of the NEXRAD network, which added higher spatial resolution and Doppler velocity measurements, marked a turning point for research, as these improvements enabled the quantification of the mean direction and speed of moving targets, which transformed weather radar data into a valuable resource for studying large-scale migratory flow (Gauthreaux and Belser, 2003; Kelly *et al.*, 2012). The next major upgrade, completed in 2013, introduced dual-polarisation radars (Stepanian *et al.*, 2016), which allow discrimination between different types of scatterers in the aerosphere. For ornithologists, this meant the possibility of automatically separating bird echoes from precipitation or insects. Because American weather radar data are openly accessible, the NEXRAD network has fostered a wealth of research on the timing, intensity, and spatial patterns of migration across North America (e.g., Van Doren and Horton, 2018).

In Europe, most operational weather radars use C-band (5 cm wavelength), while a smaller number of S-band radars are installed in southern France, including Corsica, Greece, and the Balkans (Huuskonen, Saltikoff and Holleman, 2014; *EUMETNET*, 2025). S-band radar operates at longer wavelengths than C-band radar and is less affected by signal attenuation from heavy rainfall; thus, it can detect targets over longer ranges. In contrast, C-band radar offers a higher spatial resolution but is more susceptible to signal loss under intense precipitation (Gu *et al.*, 2011).

Thirty-three European countries (as of 2025) participate in the European National Meteorological Service Network *EUMETNET*, which aims at fostering cooperation in the field of meteorology. Within this framework, the Operational Programme for the Exchange of Weather Radar Information (*OPERA*) coordinates the exchange and harmonisation of weather radar data across the network. *OPERA* aims at “facilitating the exchange of expertise on weather radar issues and creating high-quality pan-European radar composite products” (*EUMETNET*, 2025). Currently, it links over 215 radars across the 33 member states (Saltikoff *et al.*, 2019; *EUMETNET*, 2025). Although the European network is more heterogeneous than NEXRAD in terms of radar hardware, scanning protocols, and data formats, *OPERA* provides harmonised products in a common format (Michelson *et al.*, 2014). It represents one of the largest operational radar infrastructures worldwide and has become increasingly relevant not only for meteorology but also for biological monitoring and aeroecological research (Bauer *et al.*, 2017; Shamoun-Baranes *et al.*, 2019; Desmet *et al.*, 2025).

However, data accessibility and standardisation differ markedly between regions. In the United States, the National Oceanic and Atmospheric Administration (NOAA) manages the NEXRAD data archive, which is publicly available through the National Climatic Data Centre (NCDC). Standardisation across the network ensures that data from all radars are comparable (Shamoun-Baranes *et al.*, 2022). By contrast, in Europe, the situation is more fragmented.

While potentially, the digital infrastructure that OPERA is aiming to provide would allow a harmonised and easy to access data archive, heterogeneity in the radar types, the settings during operation, data formats, and especially data quality for aeroecological purposes, as well as regulatory differences between regions and nations limit the access, exchange, and usability of the weather radar data in Europe for ecologists (Huuskonen, Saltikoff and Holleman, 2014; Bauer *et al.*, 2017).

Historically, each European country developed its own radar infrastructure. Only in 1999 did these systems begin to be integrated through OPERA, which collects and distributes data via the Odyssey platform. And there lies the issue that is inherent to the whole system up to now: Odyssey was designed primarily for meteorological use and therefore provides data that has already been filtered of non-meteorological echoes (Huuskonen, Saltikoff and Holleman, 2014; Bauer *et al.*, 2017). Recognising this limitation, the European Network for the Radar Surveillance of Animal Movements (ENRAM) was established in 2012 to promote access to biological radar data and facilitate collaboration across countries (Shamoun-Baranes *et al.*, 2019). Despite these efforts, recent budgetary restrictions threaten to reduce access further, as OPERA plans to distribute only pre-cleaned radar data, effectively removing biological information from future archives (Shamoun-Baranes *et al.*, 2022). If raw polar volume data are no longer stored centrally, researchers will need to access national archives individually, making large-scale ecological studies considerably more complex. Europe thus finds itself at a critical juncture for the future of radar aeroecology: continued access to raw weather radar data is essential for advancing biodiversity monitoring and improving the coordination of conservation strategies across national borders.

The alternative for ornithological research today is to access Level III data products, such as vertical profiles of bird density, flight speed and flight direction. These can be accessed via the Aloft data portal (<https://aloftdata.eu>). However, as some of the meteorological services within OPERA only provide filtered data for meteorological purposes, not all the available Level III data products from Aloft can be used for aeroecological research. Nevertheless, ornithologists have demonstrated the potential of these Level III data products by using them to study and visualise large-scale night-time bird migration patterns and reactions to atmospheric conditions (Dokter *et al.*, 2011; Weisshaupt *et al.*, 2018; Nilsson *et al.*, 2019; Nussbaumer *et al.*, 2021).

Ideally, unfiltered Level II weather radar data would be freely available across Europe for scientific purposes (Shamoun-Baranes *et al.*, 2022). However, access to such data remains restricted due to legal and institutional barriers relating to data ownership, commercial use, and privacy. These barriers often limit the availability of raw data. For analyses requiring data at a fine spatial scale, contacting national meteorological institutes directly is often the only solution. Despite the challenges involved, analysing weather radar data in aeroecology could be important in advertising and promoting the value of an easily accessible archive of unfiltered Level II data, which could encourage policymakers to provide the necessary infrastructure for archiving and sharing data (Desmet *et al.*, 2025).

Stepanian *et al.* (2016) describe the range of Level II data products that are most frequently used to study biological targets and that are provided by modern Doppler and dual-polarisation weather radars. Additionally, Gauthreaux and Diehl (2020) have described how each of these products can be used in aeroecology. The reader is advised to study these research articles for details. Here, I will only provide a summary. In doing so, I have adapted

the terminology of the data products to align with the European OPERA Data Information Model (ODIM) (Michelson *et al.*, 2014). All these variables are stored in a polar grid centred on the radar location. For each elevation angle, typically beginning at 0.5°, there is one such grid. The grid is divided into azimuth gates around the radar; for ODIM, these are usually 1-degree bins and 400-metre range gates along each azimuth. The unique combination of range and azimuth gates for each scan is referred to as a “volume pixel”. (Michelson *et al.*, 2014). High spatial accuracy sufficient for studying birds is usually achieved between 5 and 35 kilometres from the radar. Closer ranges are often affected by clutter, and further away, the spatial accuracy is too low for reliable bird density estimates (Dokter *et al.*, 2019).

- **Logged total uncorrected reflectivity factor** (TH and TV, one for each polarisation) quantifies the proportion of transmitted energy that is returned to the radar, and is the primary measure used to estimate bird densities in the air. Reflectivity is stored separately for horizontally and vertically polarised waves. Therefore, weather radar is inherently different from ornithological radar because it stores information within spatially distinct units and not for individual scatterers. The same applies to all other radar products.
- **Radial velocity** (VRADH and VRADV) measures the component of the target's velocity that is parallel to the radar beam. Considering the radial velocity across a whole scan enables the mean direction of movement and flight speed relative to the ground to be estimated.
- **Spectral width of radial velocity** (WRADH and WRADV) represents the variability of radial velocity within a volume pixel. This metric often indicates atmospheric turbulence and can be used to differentiate between weather, birds and insects, with birds usually showing higher spectral width values than the other two targets due to hydrometeors and insects being much more affected by the wind than birds.

These three, so far mentioned products are available for Doppler weather radar. Dual-polarisation products further improve the distinction between biological and meteorological echoes by providing the next additional products.

- **Logged differential reflectivity** (ZDR) is the ratio between horizontally and vertically polarised reflectivity factors. In other words, it depends on the RCS of the sampled objects in both polarisations. For rain and hail, ZDR is centred around zero. ZDR is probably one of the best indicators for insects in the radar data, as these usually show relatively high values. For birds, ZDR is usually somewhere in between rain and insects. For birds, bats and insects in general, the distribution of ZDR values is typically wider than for rain and hail.
- **Differential phase** (PHIDP) measures phase shifts between horizontally and vertically polarised signals. The phase of each wave can be modified as it travels through a medium and/or scatters off an object, depending on the height and length of the object. For rain, the phase shifts are predictable and narrowly distributed. For aeroecology, the value of PHIDP lies mostly in separating bats from other animals³.

³ The reason why bats have much higher PHIDP values than other targets remains unknown. It is likely that this distinction is caused by dielectric differences resulting from their internal anatomy or flight membranes (Gauthreaux and Diehl, 2020).

- **Correlation coefficient** (RHOHV) quantifies the similarity between the returning waves that are horizontally and vertically polarised. Values for rain and hail are typically around 0.95 with a very narrow distribution, whereas biological targets demonstrate greater heterogeneity.

The above multi-dimensional data products enable increasingly reliable detection and classification of migratory birds in weather radar data and form the technical foundation of modern radar-based aeroecology.

1.5 Research plan and study design

1.5.1 Project aim

Although numerous studies have demonstrated that ALAN affects the behaviour and movement patterns of migratory birds, methodological limitations continue to limit our understanding of these effects. Most large-scale studies have relied on weather radar, which provides a powerful and extensive view of migratory movements. However, the way in which Level II data and Level III products are aggregated and stored restricts the detection of fine-scale behavioural reactions, such as changes in airspeed or flight altitude based on individual responses to local light sources. Furthermore, the lowest airspace, which is crucial for understanding collision risk, is frequently underrepresented in weather radar studies due to the beam geometry, ground clutter, and topographic obstruction. Conversely, although tracking radar is a powerful tool for observing the fine-scale behaviour of individual birds, it lacks the capacity to quantify migratory fluxes in the air. Consequently, it only provides limited insight into how migration is redistributed vertically or horizontally in response to ALAN. This methodological divide separates individual-level behavioural mechanisms from population-level migration patterns. Ornithological radar bridges these two perspectives by enabling the simultaneous monitoring of both individual trajectories and collective migration fluxes. It performs particularly well between 50 and 1000 metres above ground level, thereby covering the altitude layers most important for drawing conclusions about enhanced collision risks in response to ALAN.

The attraction of migrating birds to light and the resulting increased risk of collisions with human infrastructure has been well documented in large, heavily light-polluted urban areas. Much less is known, however, about how birds respond to ALAN in more natural, dimly lit landscapes. Although Cabrera-Cruz et al. (2021) and Osterhaus et al. (2025) have studied fine-scale behavioural responses to low-level ALAN, their results do not account for overall bird density. It is particularly important to understand how migrating birds respond to low-level, patchy ALAN at ecological barriers such as lakes and seas, where they transition between relative darkness and illuminated environments. Furthermore, Van Doren et al. (2021, p. 5) proposed that “migrants flying over water may show a particularly strong attractive response to coastal light pollution, possibly in combination with a general tendency to seek nearby land.” In other words, the attraction of night-time illumination for avian migrants may be particularly strong during sea-crossings and immediately after landing. Moreover, the contrast between dark water surfaces and illuminated shorelines in coastal environments provides a natural experiment to examine how ALAN influences orientation and flight behaviour. This is of particular interest along coastlines where sea-crossings occur alongside coastal following behaviour. Comparing the movements of birds that have crossed the sea

with those that have followed the coastline makes it possible to assess how light pollution shapes migratory behaviour in these distinct ecological contexts, and to better understand the role of ALAN at the interface between aquatic and terrestrial habitats.

Beyond quantifying spatial attraction to light, understanding how ALAN alters the behavioural organisation of migration is essential for identifying the mechanisms underlying light-induced disorientation. Changes in airspeed may directly indicate confusion and disorientation (Van Doren *et al.*, 2017), which could increase energy expenditure and, in combination with shifts in flight altitude, elevate the risk of collisions. Yet, these parameters remain poorly quantified in natural field settings, largely because in-flight behavioural responses to ALAN have rarely been analysed. Furthermore, little is known about how such behavioural changes interact with atmospheric conditions, particularly those affecting visibility.

Combining ornithological radar observations from nearby light-polluted and near-natural sites with atmospheric predictors from ERA5 reanalysis data (Hersbach *et al.*, 2020) allows us to examine how ALAN interacts with environmental conditions to shape the vertical and horizontal structure of nocturnal bird migration. This integrative approach captures fine-scale behavioural adjustments across migratory fluxes and provides a mechanistic basis for linking local light conditions to broader migration patterns.

1.5.2 Study area and radar monitoring

For this research project, the Swiss Ornithological Institute provided four BirdScan MR1 ornithological radar devices for a period of two years. While the radar monitoring was planned for the years 2023 and 2024, a study area had to be defined in 2022 first. Following the aim of this study, there was a clear set of criteria which the study area should fulfil.

Ideally, the study area would be relatively easy to reach from the Swiss Ornithological Institute, as the radar devices needed to be transported via car, and needed to be reachable relatively fast for the possibility of a within-monitoring repair, and because of full maintenance back in Switzerland during the winter 2023/2024.

Geographically, the study area should be located along a coastline with patchy and relatively low-intensity ALAN. Furthermore, the study area should feature frequent sea-crossing (avian movement across the Adriatic Sea from Italy to Croatia) and coastal (avian movement along the Croatian coastline to the northwest) migration directions. Combined with the reachability, this promotes an area in southern Europe. However, most coastal sites across southern Europe are either affected by high-intensity and continuous light pollution (Figure 1.5) or, from a flyway perspective (see Figure 1.1), it is unlikely that coastal and sea-crossing migration directions are about equally present.

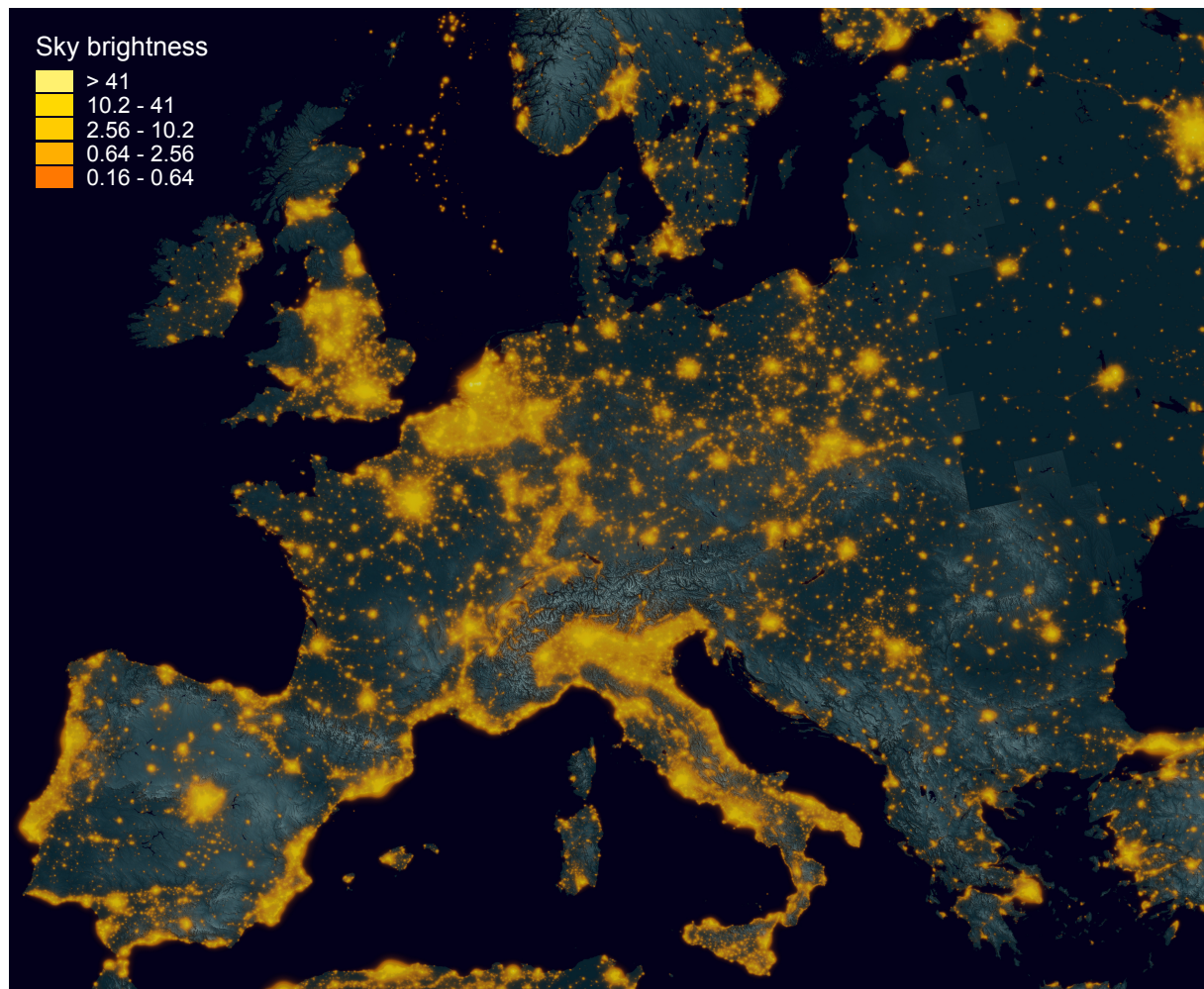


Figure 1.5. **Light pollution across Europe.** The map illustrates ALAN as skyglow or sky brightness. For reference, sky quality with brightness values above 2 is considered “poor” (Duriscoe *et al.*, 2018). Once brightness values reach 10 or above, the Milky Way becomes invisible to the naked eye, and only the brighter stars can still be seen.

Focusing on southern Europe for the water barrier and the relatively good reachability, the monitoring period would focus on the spring migration season, when birds cross the Mediterranean Sea before landfall. The regions of Istria and Dalmatia in Croatia particularly stand out due to their patchy, low-intensity light pollution (Figure 1.5 and Figure 1.6), and a location within the African-Palearctic migration system that features co-occurring sea-crossing and coastal migration directions. Good connections to local Croatian ornithologists further promoted this selection. Ultimately, these personal connections were immensely important for selecting the radar sites and carrying out the data collection, as the radar devices would inevitably be located on private property. Local ornithologists established contact with the property owners. Thus, the exact locations of the radars were defined collaboratively. The best locations were selected from a set of possible sites in QGIS using the annual cloud-free composite from the Visible and Infrared Imaging Suite (VIIRS) Day Night Band (DNB) (Elvidge *et al.*, 2021, 2022).

We deployed four BirdScan MR1 ornithological radars along the Croatian coast. The radars were installed in pairs, two in Istria and two in Dalmatia, to allow for comparative analyses of bird migration under contrasting levels of ALAN. In Istria, radars were positioned in the city of Rovinj on the balcony of a private house (45.0826° N, 13.6370° E; 17 m asl; Figure 1.7) and at the nearby ornithological reserve Palud, in the backyard of an agritourism accommodation

and restaurant, where the surrounding landscape resembles a mixture between forested and agricultural habitats (45.0397° N, 13.6974° E; 17 m asl; Figure 1.8). In Dalmatia, the radars were installed in the city of Zadar on the rooftop of the OTP bank (44.1204° N, 15.2404° E; 19 m asl; Figure 1.9), and at a house that belongs to the Park prirode Vransko jezero, just at the north-western shore of Vransko Lake (43.9282° N, 15.5098° E; 1 m asl; Figure 1.10), here referred to as Vransko Lake. The natural reserve is said to be an important stopover area for migrating birds, especially for wader species (Tutiš and Radović, 2003). The distances between the paired sites were 6.7 km in Istria and 30.4 km in Dalmatia. The distance from the coastline to each site was 450 m in Rovinj, 540 m in Palud, 1550 m in Zadar, and 2350 m at Vransko Lake.

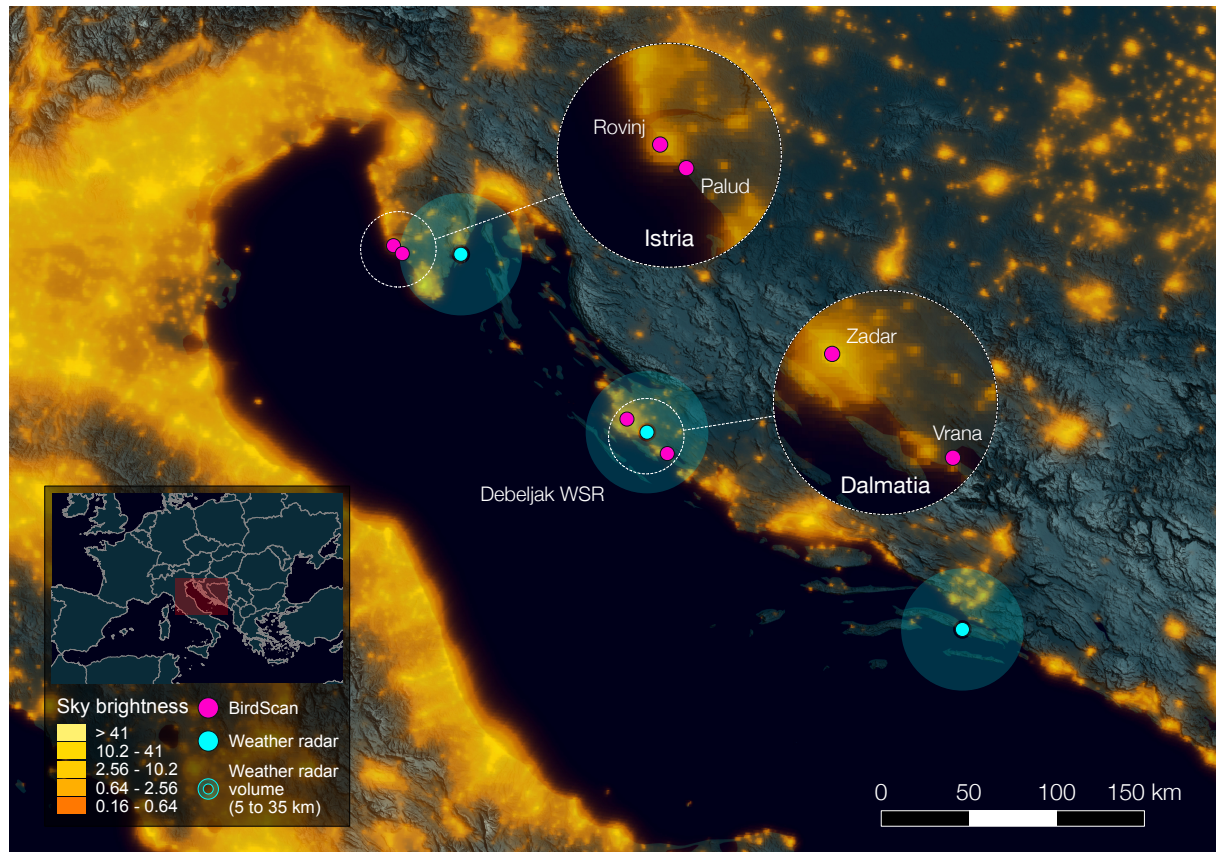


Figure 1.6. **Map overview of the study area.** It illustrates artificial skyglow and the locations of the four BirdScan MR1 radars and three coastal weather surveillance radars in Croatia, as well as the surveyed area in which bird migration monitoring is spatially accurate (indicated by a shaded circle). The dotted circles mark the zoomed-in areas.



Figure 1.7. **BirdScan MR1 in Rovinj.** The radar was installed on a private house, located in the centre of the old town. Picture courtesy of Will Leo Hawkes.



Figure 1.8. **The surroundings of the radar site at the Palud ornithological reserve.** Rovinj is visible in the background. The area is covered by trees and semi-open agricultural land. Picture courtesy of Will Leo Hawkes.



Figure 1.9. **BirdScan MR1 in Zadar.** The radar was installed on the roof of the OTP bank building, located relatively centrally in Zadar. Due to the metal structures on the roof, the radar had to be placed on wooden pallets to prevent interference with the surrounding building parts. Picture: Simon Hirschhofer.



Figure 1.10. **The surroundings of the radar site at Vransko Lake.** The radar is located close to the lake's shore (marked with the red circle). Picture courtesy of Will Leo Hawkes.

Each radar pair represents a gradient of light pollution, with one site within an area of relatively high ALAN levels (Rovinj and Zadar) and the other site characterised by a near-natural nightscape (Palud and Vransko Lake, Figure 1.11).

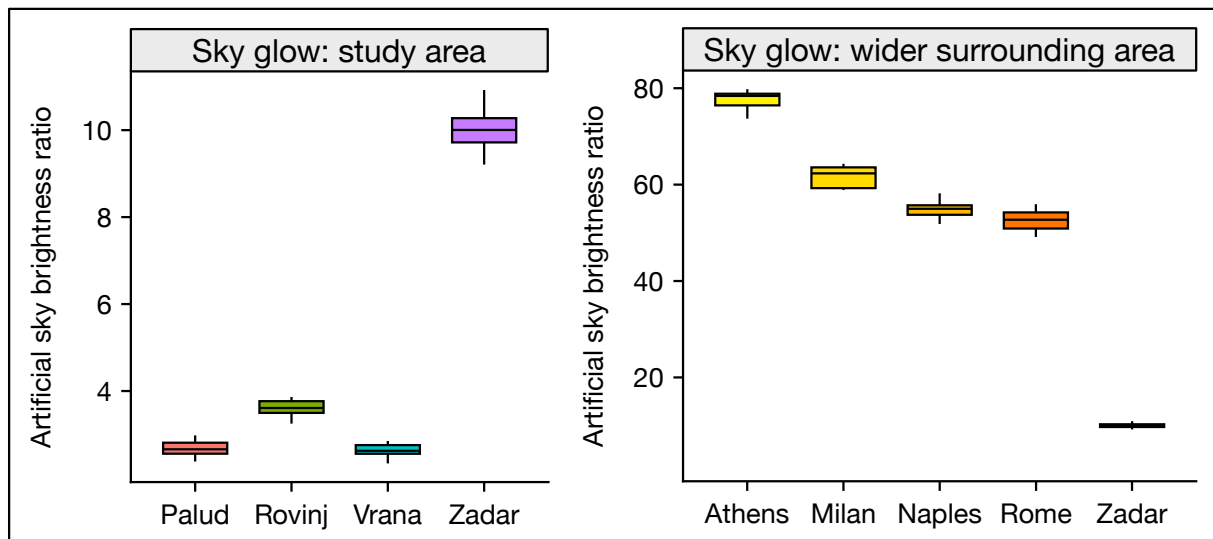


Figure 1.11. **Quantification of skyglow in the study area and its wider surroundings.** Raster cell values were sampled within a 1000 m radius around each location. Skyglow was computed using a 300 km focal window from the VIIRS dataset (Elvidge *et al.*, 2021), in accordance with the methodology outlined by Duriscoe *et al.* (2018). The four brightest cities in the surrounding area were visually selected.

On a larger geographical scale, the four sites are located along the eastern Adriatic coast, which runs from north-west to south-east. The minimum distance to cross the Adriatic Sea between Istria and the Italian mainland is approximately 130 km, and around 160 km further south in Dalmatia, both measured on an SW to NE transect. For a migrating bird, this equates to a crossing time of around 2.4 hours to reach Istria and 3 hours to reach Dalmatia, assuming a mean groundspeed of 15 m/s. This is a realistic yet conservative estimate for nocturnal migrants (Bruderer and Boldt, 2001). This delay in crossing the sea could give rise to a separation of coastal migrants from sea-crossing migrants within a single night, as the vast majority of birds are expected to take off synchronously just after sunset (Akesson, Alerstam and Hedenstrom, 1996).

The topography of Istria and Dalmatia differs markedly. Istria is relatively flat, with the foothills of the Dinaric Alps located around 70 km northeast of Rovinj and Palud. In contrast, Dalmatia is mountainous, with the Velebit, which is also part of the Dinaric Alps, lying only 30 to 40 km northeast of Zadar. The highest local peak within the Velebit, Vaganski Vrh, reaches 1757 m. The coastal morphology also varies. The Istrian coastline is relatively continuous, whereas the Dalmatian coast is fringed by numerous islands, which may provide stopover sites for migratory birds and influence local wind patterns.

In addition to the four BirdScan MR1 radar devices, three operational C-band weather radars from the Croatian Meteorological and Hydrological Service are located along the Adriatic coast (Figure 1.6): Goli (45.0205° N, 14.1223° E; 553 m asl), Debeljak (44.0455° N, 15.3765° E; 208 m asl, Figure 1.12) and Uljenje (42.8944° N, 17.4783° E; 463 m asl). The Goli and Uljenje weather radars were both built at quite high elevations, making them rather unsuitable to study bird migration in the context of light pollution, at least when seeking to draw ecologically and conservation-relevant conclusions. Furthermore, the Goli weather radar is located too far away from the coastline and is therefore not ideally positioned to observe the arrival of migrants crossing the sea from Italy. The location of the Debeljak weather radar instead is ideal for the monitoring of sea-crossing bird migration and to study the effect of ALAN on migrating birds, as the Debeljak weather radar lies centrally between the nearby dark and bright BirdScan MR1 locations, Vransko Lake and Zadar.



Figure 1.12. **The Debeljak weather surveillance radar.** Picture courtesy of Will Leo Hawkes.

1.5.3 Research questions

This PhD project is structured into three consecutive chapters (Chapters 2 to 4) that culminate in a multiscale regional analysis of bird migration phenology along the Croatian coast and of how ALAN affects the in-flight behaviour of migrating birds.

Despite growing evidence that ALAN affects nocturnally migrating birds, three major research gaps remain insufficiently resolved in the Croatian coastal context and more broadly. First, the main migratory fluxes along and across the Adriatic coast have not yet been quantified continuously with radar. Second, it remains unclear whether relatively low-intensity, patchy ALAN causes measurable in-flight behavioural changes such as reduced airspeed or flight altitude, and whether such responses depend on migration context. Third, the extent to which dim coastal illumination redistributes broad-front migration at a landscape scale remains poorly understood. This thesis addresses these gaps using complementary ornithological and weather radar observations.

A first radar-based quantification of bird migration at the coast of Croatia

Current knowledge of the phenology of spring bird migration in Croatia has been based on ringing, field observations and a limited number of tracking studies (Stipčević, 1997; Radović, Kralj and Tutiš, 1999; Kralj *et al.*, 2013, 2020; Mellone *et al.*, 2013). While these studies have outlined broad migration patterns, they offer limited insight into the fine-scale temporal dynamics required to characterise migration intensity and direction on an individual night basis. Large-scale quantification of simultaneous migratory fluxes around the Mediterranean basin, based on moonwatching, indicated that Croatia lies within the region where the eastern and central flyways converge (Bruderer and Liechti, 1999). It is therefore assumed that spring migration along the Adriatic coast comprises two dominant movements: a north-eastern route across the Adriatic Sea and a north-western route along the Croatian coastline.

However, these migratory fluxes have never been quantified continuously throughout a complete spring migration season. Quantifying migration intensity, timing and direction along and across the Adriatic is a necessary first step towards assessing whether distinct sea-crossing and coastal components can be identified and analysed separately. This is the focus of Chapter 2, which provides the first radar-based characterisation of nocturnal spring migration at the Croatian Adriatic coast. This is achieved by examining migration intensity and flight directions across sites, throughout the season and within individual nights. By establishing the main migratory fluxes and their temporal structure, this chapter lays the foundation for subsequent analyses of how different migratory components respond to ALAN.

RQ1.1: *What are the main migratory fluxes of nocturnally migrating birds at the Croatian Adriatic coast during spring migration?*

RQ1.2: *Do these migratory fluxes separate into distinct sea-crossing and coastal-following components, such that the two directions can be analysed separately in relation to ALAN?*

HP1: *Nocturnal migration activity at the Croatian Adriatic coast is dominated by two main components: sea-crossing and coastal migration. These components can be identified based on differences in the shape of within-night migration intensity profiles.*

Local-scale reactions of birds to light pollution

Although the effects of ALAN on migrating birds have been widely discussed, there is still a substantial lack of knowledge regarding their fine-scale behavioural responses to low-level illumination. There is particularly little evidence for subtle signs of disorientation, such as reduced airspeeds, or for factors relevant to collisions, such as reduced flight altitudes. Furthermore, the interaction between ALAN and impaired visibility in shaping these behavioural adjustments remains poorly understood, even though reduced visibility has long been linked to elevated collision rates.

Chapter 3 again uses the BirdScan MR1 data and builds on Chapter 2. By distinguishing sea-crossing migration from coastal migration, the overall migratory activity can be separated into different geographic contexts. Birds that cross the sea before approaching the coast may react differently to ALAN because the illuminated coastline contrasts with the surrounding darkness. This differs from birds migrating along the coastline, which regularly encounter light-polluted areas. These groups may also rely on different navigational cues, leading to different in-flight responses. Understanding these differences should provide new insight into how local landscape features influence the consequences of ALAN exposure for migratory behaviour. A particular focus is whether relatively low-intensity coastal ALAN already produces measurable behavioural responses.

RQ2.1: *How do airspeeds and flight altitudes of birds differ between light-polluted and near-natural sites?*

RQ2.2: *Do these reactions differ between birds that crossed the sea and birds that followed the shoreline?*

RQ2.3: *What is the interactive effect between ALAN and impaired visibility on airspeeds and altitudes?*

HP2: *Birds show lower airspeeds and reduced flight altitudes in response to ALAN for both, coastal and sea-crossing directions. Because the signs of confusion are similar in both directions, the reactions are similar. Impaired visibility amplifies these reactions.*

Redistribution of sea-crossing birds in response to ALAN from a weather radar

Weather radar has become an essential tool for studying large-scale patterns of nocturnal bird migration. Along the Croatian coastline, weather radar data can complement BirdScan MR1 radar monitoring. Given that sea-crossing and coastal migration directions can clearly be separated in this region by focusing on distinct nights and times within a season, the attraction to light can specifically be investigated for sea-crossing migrants, from whom a stronger reaction is expected.

The Debeljak weather radar is situated between the light-polluted urban area of Zadar city and the near-natural landscape surrounding the Vransko Nature Reserve, an important known stopover site for migrating birds. This geographical configuration provides an ideal opportunity to quantify sea-crossing migrants in both airspaces and compare their densities throughout the night.

Both BirdScan MR1 and weather radar systems are used to quantify bird migration. BirdScan MR1 is used to quantify migration intensity along the sea-crossing and coastal gradients,

while weather radar is used exclusively to quantify bird densities during nights dominated by sea-crossing migration. Together, these systems make it possible to compare the responses of the two groups to ALAN and to gain deeper insight into the role of relatively dim coastal illumination for migrating birds in coastal ecosystems (Chapter 4).

RQ3.1: *Are there differences in bird density between an urban, light-polluted area and a nearby, near-natural area during nights dominated by sea-crossing migration?*

RQ3.2: *How does this difference between light-polluted and near-natural areas change over the course of a night, and could this reflect temporal dynamics in barrier crossing and the timing of landfall?*

RQ3.3: *How does visibility affect attraction by ALAN?*

HP3: *Bird densities and migration intensity are higher over light-polluted areas. This increase is more pronounced for sea-crossing migration than for coastal migration. The attraction is strongest during sunset reorientation and towards the end of the night, while searching for a suitable stopover site. Impaired visibility amplifies the attractive effect of ALAN on birds.*

1.5.4 Overarching research aim and structure of this thesis

The following three Chapters 2 to 4 adopt a sequential approach to understanding the fundamental patterns of avian spring migration in Croatia and how these are affected by coastal ALAN. The chapters are based on separate journal publications. The first article (Chapter 2, published in *Movement Ecology*) represents the first radar study of avian spring migration phenology on the Croatian coast. The study aimed to distinguish between sea-crossing and coastal migration using functional data analysis. The second article (Chapter 3, published in *Biological Conservation*) provides a detailed assessment of behavioural responses to dim ALAN in the Istria region of northern Croatia, as captured in the BirdScan MR1 data. The third article (Chapter 4, submitted to *Remote Sensing in Ecology and Conservation*) complements the second by using weather surveillance radar to examine the attraction of birds to dim ALAN on a larger scale. Moreover, this thesis proposes a multiscale approach that combines perspectives across spatial scales to better understand how individual behavioural responses shape large-scale migration patterns. This is achieved by combining BirdScan ornithological radar with weather radar.

2 Avian spring migration at the east Adriatic coast: coastal and sea-crossing dynamics of intensity, timing, and flight directions

Simon Hirschhofer^{1,2}, Peter Ranacher¹, Barbara Helm², Davor Ćiković³, Robert Weibel¹, Sanja Barišić³, Vesna Tutiš³, Louie Taylor³, Maja Bjelić Laušić⁴, Baptiste Schmid²

¹ University of Zurich, Department of Geography, Zurich, Switzerland

² Swiss Ornithological Institute, Department of Bird Migration, Sempach, Switzerland

³ Croatian Academy of Sciences and Arts, Institute of Ornithology, Zagreb, Croatia

⁴ Public Institution Nature Park Vransko Jezero, Biograd na Moru, Croatia

Author contributions: **SH:** conceptualisation, data curation, formal analysis, investigation, methodology, project administration, software, validation, visualisation, writing—original draft, writing—review and editing. **BS:** conceptualisation, data curation, funding acquisition, investigation, methodology, project administration, resources, software, supervision, validation, writing—original draft, writing—review and editing. **PR:** conceptualisation, methodology, supervision, writing—review and editing. **BH:** conceptualisation, funding acquisition, project administration, resources, supervision, writing—review and editing. **DC:** writing—original draft, writing—review and editing. **RW:** conceptualisation, funding acquisition, supervision, writing—review and editing. **SB:** writing—original draft, writing—review and editing. **VT:** writing – original draft, writing—review and editing. **LT:** project administration. **MBL:** project administration.

Published as:

Hirschhofer, S. et al. (2025) 'Avian spring migration at the east Adriatic coast: coastal and sea-crossing dynamics of intensity, timing, and flight directions', *Movement Ecology*, 13(1), p. 44. <https://doi.org/10.1186/s40462-025-00572-3>.

Data and code:

Hirschhofer, S. et al. (2025). R scripts and data for the article: 'Avian spring migration at the east Adriatic coast: coastal and sea-crossing dynamics of intensity, timing, and flight directions', *Movement Ecology*. Zenodo. <https://doi.org/10.5281/zenodo.15674524>.

Erratum submitted to *Movement Ecology*:

In the original manuscript, unexpectedly low migration intensity and a wide distribution of flight directions were reported for the Vransko Lake radar site. The results were discussed only briefly, acknowledging the inability to exclude a technical malfunction of the radar, and highlighting the need to confirm the observed migration pattern by collecting and analysing further data.

New insights from cross-calibrations with other radar devices after the manuscript was accepted for publication confirmed that the data from Vransko Lake was indeed affected by a major hardware failure of the radar receiver. Therefore, the data from Vransko Lake had to be removed from the analysis post-publication. Despite the removal of these data, the general conclusions of the study, however, remained predominantly unchanged.

The version provided here is an updated, consolidated version of the research article that includes the changes from the erratum.

The full text of the erratum is provided in Appendix A.

Supporting Information in Appendix B.

2.1 Abstract

Background: Each spring, migratory birds converge along the Croatian coast from various directions, creating a dynamic intersection of flight paths. Many birds are thought to cross the Adriatic Sea, while others follow a northward route along the coastline. As most migratory birds initiate flight shortly after sunset, we hypothesised that sea-crossing migrants would arrive with a delay at the Croatian coast, compared to migrants that were following the coast, resulting in potentially intricate spatiotemporal patterns that remain poorly understood.

Methods: We deployed four ornithological radar devices along the Croatian coastline: two in southwestern Istria and two in northern Dalmatia. One Dalmatian site had to be removed from the analysis due to a hardware failure of the radar. These radars tracked migratory bird activity up to 1000 m above ground, recording intensity and flight directions and their variations across sites, seasons, and individual nights. We conducted an exploratory analysis of these variations, applied functional principal component analysis and hierarchical clustering to summarise within-night activity profiles, and compared these profiles between sites and across the migration season, alongside associated flight direction distributions.

Results: During the early migration season, migration intensity was similar across all technically active sites, but site-to-site variation increased markedly in May. In March, flight directions were predominantly towards NNE, indicating mainly sea-crossing migration throughout the night. In April, NW directions dominated the first half of the night, shifting to scattered N directions later; in Dalmatia, even strong W components were observed early in the night. By May, the W to NW movement towards the Italian coast was typical for early-night activity. Later in the night, flight directions shifted towards NE over Istria and N at the Dalmatian site in Zadar. Contrary to our expectations, within-night intensity profiles could not be fully linked to specific directional patterns.

Conclusion: This study points to the complex interplay between coastal and sea-crossing migration along the Croatian coast. Our results demonstrate significant variability in the timing of migration within single nights in the context of aquatic barriers. Crossing such a barrier results in downstream delays compared to birds migrating along the barrier. Between nights, one behaviour or the other may dominate the overall activity, causing the shifts in within-night timing. In addition, barrier crossing is likely to be strongly influenced by weather conditions, contributing to the variability in the within-night timing of migration. However, measured flight directions were not always consistent with within-night timing, highlighting the complexity of

avian migration in the context of aquatic barriers. This highlights the need for further research with high temporal resolution to gain a deeper understanding of migration behaviour in response to such barriers.

2.2 Introduction

In the African-Palearctic bird migration system, Croatia, situated in southeastern Europe, serves as a connection point for the system's three main flyways - western, central, and southeastern - linking Europe and Africa (Busse, Zaniewicz and Cofta, 2015). Ringing recoveries and observational studies across the Adriatic region suggest that migration along the central flyway on an SSW-NNE axis, and south-eastern flyway on a SSE-NNW axis predominate over western flyway directions on a WSW-ENE axis (Kiepenheuer and Linsenmair, 1965; Bruderer and Liechti, 1999; Kralj *et al.*, 2013). During the spring migration season, these general directions result in two principal modes of migration. The first is coastal migration, following the coastline from SE to NW. The second is the sea-crossing migration from SSW to NNE, in which birds traverse the Adriatic Sea between Italy and Croatia, which is on average 160 km wide. In contrast to some inland migration, where the number of migrants can be correlated over a large area (Tschanz *et al.*, 2019), the complexity of Croatia's coastal topography is expected to give rise to intricate spatio-temporal dynamics. The delay caused by crossing a barrier, coastal and sea-crossing migration should result in distinct differences in the within-night timing of the two streams (Fortin, Liechti and Bruderer, 1999; Weisshaupt *et al.*, 2018). During the spring migration, short-distance migrant activity precedes the arrival of the first long-distance migrants returning from sub-Saharan Africa in mid-April. (Gargallo *et al.*, 2011). These two groups might also lead to directional differences, as well as shifts in within-night timings, as some long-distance migrant species are known for their prolonged flights over open seas (Adamík *et al.*, 2016).

Despite Croatia's importance as a central region in the migration system, current understanding relies mainly on bird ringing (Kralj *et al.*, 2013), observational research (Stipčević, 1997; Radović, Kralj and Tutiš, 1999; Kralj and Dolenec, 2008), and limited tracking studies of non-passerine species (Mellone *et al.*, 2013; Kralj *et al.*, 2020; Monti *et al.*, 2024). Ringing birds, e.g., the capture, marking, and recapture of individual birds, is the oldest method for researching migration patterns in a standardised way. Bird ringing data are invaluable for establishing migratory networks between breeding and wintering sites, including major stopovers at the population level, and have been successfully used to improve conservation practices internationally (Anderson and Green, 2009). In Croatia, ringing has been performed since 1910, yielding comprehensive migratory networks and estimated phenologies for 308 migratory bird species (Kralj *et al.*, 2013). Observational research often provides insight into migratory phenology, such as species composition at single sites (e.g. waders, 8). However, these methods have limitations in depicting active, in-flight migration and require extensive effort to draw quantitative insights (Thorup *et al.*, 2014).

Radar offers a standardised way to quantify migrants at passage sites (Liechti, Bruderer and Paproth, 1995; Schmaljohann *et al.*, 2008). Radar monitors migration continuously, regardless of daylight or cloud cover, and is only limited by data removal due to rainfall, during which, however, a majority of birds tend to pause their migration (Erni *et al.*, 2002). We focus here on dedicated ornithological radar, which collects information at the level of individual birds. A bird entering the radar beam can be tracked as it crosses the beam. From its echo, the radar

gathers information on flight direction, with which it is possible to disentangle directed migratory movement from undirected local activity, which has been shown to increasingly dominate the overall avian activity towards the end and outside of the migration seasons (Tschanz *et al.*, 2019; Shi *et al.*, 2021). Furthermore, speed relative to the ground, altitude and even wing flapping patterns as a function of echo intensity over time are estimated. Individual echoes are used to calculate hourly passage rates, known as the migration traffic rate (MTR), which takes into account the altitude-dependent detection probability bias inherent in ornithological radar (more in the methods). These can be used to analyse seasonal phenology, but also to gain an in-depth understanding of within-night timing by assessing nightly profiles.

Understanding movement patterns along major flyways is essential for identifying bottlenecks where birds congregate in large numbers (Hirschhofer *et al.*, 2024) and key stopover sites that provide the necessary conditions for resting and refuelling (Kirby *et al.*, 2008; Runge *et al.*, 2015). Until recently, migration research has primarily focused on aggregating migration phenology at a nightly scale, with an emphasis on seasonal timing, resulting in the notation that more than half of the total migration volume occurs within just one-quarter of the nights in the spring season (Hirschhofer *et al.*, 2024), here referred to as seasonal peaks (Horton *et al.*, 2021). However, high-resolution time series of intra-night variability in migration intensity, covering entire migration seasons, remain understudied.

Quantitative data with high temporal resolution are essential for studying migration patterns in regions with geographic barriers, as within individual nights, the timing of peak migration intensity is strongly influenced by upstream topography (Bruderer and Liechti, 1999; Kranstauber, Bauer and Shamoun-Baranes, 2023), while during barrier crossings, weather conditions, particularly wind, play a crucial role in causing delays or allowing for a faster passage (Bradarić *et al.*, 2024). A deeper understanding of these dynamics is crucial for the timely coordination of conservation efforts (Runge *et al.*, 2014), such as the Lights Out initiative in the US (Van Doren and Horton, 2018) or the temporary shutdown of wind turbines at sensitive sites (Drewitt and Langston, 2006).

Traditionally, researchers have used pointwise statistical metrics such as the timing of the nightly peak migration intensity relative to sunset or the interquartile range (IQR) of migration intensity based on standardised nighttime hours to describe variations between migration nights. Yet, these approaches can obscure some of the differences between observations by missing information on the profile of migration intensities, defined here as the within-night migration intensity as a function of hour after sunset. Relating to migration in the presence of partial barriers, one pattern that might be missed is the occurrence of simultaneous barrier-crossing and barrier-following movement, which would result in separate timings of peak activity. To address this, a new approach conceptualises migration intensity measurements throughout a night at a given location as continuous functions over time. These functions can then be analysed and generalised into fundamental types using functional principal component analysis (FPCA) and hierarchical clustering (Assunção *et al.*, 2020; Godard *et al.*, 2020).

If applied to bird radar data, FPCA is first used to conceptualise the hourly measured migration intensity within individual radar nights (defined as unique combinations of night and site) as functions. Next, eigenfunctions which capture the maximum variability between radar nights are estimated. The measured migration intensity profiles of individual radar nights can

then be described with just a few parameters by using the eigenvalues. Based on these eigenvalues, the profiles can be clustered and typified.

We present here the first radar-derived phenology of avian spring migration in Croatia, focusing on inter-night phenology across the season, and intra-night phenology of intensity profiles of 276 radar nights. We analyse the flight direction distributions in relation to season and shape of within-night migration intensity profiles. Using three of the originally four vertical-looking radar devices along the Adriatic coast of Croatia (Figure 2.1), we address the following research questions and hypotheses:

- 1) How do migration intensities vary across four sites over the migration season, and how do these intensities correlate within and between regions? We expect migration intensities to exhibit a strong correlation between study sites, particularly within regions. This correlation should be highest at the start of the season in March but decline toward the end of the season after mid-May due to increasingly undirected avian activity.
- 2) How do flight directions vary across sites, regions, and time during the migration season? In general, we expect to detect migration along two main directions. Coastal migration is expected to favour NW directions, while sea-crossing migration should favour NE. Flight directions are anticipated to differ more between regions than within them, align closely in March and April, and become more dispersed later in the season, when local movements gradually take over the overall activity.
- 3) How does the timing of the nightly migration peak relate to shifts in migration direction along the coast versus across the sea? Coastal migration is expected to show an early intensity peak with predominant NW flight directions, while sea-crossing migration should show a delayed peak with predominant NE directions. Nights with strong activity along both routes may exhibit bimodal directions, shifting from NW after sunset to NE later in the night.

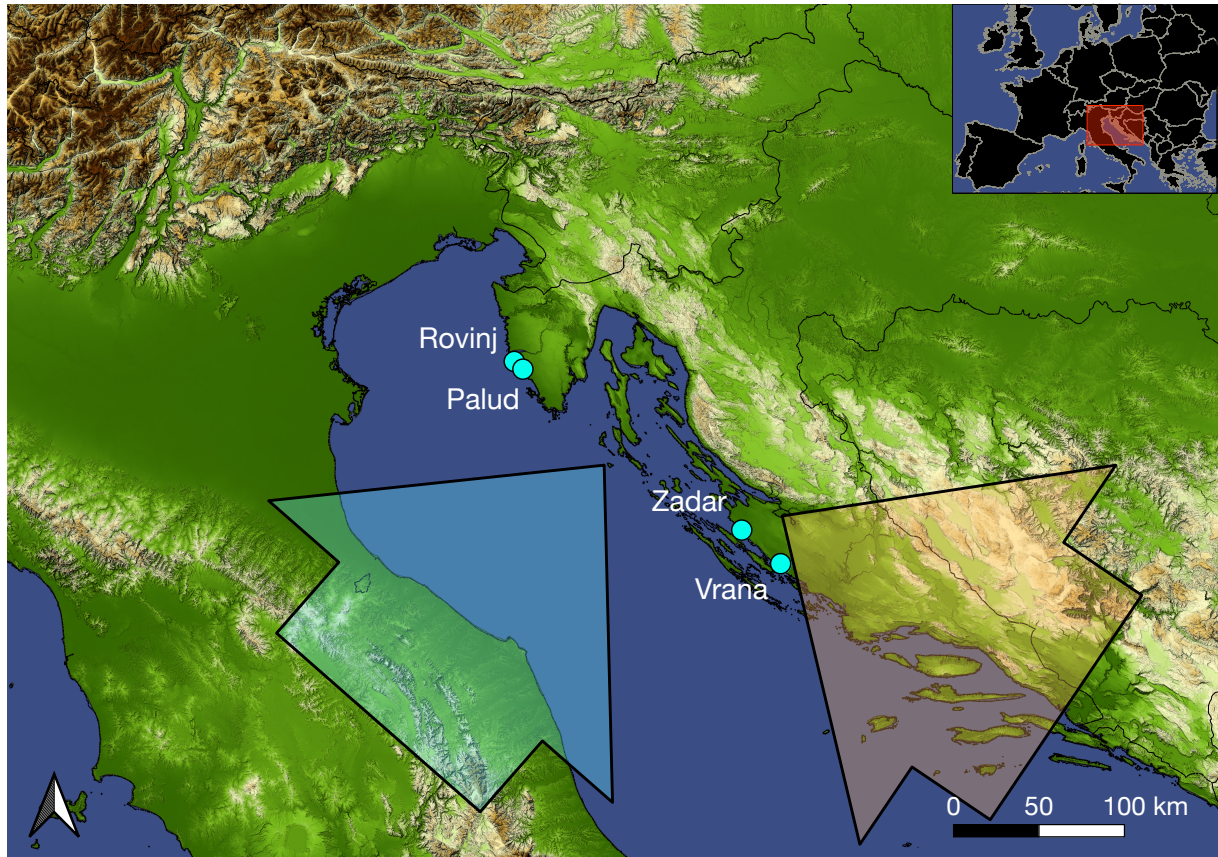


Figure 2.1. **The locations of the four radar sites in Rovinj, Palud, Zadar and Vrana, each equipped with a BirdScan MR1 ornithological radar.** Broad arrows indicate the expected directions of coastal (reddish) and sea-crossing (blueish) migration.

2.3 Methods

2.3.1 Study area

We installed four BirdScan MR1 ornithological radar devices in pairs along the Croatian coast (Figure 2.1): two in the Istrian region (Rovinj: 45° 4' 57.5034" N, 13° 38' 13.524" E; 17 m asl.; Palud: 45° 2' 22.92" N, 13° 41' 50.928" E; 17 m asl.), and two in the Dalmatian region (Zadar: 44° 7' 13.656" N, 15° 14' 25.476" E; 19 m asl.; Vrana: 43° 55' 41.736" N, 15° 30' 35.1714" E; 1 m asl.). Distances between the paired sites are 6.7 km (Istria) and 30.4 km (Dalmatia).

On a larger geographical scale, these four sites are located along the East Adriatic coast, which follows an NW-SE axis. Across the sea, the distance between Istria and the Italian mainland is approximately 130 km, following an SSW to NNE transect. Further south in Dalmatia, this distance increases to approximately 200 km.

The topography of the study areas varies significantly. Istria is relatively flat, with the northern foothills of the Dinaric Alps (Kras area) located about 70 km northeast of Rovinj and Palud. In contrast, the mountainous area is much closer to the Dalmatian sites, with the Velebit mountain range (part of the Dinaric Alps) located about 30-40 km northeast of Zadar and Vrana. The highest peak in this range, Vaganski Vrh, reaches 1,757 m. The coastal features also differ between regions. The Istrian coast is relatively uninterrupted, while the Dalmatian coast is characterised by numerous islands. These islands potentially offer suitable stopovers

for migratory birds and may influence local wind patterns, potentially affecting migration routes and timing (Stipčević, 1997; Radović *et al.*, 2008).

2.3.2 Radar monitoring

We used BirdScan MR1 ornithological radar (manufactured by Swiss Birdradar Solution AG), a modified X-band marine radar (Bridgemaster©, 25 kW, 9.4 GHz, wavelength ca. 3.2 cm), capable of retrieving echoes of small passerines up to 1000 m agl. The vertical-looking 20 dB horn antenna (17.5° nominal beam angle at -3dB) rotates at 0.8 Hz on a 0.2 ° nutated axis, which allows the measurement of flight directions and ground speeds of birds aloft (Schmid *et al.*, 2019). Birds are automatically detected by the radar software. Bird echoes are further classified based on radar cross section and wing flapping pattern (Zaugg *et al.*, 2008; Schmid *et al.*, 2019). For the present study, we focused on small- to medium-sized, constant- and intermittent-flapping birds (here referred to as wader-type or passerine-type), which underlines the emphasis on nocturnally migrating birds by maximising the exclusion of local activity of larger seabirds. This resulted in the removal of 269,959 out of a total of 457,064 echoes (see Supporting Information). Focusing only on nocturnal migrants further reduced the data to 156,211 echoes.

The radar data covers the spring migration season of 2023 from March 1 to May 31. Technical problems led to gaps in the time series: Rovinj from March 29 to April 11; Palud from March 1 to March 3, and from April 28 to April 29. The Vrana data had to be completely excluded from the analysis due to a serious hardware failure of the radar. In total, this left us with 276 radar nights (unique combinations of radar site and night of the year). The radar can falsely interpret rain as bird echoes. To prevent these false positives, we set the migration intensity to zero during rainfall. Rainfall periods are detected by the radar software but must be manually checked and adjusted. Corrections were done based on visualised raw data, up to a temporal resolution of one minute. We focused on nocturnal migration only and defined the length of the night as the time between civil dusk and civil dawn, which was calculated for each site separately using the *suncalc* R package (Thieurmél and Elmarhraoui, 2022). From this point onwards, all dates in the text and figures refer to the date on which the sunset took place.

From individual bird echoes, the radar software computes the MTR, which is a measure of migration intensity that accounts for the altitude-dependent sample bias of the radar. In short, the surveyed volume increases with increasing distance to the radar. Thus, for example, a bird detected at 100 m agl gets a higher weight in the computation of the MTR than a bird sampled at 800 m agl. The weighting is here referred to as the MTR factor (MTR_f). The MTR as a measure of migration intensity translates into the number of birds per hour per virtual transect of one kilometre, or, in other words, the hourly average number of birds in a 500 m radius around the radar. The theory, computation, and validation of the MTR are described in detail in a previous publication (Schmid *et al.*, 2019).

To evaluate the similarity of migration intensity between sites, we used Spearman's correlation coefficient ρ (rho) to account for the non-normal distribution of the MTR. Due to the malfunctioning sensor of the Vrana radar, we excluded the data from this site from the correlation analysis.

To describe the flight direction statistics, we used the individual echoes directly. Throughout the whole season, we collected 99,823 passerine- and wader-type echoes with directional information (out of a total of 149,195 nighttime echoes). To investigate the degree of directional alignment, we computed the mean resultant vector length (MRL) after Fisher (1993), while adding the MTR factor as weights for the echoes:

$$MRL = \frac{1}{n} \sqrt{\left(\sum_{n=1}^n \cos \theta_n \cdot MTR f_n \right)^2 + \left(\sum_{n=1}^n \sin \theta_n \cdot MTR f_n \right)^2}$$

where n are the echoes, θ_n are the flight directions of these echoes in radians, and $MTR f_n$ are the MTR factors for these echoes. The scale of the MRL is then $[0, 1]$, where 1 means that all birds fly in the same direction, while increasingly smaller ρ means a smaller degree of alignment (Fisher, 1993). For a statistical summary, we also calculated the weighted mean and weighted IQR of flight directions.

2.3.3 Conceptualisation of nightly migration intensity profiles

We analysed nightly migration intensity profiles using FPCA, a statistical method for describing, modelling, and summarising sets of functions - in this case, the within-night migration intensity profiles. FPCA reduces the dimensionality of this set of profiles while preserving maximum variability, enabling distinctions between profile types based on overall migration intensity, peak timing, and the potential presence of multiple peaks, which may arise from simultaneous coastal and sea-crossing migration. First, instead of point measurements of hourly MTR, each radar night is described by a function:

$$MTR_r(t) = f_r(t) + \varepsilon_r(t)$$

where $MTR_r(t)$ is the migration intensity profile of a radar night r , $f_r(t)$ is the deterministic part of the function, and $\varepsilon_r(t)$ is the error term. Due to the seasonal shift of day and night length, we first normalised the time grid of individual radar nights to percentages, so that nightly migration intensity profiles can be described independently from seasonality. This also means that the time grid was coarser in early spring, when nights were longer, than in late May. With FPCA, the deterministic part of the function above can be expressed by a set of k continuous eigenfunctions, or functional principal components (FPCs), $\phi_1(t)$ to $\phi_k(t)$. These FPCs comprise information on all radar nights. The eigenvalues of these FPCs, $\xi_{r,1}$ to $\xi_{r,k}$, here referred to as FPC scores, model the variation between radar nights. These are different between radar nights and can best be described as weights on the FPCs. We used the *fdapace* R package (Zhou *et al.*, 2022) to compute the FPCs $\phi(t)$ and the scores ξ_r . From the set of FPCs, we selected the first three $\phi_1(t)$, $\phi_2(t)$, and $\phi_3(t)$, describing more than 85% of the total variation in the data. In *fdapace*, the FPCs and FPC scores describe change relative to a mean function $\mu(t)$. After the FPCA, the deterministic part of each radar night $f_r(t)$ can be described by the mean function $\mu(t)$, where the linear combination of FPCs $\phi(t)$ and their scores ξ_r is added:

$$f_r(t) = \mu(t) + \xi_{r,1}\phi_1(t) + \xi_{r,2}\phi_2(t) + \xi_{r,3}\phi_3(t)$$

Simulated profiles of different eigenvalues of the first three eigenfunctions are displayed in the Supporting Information.

2.3.4 Clustering intensity profiles

Now that the nightly migration intensity profiles had been described by FPCA, the next step was to group these profiles by migration intensity and time of the intensity peak. We performed a hierarchical clustering based on the FPC eigenvalues $\xi_{r,1}$, $\xi_{r,2}$, and $\xi_{r,3}$. We used the Minkowski distance to calculate the similarity between the eigenvalues of the radar nights, and then Ward's method to hierarchically aggregate the radar nights using the `hclust` function from the *stats* R package (R Core Team, 2013). Based on the dendrogram structure, we defined four clusters, achieving a cophenetic correlation coefficient of 0.61, which signalled an acceptable representation of the paired distances between the eigenvalues.

We characterised the typical activity profile per cluster by first finding the cluster centres, which we did by calculating the mean value of ξ_1 , ξ_2 , and ξ_3 for all radar nights within a cluster, and then simulating the resulting cluster centre activity profile from these averaged eigenvalues.

To investigate whether the nightly migration intensity and time of the peak were related to sea-crossing or coastal migration, we analysed flight direction distributions per cluster and site.

2.4 Results

2.4.1 Migration intensity

We observed strong variation in migration intensity between successive nights (Figure 2.2). Monthly migration intensity means were lowest during April, and higher during March (Istria) and May (Zadar). Over the whole season, the migration intensity was similar between the neighbouring sites Palud (mean MTR = 483; max MTR = 1889 on March 13; IQR = 427) and Rovinj (mean MTR = 513; max MTR = 2392 on March 13; IQR = 479) in Istria. In Zadar, we measured the strongest intensity during May (mean MTR = 516; max MTR = 3317 on May 22; IQR = 420).

The similarity of migration intensity across sites was highest during March (Rovinj and Palud: $\rho = 0.92$, $p < 0.05$; Rovinj and Zadar: $\rho = 0.71$, $p < 0.05$, Palud and Zadar: $\rho = 0.78$, $p < 0.05$), decreased during April (Rovinj and Palud: $\rho = 0.91$, $p < 0.05$; Rovinj and Zadar: $\rho = 0.59$, $p < 0.05$, Palud and Zadar: $\rho = 0.66$, $p < 0.05$), and was lowest during May (Rovinj and Palud: $\rho = 0.70$, $p < 0.05$; Rovinj and Zadar: $\rho = 0.58$, $p < 0.05$, Palud and Zadar: $\rho = 0.25$, $p = 0.19$).

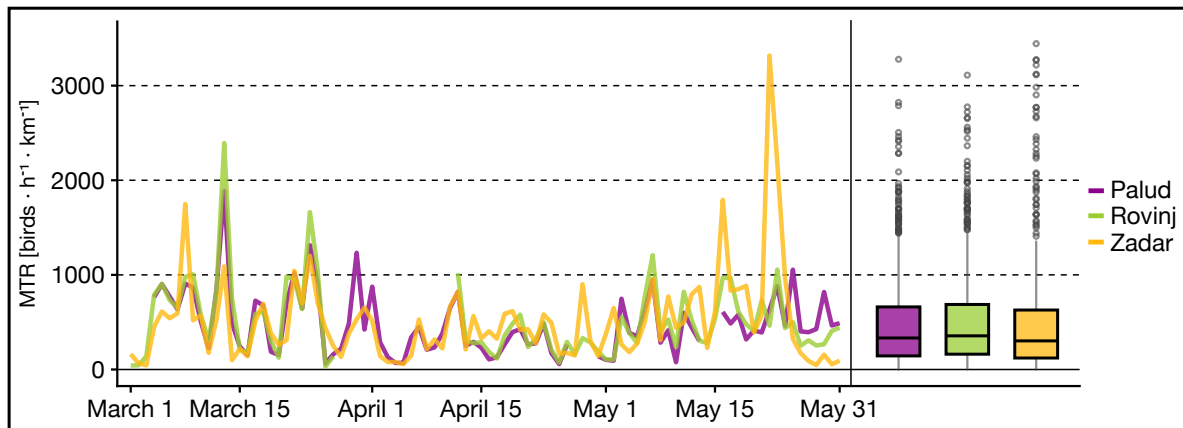


Figure 2.2. **Phenology of the 2023 spring migration season at the Croatian coast.** Left: Timeline plot of the nightly mean migration intensity for the three operational sites. Right: Summary of migration intensities at each site shown as boxplots, including the median, interquartile range, and outliers.

2.4.2 Flight directions

We found flight directions to be similar between the Istrian sites (Palud: mean direction = 5.2° (N), MRL = 0.72; Rovinj: mean direction = 2.9° (N), MRL = 0.72). Compared to the site from Istria, flight directions in Zadar were more aligned to the coast (Zadar: mean direction = 339° (NNW), MRL = 0.68).

In Istria, the directional distributions predominantly showed a concentrated NNE migration during the first three quarters of March, gradually shifting to more dispersed N and even NW to NNW directions as the season progressed. Over Zadar, the dispersal and directional shifts in April and early May were even more pronounced than in Istria. Towards the end of May, directional concentration decreased notably at all sites (Figure 2.3). In general, the degree of directional alignment was highest in March and lowest in May for all sites (Palud: March = 0.77, May = 0.66; Rovinj: March = 0.81, May = 0.64; Zadar: March = 0.71, May = 0.56).

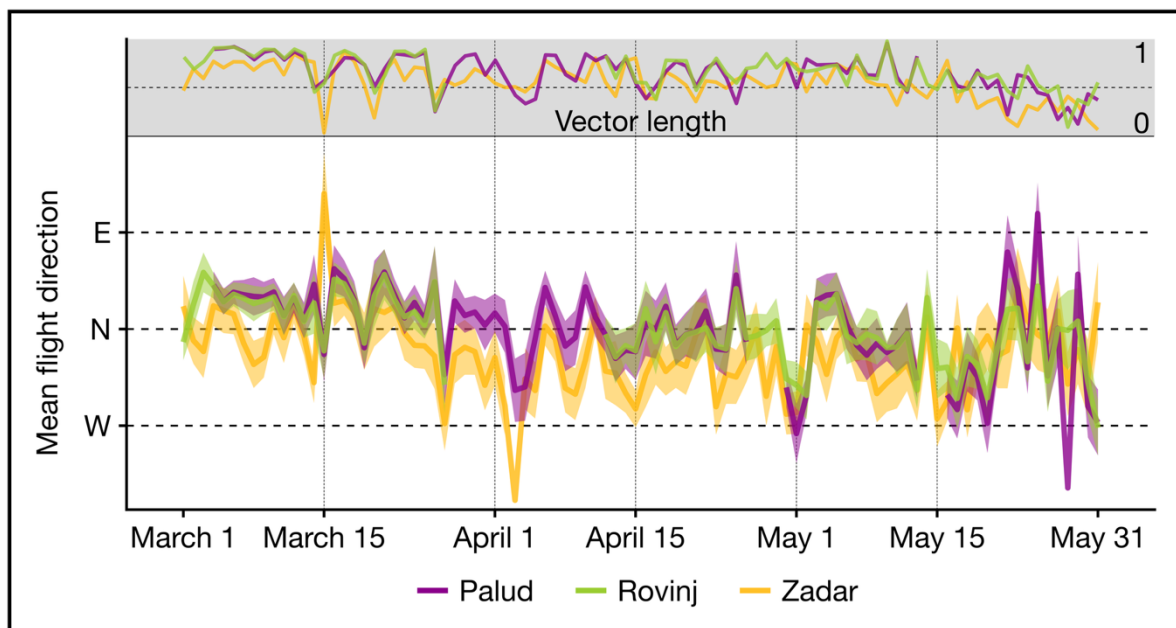


Figure 2.3. **Nightly flight direction means and interquartile ranges for each radar site during the spring migration season 2023.** Inset plots show the concentration of flight direction as the mean resultant vector length (MRL).

On a finer temporal scale, we found that during March, the distribution of flight directions remained relatively constant throughout the night, with NNE migration from the sea towards inland. Migration at the Dalmatian coast was slightly more scattered than on the Istrian peninsula (Figure 2.4). In April, directional patterns began to diverge between the first and second half of the night: early-night migration featured NW to NNW components, with even W directions over Dalmatia. Later in the night, flight directions shifted towards N and NE over Istria, while the Zadar station showed more scattered directions around NW to N. By May, this pattern became even more pronounced, with W to NW migration dominating the first half of the night, whereas later in the night, the bulk of directions shifted towards NE over Istria and N above Zadar.

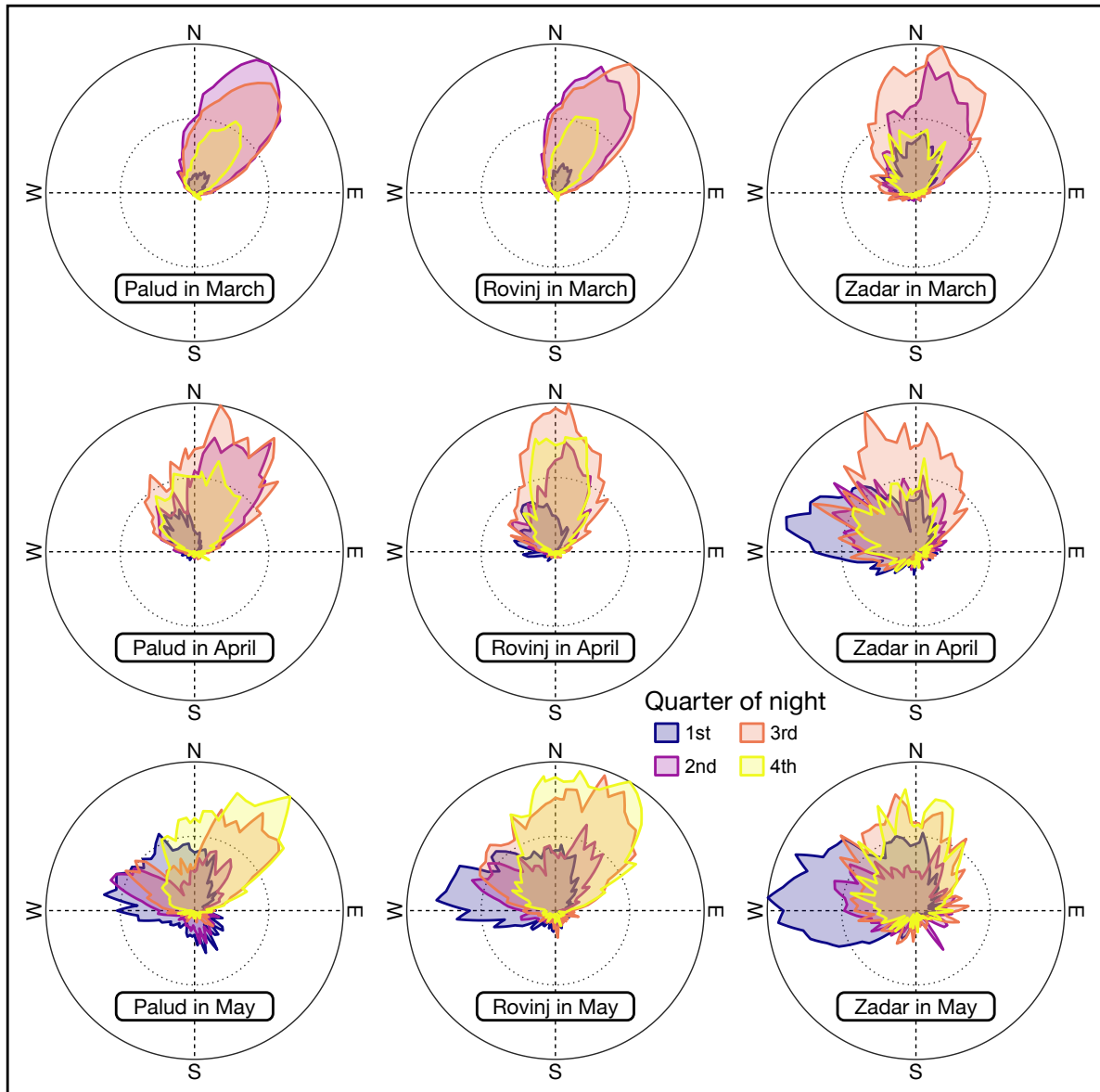


Figure 2.4. **Distribution of recorded flight directions per site and month.** Bird echoes have been quantified per 5-degree segment of the circle and standardised for comparability. Colours represent quarters of the night with blue just after sunset, purple before midnight, orange just after midnight, and yellow before sunrise.

2.4.3 FPCA and clustering

FPCA reduced the variability in the migration intensity profiles of individual radar nights, with two principal components explaining 83.8% of the total variability. The first FPC, accounting for 73.6%, primarily reflects variations in amplitude: radar nights with low mean MTR correspond to low eigenvalues, while high eigenvalues indicate consistently high MTR throughout the night. The second FPC, explaining 10.2%, represents shifts in peak migration timing relative to the mean profile - lower eigenvalues correspond to earlier peaks, while higher values indicate delayed peaks.

The hierarchical clustering of the eigenvalues of the first two FPCs identified three groups of distinct intensity profile shapes. These can best be described by mean intensity and timing of the intensity peak (Figure 2.5). In short, Cluster 1 was characterised by low migration intensity

with an average timing of the intensity peak (mean MTR = 263, time of peak = 47% of the night's time passed since sunset). Cluster 2 and Cluster 3 both were characterised by higher migration intensities (mean MTR = 684 and MTR = 810, respectively) but differed in timing. Cluster 2 showed an earlier timing of peak intensity (time of peak = 46%) compared to Cluster 3 (time of peak = 64%).

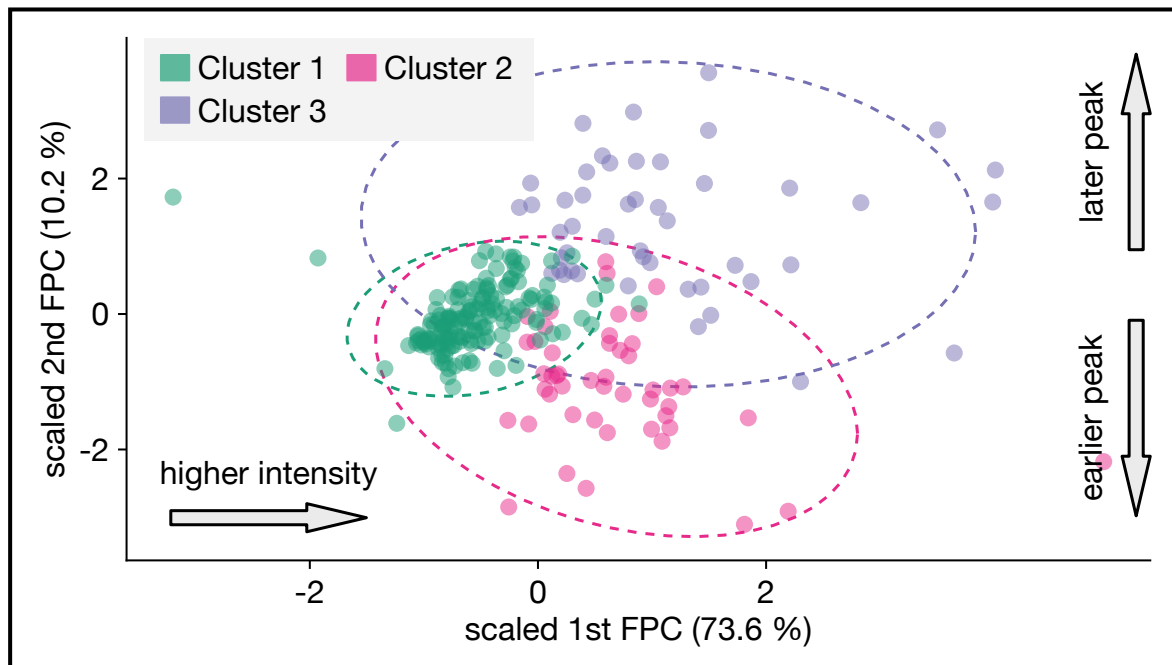


Figure 2.5. **Distribution of scaled first and second FPC scores.** The points were coloured according to cluster membership and supplemented with 95% confidence ellipses. The first FPC modifies the amplitude of the migration intensity profiles, the second FPC represents a shift in the timing of the peak intensity within a night.

As an alternative to examining the distribution of flight directions per month, we were interested in how directional patterns varied between different shapes of migration intensity profiles, particularly between those with an early (Cluster 2) and late (Cluster 3) peak in migration intensity, which intuitively reflect coastal and sea-crossing migration. To analyse how inferred coastal and sea-crossing migration, or migration direction in general, is associated with specific differences in migration intensity and within-night timing, we compared the site-specific flight direction distributions to the four migration intensity profile types.

Within clusters, on a nightly scale, the average flight directions were generally similar between the two Istrian sites, while the Dalmatian site in Zadar consistently showed a stronger W component. In the low-intensity Cluster 1, the flight directions in Istria were distributed around the NW, while in Zadar, they were oriented towards the NW. A similar pattern was observed in Clusters 2 and 3, with Zadar consistently showing a greater deviation towards W compared to the Istrian sites (Figure 2.6).

Pronounced differences in cluster-wise flight direction distributions only appeared for within-night patterns. At this level, distinct distributional patterns emerged, with time-dependent shifts in the shape of the migration intensity profile. Here, we focus on Clusters 2 and 3, which differed in the timing of the intensity peak, being either early or delayed, respectively. On nights with an early intensity peak, flight directions in Istria remained consistently oriented towards the NNE throughout the night. In contrast, migration over Zadar initially showed an

intense westward movement before shifting to the NNW later in the night. On nights with a delayed intensity peak, migration in Istria shifted from NW to NE as the night progressed. Over Zadar, early night flights had a strong westward component before gradually shifting to the N.

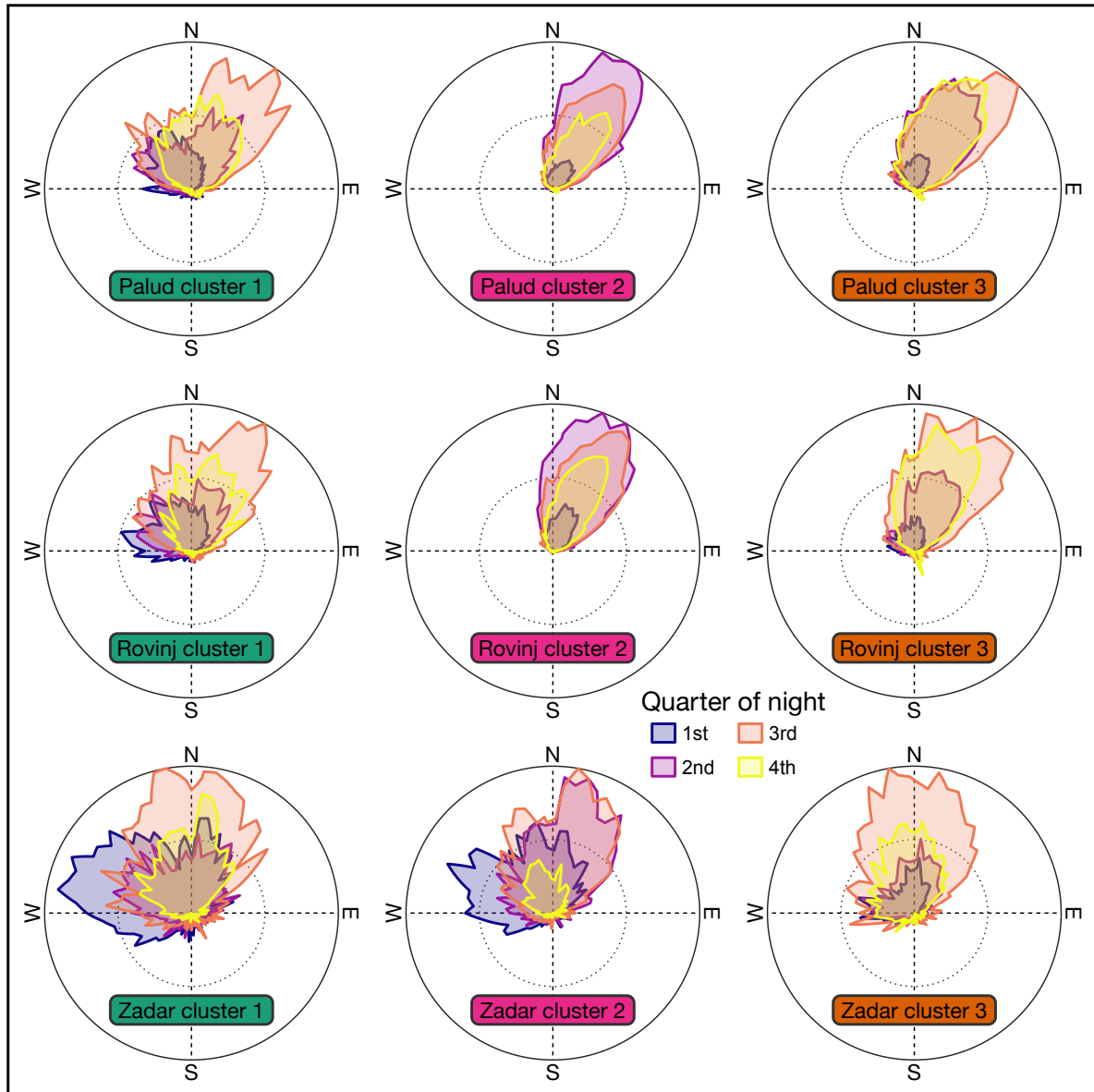


Figure 2.6. **Distribution of recorded flight directions per site and cluster.** Bird echoes have been quantified per 5-degree segment of the circle and standardised for comparability. Colours represent quarters of the night with blue just after sunset, purple before midnight, orange just after midnight, and yellow before sunrise.

2.5 Discussion

Our study provides first insights into the nocturnal fluxes of avian spring migration along the Croatian coast. We identified two periods of generally high migration intensity, one in March and another in May. Migration intensities between neighbouring sites were strongly correlated at the beginning of the season but showed increasing spatial variation towards the end. Flight directions followed a similar pattern. At the beginning of the season, seaward directions dominated at all sites. From April onwards, coastal migration became increasingly common, while sea-crossing directions continued to dominate after midnight. We applied functional principal component analysis (FPCA) to the within-night migration intensity profiles and performed hierarchical clustering based on mean migration intensity and timing of intensity peaks. This analysis revealed four clusters that summarised the profile shape. However, these clusters did not correspond to unambiguously separable flight direction distributions. Consequently, the within-night timing of peak bird activity alone cannot be directly linked to the dominant migration direction on a given night.

2.5.1 Migration intensity and flight directions in comparison

We have identified two peaks of migration activity throughout the season. One spanning March and another from early to mid-May. Although overall bird activity remained high until late May, a marked decrease in the concentration of flight direction concentrations suggests that local movements may be involved (Tschanz *et al.*, 2019; Shi *et al.*, 2021). Years of ringing efforts across several small islands between Europe and Africa have shown that early migration in March consists mainly of short-distance migrants, while long-distance migrants replace the population of actively migrating birds in April and May (Gargallo *et al.*, 2011). Although it is not possible to differ between short- and long-distance migrants, our radar data generally reflect these findings, though an unexpected reduction in migratory activity in April. This could be attributed to weather effects, as atmospheric conditions are known to cause high variability in migration phenology between years (Stipčević, 1997; Radović, Kralj and Tutiš, 1999; Gargallo *et al.*, 2011). The high synchrony in March across all our study sites supports the idea of a homogeneous group of short-distance migrants in early spring. Increasing directional scatter towards the end of May suggests that local movement is becoming more involved in the overall activity (Tøttrup *et al.*, 2012; Blackburn *et al.*, 2019).

Simultaneously, from April to May, we detected increasing movement towards NW to N directions, rather than the general N to NE direction. This aligns with previous tracking studies suggesting that spring migration along the south-eastern flyway occurs later in the season (Briedis *et al.*, 2020). The decreasing synchrony in migration intensities among study sites may be due to an increasing mix of sea-crossing and coastal migration in early May, followed by the end of the migration season in the second half of May.

A hardware failure with the Vrana radar affected the collection of quantitative data and forced the exclusion of this site from the analysis. As Lake Vrana is considered to be one of the most important bird sites in Croatia (Tutiš and Radović, 2003), additional data could be interesting to analyse in the future.

2.5.2 Nightly timing of migration

The FPCA and hierarchical clustering identified two clusters of migration intensity profiles, primarily differentiated by mean nightly migration intensity, and two other clusters by timing of peak intensity. Most radar nights were identified by a low overall migration intensity. On the other hand, the cluster with the highest intensity was assigned to the lowest number of nights. This allocation follows previous analyses where more than 50% of migratory departures occurred in only about 25% of nights during a season (Horton *et al.*, 2021; Nussbaumer *et al.*, 2021; Hirschhofer *et al.*, 2024). The two profiles that differ in the time of the peak intensity fall between the two groups just mentioned in terms of average intensity. These can be characterised as medium-intensity with an early peak in the first or second quarter of the night, and medium-intensity with a late peak, clearly after midnight.

Experimental evidence indicates that the timing of the onset of migratory behaviour in relation to sunset remains consistent between consecutive nights (Coppack, Becker and Becker, 2008), if not modified by the weather (Åkesson and Hedenström, 2000). Contrary to typical migration patterns where peak activity occurs shortly after sunset (Michev *et al.*, 2020), the Croatian coast data showed significant variability. Variability in the nightly timing of peak migration was often linked to geographic barriers, such as mountains or larger bodies of water, located upstream of the migratory flow (Kranstauber, Bauer and Shamoun-Baranes, 2023). In our case, the variability is likely due to the Adriatic Sea acting as a geographic barrier. This gets support by nights where coastal migration dominated, indicated by W and NW directions prevailing the overall distribution (e.g., Zadar in May), with initially high migration intensities right after sunset. Remarkable in the context of the research described above, however, is the great variability of the site-specific nocturnal timing between consecutive nights. Considering the associated flight directions, we conclude that this variability is caused by the two migration regimes, coastal and sea-crossing migration. In addition, the timing of migratory birds crossing the Adriatic should be strongly influenced by winds (Bruderer and Liechti, 1999). However, how exactly this timing depends on winds in our case remains the subject of future analyses. Finally, strong winds are likely to change not only the timing of arrival of sea-crossing birds, but also their relative numbers compared to those that remain on the ground or over the Italian mainland in strong headwinds.

A comparison of within-night migration intensity with flight direction distributions reveals the necessity to differentiate between the general patterns observed at the beginning and end of the season. In March, the predominant direction was N to NE at all sites and during the whole night, indicating that many likely short-distance migrants crossed the Adriatic Sea from the Italian to the Croatian coast, resulting in a temporal prevalence of sea-crossing migration compared to migration along the coast. Differences in within-night timing during this period may be due to varying wind conditions encountered on the route. In contrast, the prevalence of NW flight directions during the first one or two quarters of the night in April and May suggests a significant increase in coastal migration during the first one or two quarters of the night, while N to NE directions after midnight until sunrise again suggest sea-crossing from Italy to Croatia. As we hypothesised that the timing of peak migration would depend on either prevalent coastal (early peak) or sea-crossing (late peak) migration, we thus did not expect to find within-night migration intensity profiles with an early peak during March. We thus must reject our assumption that we can tell coastal migration apart from sea-crossing by only investigating within-night migration intensity profiles. Further research must look for alternative drivers behind the difference in nightly timing of birds at the coast of Croatia. We,

however, assume that winds might speed up migrants that crossed the Adriatic Sea, thus leading to early intensity peaks on a set of consecutive nights in early March. Such an analysis, however, must include winds along the whole backwards-projected trajectory across the sea. Between the mid- to late season, the distribution of flight directions indicated a significant increase in coastal migration during the first one or two quarters of the night, while likely sea-crossing migration became the dominant recorded pattern after midnight until sunrise. In view of the growing influence of coastal and sea-crossing migrants in shaping observed migration patterns from mid to late season, we infer that the early peaked radar nights observed between mid-April to mid-May seemed to show massive departures from the Croatian coast towards the NW and even W, while the late peaks result mainly from migrants having crossed the Adriatic Sea from the S before arriving at the radar site. We were surprised by these westward movements, as this has not been described before.

The Dalmatian radar site at Zadar exhibited the greatest variation in flight directions throughout the night and across the three clusters of intensity profiles. It serves as an exemplary illustration of the distinction between early and late nightly peak intensity and the corresponding flight direction distributions, whereby the Dalmatian site may additionally include local flights between the coast and offshore islands. In Zadar, an early peak was associated with a general W to NW direction after sunset and a shift from W to N after midnight, which still indicates migration along the coast. This contrasts with the flight directions observed at Istria's Palud and Rovinj over the course of the nights, with relatively homogeneous flight directions between clusters. Here, a higher prevalence of sea-crossing migration towards the N to NE may be due to the shorter coast-to-coast distances between Italy and Istria (Palud, Rovinj) compared to Dalmatia (Zadar). It is also likely that a significant number of migrants cross the sea well south of Dalmatia before following the coast, similar to red kites that have been tracked (Literák *et al.*, 2021). This assumption is supported by the breeding area of the Eleonora's falcon, an aerial predator that depends on migrating passerines to feed its chicks. In Croatia, these falcons can only be found on the islands between Croatia and Italy, south of Dalmatia. (Lukač, Stipčević and Tvrtković, 1997). This just goes to underline that the interplay between barrier-crossing and barrier-following birds complicates the migration patterns measured in the field.

2.5.3 Limitations of the study

With data from only one spring migration season, we can only make limited generalisations from this study. Previous research has amply demonstrated that migration intensity can vary greatly between years, probably largely due to weather effects (Haest, Hüppop and Bairlein, 2018) and geographic barriers (Kranstauber, Bauer and Shamoun-Baranes, 2023; Hirschhofer *et al.*, 2024). However, as this is the first radar-based study in the area, our results still provide valuable insights into migration directions along the Croatian coast.

2.6 Conclusion

The radar data recorded in spring 2023 provide quantitative evidence to support the assumption that the coastal region of Croatia is traversed by a multitude of migratory birds in a variety of directions. Three principal migratory cohorts may be discerned: one proceeding in an NW direction along the coast, another in an NE direction from the Adriatic Sea towards

the inland, and surprisingly a third, occurring only in May in Dalmatia, towards the W. The convergence of coastal and sea-crossing migration results in complex spatiotemporal patterns. We here highlight that the site-specific nightly timing of migratory birds does not remain consistent between consecutive nights. Rather, it is subject to considerable variability over a single migration season, which is likely dependent on the currently dominant coastal or sea-crossing migration. Future research will be needed to explain how synoptic meteorology, i.e. synchronous weather conditions over the Italian coast, the Adriatic Sea and the Croatian coast itself, shapes these patterns. A deep understanding of these drivers is needed for the future implementation of dynamic aero conservation actions, such as the temporal reduction of artificial illumination or shutdown of wind turbines in accordance with the timing of migration.

3 When nocturnally migrating birds encounter low-level light pollution patches: a case study from the Croatian coast

Simon Hirschhofer^{1,2}, Peter Ranacher¹, Robert Weibel¹, Barbara Helm², Davor Ćiković³, Sanja Barišić³, Louie Taylor³, Maja Bjelić Laušić⁴, Baptiste Schmid²

¹ University of Zurich, Department of Geography, Zurich, Switzerland

² Swiss Ornithological Institute, Department of Bird Migration, Sempach, Switzerland

³ Croatian Academy of Sciences and Arts, Institute of Ornithology, Zagreb, Croatia

⁴ Public Institution Nature Park Vransko Jezero, Biograd na Moru, Croatia

Author contributions: **SH:** conceptualisation, data curation, formal analysis, investigation, methodology, project administration, software, validation, visualisation, writing - original draft, writing - review and editing. **BS:** conceptualisation, data curation, funding acquisition, investigation, methodology, project administration, resources, software, supervision, validation, writing - original draft, writing - review and editing. **PR:** conceptualisation, methodology, supervision, writing - review and editing. **RW:** conceptualisation, funding acquisition, supervision, writing - review and editing. **BH:** conceptualisation, funding acquisition, project administration, resources, supervision, writing - review and editing. **DC:** writing - original draft, writing - review and editing. **SB:** writing - original draft, writing - review and editing. **LT:** project administration. **MBL:** project administration.

Published as:

Hirschhofer, S. et al. (2026) 'When nocturnally migrating birds encounter low-level light pollution patches: a case study from the Croatian coast', Biological Conservation, 313, p. 111620. <https://doi.org/10.1016/j.biocon.2025.111620>.

Data and code:

Hirschhofer, S. et al. (2025). R scripts and data for the article: 'When nocturnally migrating birds encounter low-level light pollution patches: a case study from the Croatian coast', Biological Conservation. Zenodo. <https://doi.org/10.5281/zenodo.17598350>.

Supporting Information in Appendix C.

3.1 Abstract

Artificial light is a pollutant of growing global concern. For nocturnally migrating birds, the consequences can be fatal. Attracted and disoriented by illuminated infrastructure, birds can become victims of collisions, especially when visibility is reduced by fog and clouds. Birds crossing large, predominantly dark bodies of water can suddenly be confronted with patches

of lit coastal areas. In contrast, when flying over land along the coast, birds are sequentially confronted with lit areas and are likely to rely on different navigation cues. We deployed two ornithological radars in proximity along the Croatian coast: one at a light-polluted site and one at a near-natural site. The aim was to maximise the contrast in light pollution while keeping other site-specific factors similar. We monitored the consecutive spring migration seasons of 2023 and 2024 and modelled the effect of light pollution on the number of birds in the air, mean airspeeds and mean flight altitudes, considering atmospheric, temporal, and directional predictors. Our results are partially hampered by the fact that we had to exclude a second radar pair from the analysis due to a technical defect. Nevertheless, we found evidence for attraction towards light pollution of sea-crossing birds in the remaining radar pair. Furthermore, we found a significant contribution of light pollution to the reduction of mean airspeeds and altitudes, especially in an overcast context. Besides indicating disorientation, our results raise serious concerns about increased numbers of bird collisions associated with migration peaks and impaired visibility, even with lower-intensity light pollution.

3.2 Introduction

Human activities are known to alter established avian migration patterns across taxa (Bauer and Hoyer, 2014). Nocturnally migrating birds can be severely affected by night-time lighting (Convention on Migratory Species, 2024). As an effect, birds can suffer from confusion due to artificial light at night (ALAN), sometimes to the point where they become severely disoriented, which can ultimately lead to exhaustion, increased risk of predation or fatal collisions (Van Doren *et al.*, 2017; Korner, von Maravic and Haupt, 2022). In addition, birds have been found to be attracted to light-polluted areas when looking for a place to stop, rest and refuel, which might be especially an issue after crossing geographic barriers (Horton *et al.*, 2023).

Here, we consider phototactic effects as attraction to or avoidance of light pollution, along with behavioural responses likely caused by confusion and disorientation. Such effects have been documented in migrating birds, affecting migration intensity (Van Doren *et al.*, 2017), flight altitude (Cabrera-Cruz *et al.*, 2019), and airspeed (Van Doren *et al.*, 2017). Studies on how migratory birds respond to light pollution, however, often present a complex and even conflicting picture (Cochran and Graber, 1958; Nemes *et al.*, 2023). While most studies find that birds are attracted to areas with higher levels of light pollution, there is evidence to the contrary, showing that birds sometimes avoid light-polluted areas during flight (Korpach *et al.*, 2022) and as a stopover (Cabrera-Cruz *et al.*, 2020). Attraction and repulsion by light likely depend on context: while high levels of light pollution are found to attract migrating birds on a large scale, they act as a repellent on a local scale (McLaren *et al.*, 2018).

The context also includes the intensity of nocturnal illumination. Most studies on avian migrants' responses to light pollution have focused on high-intensity light pollution in large cities. Although findings from environments with relatively low light intensity are rare, they are nevertheless worth considering. This is because, although lower-intensity or bird-friendly lighting still influences migratory behaviour (Cabrera-Cruz *et al.*, 2021), this behavioural change is significantly less pronounced than at higher light intensities (Osterhaus *et al.*, 2025).

Furthermore, visibility plays an important role, too. Low cloud cover (LCC) and fog have been found to amplify the response to light pollution (Cabrera-Cruz *et al.*, 2021). Measurements of light intensity in light-polluted environments show that brightness can increase tenfold under thick clouds (Kyba *et al.*, 2011), providing a straightforward explanation for why migrating birds are especially attracted to artificial light under overcast conditions (Rebke *et al.*, 2019; Van Doren *et al.*, 2021; Weisshaupt *et al.*, 2022). Similarly, dense cloud cover exacerbates confusion and disorientation caused by light pollution, further reducing airspeed (Bruderer, Peter and Steuri, 1999).

Finally, there are hints that birds are particularly sensitive to light pollution after crossing a larger body of water, and might become victims of collisions with illuminated windows and other infrastructure more often (Van Doren *et al.*, 2021). Although this hypothesis has not been directly studied, the authors of the aforementioned study highlight that it should be investigated further. To our knowledge, this has not yet been done.

Attraction to light pollution poses two major risks for birds. First, artificial light can draw birds to inferior habitats with reduced quality and quantity of potential food sources (Burt *et al.*, 2023; Morelli *et al.*, 2023). Secondly, night-time lighting increases the risk of collisions with windows and other man-made structures, resulting in significant annual losses which are likely to affect population dynamics (Van Doren *et al.*, 2021). These collisions result in significant losses each year and are likely to affect population dynamics (Erickson, Johnson and Young Jr., 2005).

We selected our study area to include birds with different migration directions, which likely rely on different navigation cues. In coastal regions, migration is often bimodal: some birds cross the sea, while others follow the coastline (Bruderer and Liechti, 1998; Weisshaupt *et al.*, 2018). We here refer to them as sea-crossing and coastal migrants, respectively. Given that the sea is relatively dark, sea-crossing migrants are likely attracted to light from afar, potentially increasing migration intensity at light-polluted coastal sites compared to dark, near-natural sites. In contrast, coastal migrants likely use the coastline as a navigational landmark and may be less affected by artificial light, resulting in similar migration intensities at light-polluted and near-natural locations (Koistinen, 2000; Weisshaupt *et al.*, 2022). Nevertheless, coastal migrants may still experience confusion and disorientation when passing light-polluted areas. Our study design allows us to differentiate between responses in migration intensity and changes in flight speed and altitude for both migration directions.

A preceding study observed such bimodal directionality along the Croatian coast (Hirschhofer *et al.*, 2025). Here, one group of migrants was crossing the Adriatic Sea from the Italian coast towards Croatia on a roughly SSW to NNE axis. The other group followed the coastline along an SE to NW axis (Figure 3.1). Furthermore, light pollution is patchy along the Croatian coastline (Elvidge *et al.*, 2021), presenting opportunities for a suitable study setup.

To analyse bird migration patterns in response to light pollution patterns, two BirdScan ornithological radars were deployed along the Croatian Adriatic coast. The radars were installed 6.7 kilometres apart, in the town of Rovinj and the Palud ornithological reserve, to maximise the contrast between light-polluted and near-natural conditions while keeping other geographic factors similar. The radars recorded nocturnal spring migration from March to May in both 2023 and 2024. BirdScan quantifies bird movement based on individual radar echoes, allowing to separate migratory fluxes by migration direction. We used this capability to study how birds respond to light pollution when migrating over the sea versus along the

coast, focusing on migration intensity, mean airspeed, and mean flight altitude. Based on the literature, we formulated the following hypotheses:

Migration intensity of sea-crossing migrants is higher at the light-polluted site than at the dark site, after controlling for atmospheric conditions and seasonality. For coastal migrants, the association between light pollution and migration intensity is weaker or absent. Low cloud cover (LCC) is negatively associated with migration intensity, while also modifying the relationship between light pollution and migration intensity, such that the effect of light pollution is stronger on nights with higher LCC.

Mean airspeed is lower at the light-polluted site than at the dark site for both sea-crossing and coastal migrants, with a stronger reduction in sea-crossing birds. High LCC further amplifies this effect, leading to the greatest reduction in airspeed on cloudy nights at the light-polluted site.

Flight altitudes are lower over the light-polluted site than over the dark site. High LCC further reduces flight altitude, with the greatest reduction during cloudy nights at the light-polluted site.

3.3 Methods

3.3.1 Study region and radar monitoring

We deployed two BirdScan MR1 ornithological radars along the Croatian coast on the Istrian peninsula (Figure 3.1). One radar was placed in the city of Rovinj (45° 4' 57.5034" N, 13° 38' 13.524" E; 17 m asl), and the second was placed in the Palud ornithological reserve (45° 2' 22.92" N, 13° 41' 50.928" E; 17 m asl). Two additional radars were deployed in Dalmatia, in Zadar and at Vransko Lake, but technical issues prevented us from including their data (Hirschhofer *et al.*, 2025; S.H. and B.S., personal observation). The two sites differed in light pollution levels, quantified as upward radiance within a 1,000-metre raster cell neighbourhood using the monthly cloud-free day-night band composite from VIIRS (Elvidge *et al.*, 2021) for March, April, and May in 2023 and 2024 (Rovinj: $20.6 \pm 17.4 \text{ nW}\cdot\text{cm}^{-2}\cdot\text{sr}^{-1}$; Palud: $0.7 \pm 0.5 \text{ nW}\cdot\text{cm}^{-2}\cdot\text{sr}^{-1}$; see Supporting Information). The distance between the sites was 6.7 km. The distance from the coast to the radar sites was 450 m in Rovinj, 540 m in Palud.

The BirdScan MR1 is a modified marine X-band radar with a pulse length of 70 ns, a wavelength of 3.2 cm, a range resolution of 10 m, and a minimum detection range of 40 m. It detects echoes from individual small passerine birds up to 1000 metres above ground level (m agl). The radar rotates at 0.8 Hz around a 0.2° nutated axis, which enables the calculation of the birds' ground speed and direction. As an object passes through the radar beam, it is repeatedly illuminated. Birds are distinguished from other echoes and classified into broad groups based on echo intensity and observed changes in echo intensity over time, which correspond to the size of the bird and specific wing-flapping patterns. We focus here on two groups of small to medium-sized birds: continuously flapping birds (e.g. waders) and intermittently flapping birds (e.g. passerines), both with a flapping frequency of 25 Hz or less (Bruderer *et al.*, 2010). The filtering and frequency threshold help to reduce contamination from non-bird echoes and non-migratory movements by excluding larger, local birds or insects. To estimate the number of birds, echoes were corrected for detection probability (Schmaljohann *et al.*, 2008; Schmid *et al.*, 2019). Birds are not equally detectable at different

altitudes due to two main factors. First, at higher altitudes, as the bird's distance from the radar increases, the received signal weakens, reducing the probability of detecting smaller birds. Second, due to the shape of the radar beam, the projected area covered is smaller near the radar and larger farther away. To account for the second sampling bias, we applied a correction factor to calculate the hourly migration traffic rate (MTR), the number of birds passing within 500 m of the radar per hour. For further analysis, we used the R package *suncalc* (Thieurmél and Elmarhraoui, 2022) to calculate site-specific times of civil dusk and dawn (the moment when the centre of the sun is 6° below the horizon), and defined the time between as nighttime. We then averaged the MTR to reflect the mean migration intensity of radar nights.

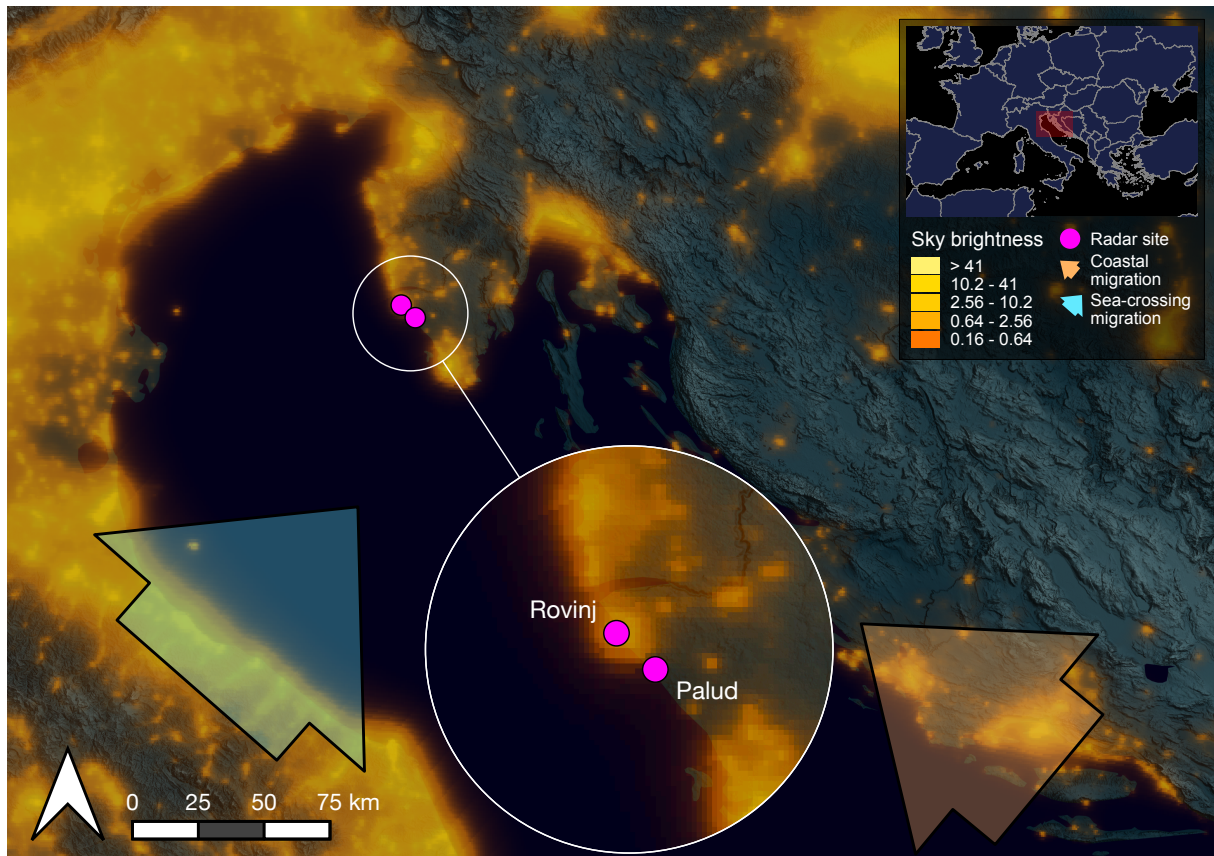


Figure 3.1. **Overview of the study area.** The map shows the two radar sites, topography, and light pollution as skyglow (the ratio of artificial to natural sky brightness). For reference, at ratios ≥ 0.5 , the Milky Way is no longer visible. The inset enlarges the Rovinj area to provide a clearer view of night-time illumination around the radar sites. The transparent blue arrow indicates the direction of sea-crossing migration, and the transparent red arrow indicates the direction of coastal migration.

We monitored the nocturnal spring migration from 1 March to 31 May in 2023 and 2024. Several radar nights were excluded from analysis due to technical problems and rain contamination, which may cause false positives. Of the total 368 radar nights, we retained 370 for the analysis.

In total, 456,827 bird echoes were recorded at the two radar sites between March and May in 2023 and 2024. Filtering for passerine- and wader-type echoes resulted in 222,747 remaining echoes for analysis, of which 160,865 contained directional information. Removed echoes were either recorded during the day, belonged to other bird classes (e.g., larger birds or swift-type birds), or had classifications with high uncertainty.

3.3.2 Distinguishing between sea-crossing and coastal migration

To quantify sea-crossing and coastal migration separately, we first defined the coastline by manually approximating a line in QGIS and determining its orientation (326°). Bird echoes with flight directions perpendicular to the coastline ($\pm 45^\circ$) were classified as sea-crossing, while those parallel ($\pm 45^\circ$) were classified as coastal. To distinguish between sea-crossing and coastal migration, we then calculated the proportion of sea-crossing and coastal echoes relative to the total number of included bird echoes per radar night. This proportion was then used to recalculate the MTR for both directions.

3.3.3 Atmospheric data

To calculate the airspeed of birds and account for atmospheric effects in the modelling, we used hourly ERA5 reanalysis data (Hersbach *et al.*, 2020) at single-altitude levels (LCC up to 2,000 m above sea level in percentage coverage, air temperature at 2 metres above ground, and air pressure at sea level), and pressure-level intervals of 25 hPa with a grid size of 0.25° (u- and v-wind components, representing west to east and south to north wind).

From the downloaded atmospheric variables, we extracted exact grid cell values for the two radar sites. LCC, temperature and pressure were provided on single levels, so no further selection was required. The processing of the wind data is described in more detail below.

To merge wind data with bird echoes, we converted echo altitudes to corresponding pressure levels using the barometric formula. We then used the wind data to calculate the airspeeds of individual birds from the measured groundspeeds, as airspeeds better reflect the in-flight behaviour of birds (Hedenström and Åkesson, 2017). We matched bird flight altitudes to pressure levels in the wind data and then calculated u- and v-movement vectors for each recorded bird from the measured groundspeed and flight direction. Airspeed is then the subtraction of the u- and v-wind vectors from a bird's u- and v-movement vectors. To reconcile the airspeeds with the aggregated MTR data, the resulting airspeed was averaged over complete radar nights, weighting each echo with the correction factor that accounts for the probability of detection.

Second, to use wind as an environmental predictor in the analysis, we calculated the mean headwind and crosswind for each radar night and separately for sea-crossing and coastal migration. We define headwind as the wind speed parallel to the mean direction of flight per night and radar site and separately for sea-crossing and coastal migration, with negative values indicating winds in the mean direction of migration and positive values indicating winds against the mean direction of migration, and crosswind as the wind perpendicular to the mean direction of flight, without distinguishing between winds from the right or left. We thereafter selected the pressure level with the highest bird activity for each radar night and migration direction and calculated the headwind and crosswind relative to the mean flight directions determined from the echo data, again weighted with the correction factor for the probability of detection.

3.3.4 Light pollution data

Following the study design, which included two regions, each containing one light-polluted and one near-natural site, we modelled light pollution as a categorical variable with the factors

light-polluted and dark. This allowed us to better account for the light pollution contrasts within regions rather than absolute brightness.

Initially, we included light pollution as a continuous variable, derived from the monthly (March to May) cloud-free averaged upward radiance of night lights from the NASA/NOAA Visible Infrared Imaging Radiometer Suite (VIIRS) day/night band low-light imaging data at 15 arcsec raster resolution (Elvidge *et al.*, 2021). The problem with absolute measurements of light pollution as a continuous variable was the strong concavity between measured light pollution, the radar locations, and the night of the year (NoY) during modelling. This led to highly unstable and unrealistic predictions of the response variables. These problems were eliminated by using light pollution as a categorical variable.

3.3.5 Modelling intensity and behaviour

To explain the variability in migration traffic rate (MTR), mean airspeed and mean flight altitude, we built 3 Generalised Additive Models (GAMs), one for each of our response variables (MTR, airspeed, and flight altitude) using the *mgcv* package in R (Wood, 2023).

Response variables were modelled using appropriate error distributions: MTR was modelled with a quasi-Poisson family and a log link to account for overdispersion and positive count data, while airspeed and flight altitude were modelled using a Gaussian family with an identity link. All models were fitted using Restricted Maximum Likelihood (REML) to reduce the risk of overfitting.

Our model structure was designed to test the effects of light pollution while accounting for environmental and seasonal drivers. We modelled the non-linear effects of continuous predictors using thin plate regression splines. The full model structure included:

- **Smooth terms:** non-linear effects of air pressure, air temperature, LCC, headwind, and crosswind, with separate smooths for sea-crossing and coastal migration.
- **Seasonal term:** a smooth term for the night number of the year (NoY), with a separate smooth for each year to account for inter-annual variation.
- **Light pollution:** a parametric term for light pollution (categorical: light-polluted/dark) and its interaction with LCC and migration direction.
- **Temporal autocorrelation:** to account for temporal autocorrelation in the time-series data, we incorporated a first-order autoregressive correlation structure (corAR1), nested within each unique combination of year and migration direction.

We assessed multicollinearity among predictors by checking for concavity, the non-linear analogue to collinearity in GAMs. After model fitting, we quantified the contribution of each predictor by calculating its percentage of explained deviance using the *gam.HPR* package (Lai *et al.*, 2024). We visualised the marginal effect of each predictor by generating model predictions using the *ggeffects* R package (Lüdtke, 2018), holding all other covariates constant at their mean or reference values.

To quantify the effects of light pollution on migration intensity, airspeed, and flight altitude, we performed a post-hoc analysis. We calculated estimated marginal means (EMMs) for the two levels of light pollution and the two migration directions using the *emmeans* R package (Lenth, 2017). We then performed pairwise contrasts between these EMMs to quantify their

differences, including standard errors and p-values, directly testing the significance of light pollution effects while accounting for other covariates.

3.4 Results

Here, we focus on the reporting of the modelled effects of light pollution and LCC on bird migration for the two radar sites at Rovinj and Palud. The Supporting Information details migration phenology, airspeeds, and flight altitudes, as well as the effects of atmospheric and temporal predictors.

3.4.1 Effect of light pollution on mean nightly migration intensity (MTR)

The Mean nightly migration intensity for the light-polluted and dark site was $187 \text{ birds}\cdot\text{h}^{-1}\cdot\text{km}^{-1}$ for sea-crossing migration ($Q_1 = 55$, $Q_3 = 234$), and $123 \text{ birds}\cdot\text{h}^{-1}\cdot\text{km}^{-1}$ for coastal migration ($Q_1 = 60$, $Q_3 = 158$). There were nights with little or no activity, as well as extreme nights with mean MTRs of $1,526 \text{ birds}\cdot\text{h}^{-1}\cdot\text{km}^{-1}$ for sea-crossing and $778 \text{ birds}\cdot\text{h}^{-1}\cdot\text{km}^{-1}$ for coastal migration. The GAM explained 66.5% of the total deviance in mean nightly MTR (adjusted $R^2 = 0.65$).

The model estimated a 22.9 % increase in the MTR from the dark to the light-polluted site for sea-crossing migration, although this difference was not statistically significant (95 % CI: -2.5 % to $+55.0$ %; $p = 0.157$). For coastal migration, the estimated increase was 4.6 % from the dark to the light-polluted site, but this difference was also not statistically significant (95 % CI: -8.3 % to $+19.6$ %; $p = 0.560$) (Figure 3.2).

LCC generally had a negative effect on MTR. The effect was significant for sea-crossing migration for both light-polluted and dark sites ($p < 0.001$ at the dark site and $p = 0.002$ at the light-polluted site), but not significant for coastal migration ($p = 0.419$ at the dark site and $p = 0.110$ at the light-polluted site). The interaction between LCC, migration direction, and light pollution explained 10.8 % of the total deviance.

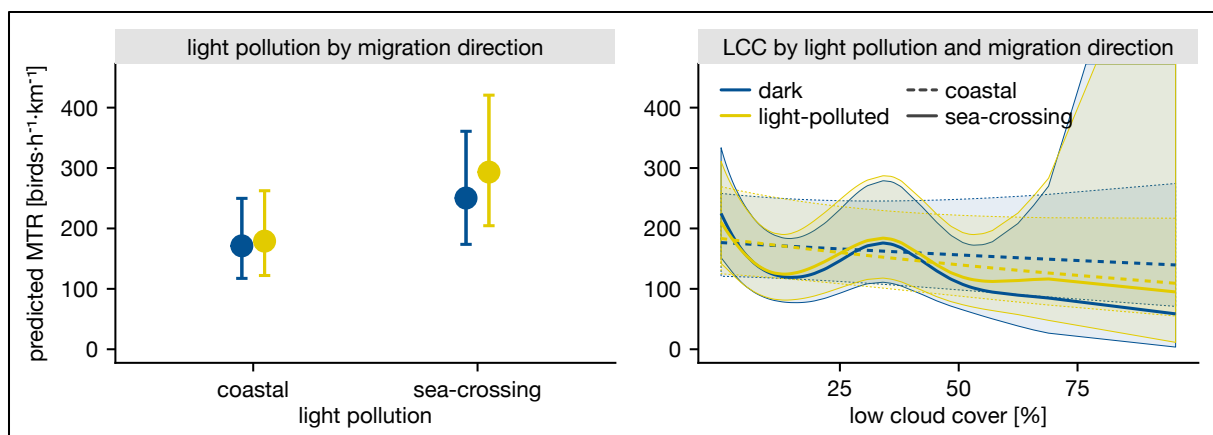


Figure 3.2. **Effects of light pollution on migration intensity (MTR) during the spring migration seasons of 2023 and 2024 in Istria.** Marginal effects of light pollution, and LCC in interaction with light pollution, for sea-crossing and coastal migration intensities. The panels show the mean estimate and 95% prediction intervals.

3.4.2 Effect of light pollution on mean nightly airspeed

The mean nightly airspeed for both sites was $11.2 \text{ m}\cdot\text{s}^{-1}$ for sea-crossing migration ($Q_1 = 9.7 \text{ m}\cdot\text{s}^{-1}$, $Q_3 = 12.6 \text{ m}\cdot\text{s}^{-1}$), and $9.6 \text{ m}\cdot\text{s}^{-1}$ for coastal migration ($Q_1 = 8.4 \text{ m}\cdot\text{s}^{-1}$, $Q_3 = 10.4 \text{ m}\cdot\text{s}^{-1}$). The GAM explained 77.8 % of the total deviance in mean nightly airspeed (adjusted $R^2 = 0.757$).

The model predicted significantly lower mean airspeeds at the light-polluted site than at the dark site for both sea-crossing and coastal migration, with a stronger effect for sea-crossing migration. Airspeeds were $0.94 \text{ m}\cdot\text{s}^{-1}$ lower (95 % CI: 0.55 to $1.33 \text{ m}\cdot\text{s}^{-1}$; $p < 0.001$) at the light-polluted site than at the dark site for sea-crossing migration, and $0.55 \text{ m}\cdot\text{s}^{-1}$ lower (95 % CI: 0.24 to $0.86 \text{ m}\cdot\text{s}^{-1}$; $p < 0.001$) for coastal migration. Light pollution accounted for 7 % of the model's total deviance (Figure 3.3).

LCC had no significant effect on mean airspeeds.

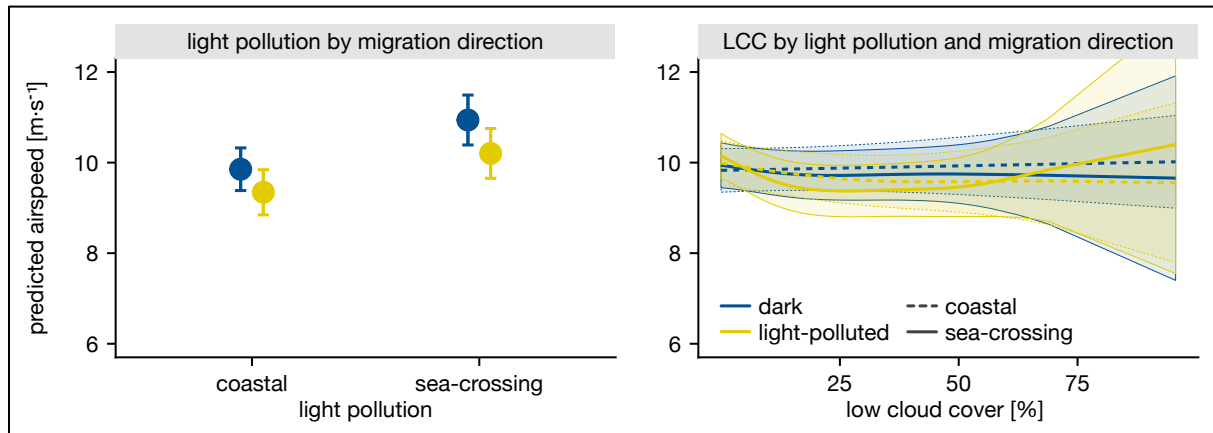


Figure 3.3. **Effects of light pollution on mean airspeed during the spring migration seasons of 2023 and 2024 in Istria.** Marginal effects of light pollution, and LCC in interaction with light pollution, for mean nightly airspeeds of sea-crossing and coastal migration. The panels show the mean estimate and 95% prediction intervals.

3.4.3 Effect of light pollution on mean nightly flight altitude

The mean nightly flight altitude for both sites was 393 m ASL for sea-crossing migration ($Q_1 = 338 \text{ m}$, $Q_3 = 447 \text{ m}$), and 359 m for coastal migration ($Q_1 = 317 \text{ m}$, $Q_3 = 405 \text{ m}$). The GAM explained 58.2 % of the total deviance in mean nightly flight altitude (adjusted $R^2 = 0.549$).

The model predicted significantly lower mean flight altitude at the light-polluted site than at the dark site for both sea-crossing and coastal migration, again with a stronger effect for sea-crossing migration. Mean flight altitude was 52.2 m lower (95 % CI: 40.44 to 63.96 m ; $p < 0.001$) at the light-polluted site than at the dark site for sea-crossing migration, and 44.7 m lower (95 % CI: 27.26 to 62.14 m ; $p < 0.001$) for coastal migration. Light pollution accounted for 16 % of the model's total deviance (Figure 3.4).

LCC had a significant effect on flight altitudes at the light-polluted site. For coastal migration, an additional decrease of 43 m was estimated ($p < 0.008$) when the sky was fully covered, while the reduction was 58 m ($p < 0.029$) for sea-crossing migration. The interactive effect between LCC, migration direction, and light pollution explained 6.8 % of the model's total deviance.

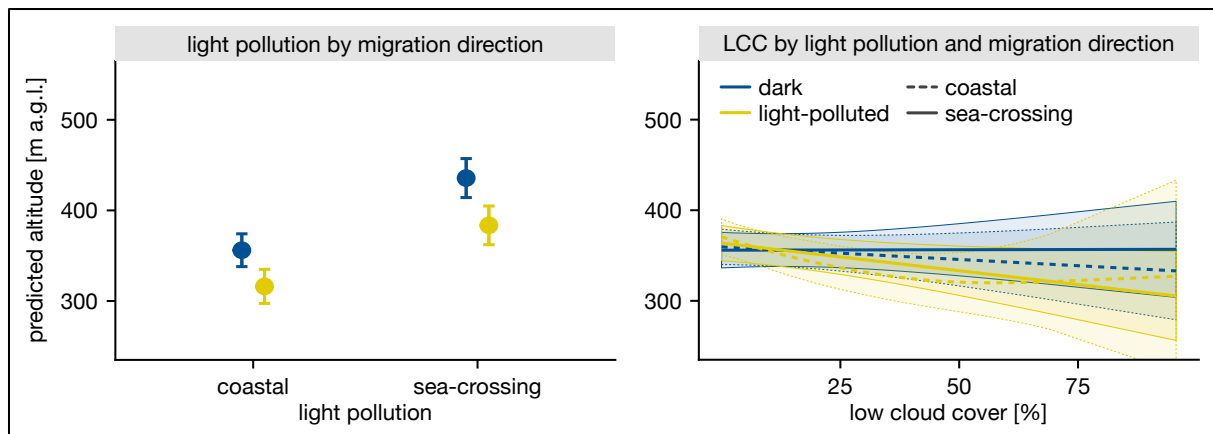


Figure 3.4. **Effects of light pollution on mean flight altitude during the spring migration seasons of 2023 and 2024 in Istria.** Marginal effects of light pollution, and LCC in interaction with light pollution, for mean nightly flight altitude for sea-crossing and coastal migration. The panels show the mean estimate and 95% prediction intervals.

3.5 Discussion

We tested the responses of nocturnally migrating birds to light pollution in terms of migration intensity (MTR), mean airspeed and mean flight altitude. Together, these variables form a measurable proxy for a phototactic response (Van Doren *et al.*, 2017) and provide insight into light-pollution-induced disorientation (Bruderer, Peter and Steuri, 1999). Here, we present the first full-season, individual-based quantification of these responses.

3.5.1 The effect of light pollution on migration intensity (MTR) and flight behaviour

Our results suggest that birds respond to light pollution, even at relatively low intensities (20.6 nW·cm⁻²·sr⁻¹ in Rovinj). Although the increase in the estimated MTR at the light-polluted site compared to the dark site was not statistically significant, the trend towards higher MTR, together with the clearly reduced airspeeds and flight altitudes, suggests that birds exhibit an in-flight behavioural response to light pollution, particularly after crossing the sea. This response appears to occur even under comparatively low levels of light pollution.

Although the two radar sites were separated by less than 7 km, our models indicated notable behavioural differences between the light-polluted site and the dark site that could not be attributed to atmospheric or seasonal effects. Most birds migrate across the Mediterranean and the Adriatic Sea on a broad front (Trösch *et al.*, 2005; Gargallo *et al.*, 2011). Although topography can divert broad-front migration (Aurbach *et al.*, 2018), the area surrounding the two radars is relatively flat. Therefore, we expect that migration across the Adriatic Sea in this region is largely unimpeded, with minimal differences over the short distance separating the two radars.

The wide confidence intervals around the estimated differences in migration intensity likely reflect the substantial natural variability in MTR between nights rather than model uncertainty alone. The MTR exhibited a wide interquartile range (55 to 234 birds·h⁻¹·km⁻¹ for sea-crossing and 60 to 158 for coastal migration) and nights with little or no detectable migration were frequent. Such variability, including sporadic peaks of very high MTR, increases the overall variance of the data and could consequently have broadened the confidence intervals in the

model. Although the GAM accounted for seasonal variation in the MTR, a considerable proportion of the variability remained unexplained, as indicated by the moderate adjusted R^2 of 0.65. This suggests that other site-specific differences in bird passage that were not captured by the GAM contributed substantially to the residual variation. Despite this uncertainty, the estimated 22 % higher MTR at the light-polluted site for sea-crossing migration suggests that light pollution may influence the spatial distribution of migrants as they approach the shoreline. In contrast, the MTR for coastal migration showed only a small, non-significant increase of 4.6 % between the dark and light-polluted sites, suggesting that light pollution may have a comparatively weaker effect when birds rely on topographic cues for navigation. This pattern is consistent with the idea that light attraction depends on birds' reliance on navigational cues: coastal migrants are likely to follow the shoreline regardless of light (Koistinen, 2000; Weisshaupt *et al.*, 2022). While the observed difference between sea-crossing and coastal MTR is not statistically significant, it highlights the need for further investigations across additional sites and migratory contexts to clarify whether this pattern is more general.

In contrast, measured airspeeds and flight altitudes exhibited narrower distributions, indicating greater consistency of these response variables between nights. In the case of airspeeds, the GAM also captured a higher proportion of the overall variability in the measurements. Thus, the models estimated significantly lower airspeeds and, more concerning, reduced flight altitudes for both migration directions when birds were over light-polluted areas. These results suggest that, although the MTR fluctuates markedly, leading to clear yet insignificant trends, the behavioural in-flight adjustments of migrating birds over illuminated areas represent a consistent response to light pollution.

Our findings regarding flight altitude, however, contrasts with previous findings, in which migrating birds increased their flight altitudes in response to light pollution (Cabrera-Cruz *et al.*, 2019). However, that study suggested that the observed altitude increase may have been a response to urban heat rather than light pollution per se. To our knowledge, the altitudinal response of migrating birds to light pollution remains poorly understood and warrants further investigation.

Further research is needed to determine whether this altitudinal response has a detrimental effect on migrating birds. There is conflicting evidence, which makes it difficult to reach a conclusion. While some studies have found that birds follow light sources as a guiding aid (Weisshaupt *et al.*, 2022), it has been assumed that the collision rate of nocturnally migrating birds increases after the crossing of aquatic barriers, particularly when visibility is reduced (Van Doren *et al.*, 2021). Although our results also suggest such a hypothesis, the model failed to provide statistically significant support for it. Ultimately, light attraction may be problematic, regardless of whether it is initially used as an orientation cue. When seeking a suitable stopover site after crossing a barrier, migrating birds that were previously drawn to light-polluted areas may encounter lower-quality stopover habitats (Horton *et al.*, 2023) or collide with urban infrastructure (Van Doren *et al.*, 2021; Korner, von Maravic and Haupt, 2022). Recent evidence further suggests that even bird-friendly lighting, such as shielded fixtures or lights with higher dominant wavelengths, can still elicit in-flight behavioural alterations (Osterhaus *et al.*, 2025). While such lighting strategies reduce the overall impact of artificial light at night, they do not entirely prevent behavioural responses. This indicates that migratory birds remain sensitive to illumination, even under mitigation-oriented designs. The cumulative negative impact of these behavioural reactions is, however, still subject to future research.

In support of the hypothesis that collision risk may be increased, we found reduced airspeeds and lower flight altitudes, which could indicate signs of disorientation in response to light pollution in migrants crossing the sea and those flying along the coast. Our study area does not include tall, illuminated buildings that can be responsible for the deaths of thousands of birds through collisions (Korner, von Maravic and Haupt, 2022). However, there is striking evidence that even a single low building with illuminated windows can result in countless bird collisions (Van Doren *et al.*, 2021). As tourism in Croatia continues to increase (Carić, 2018), likely leading to higher levels of light pollution (Cho, Sung and Ki, 2014), strategies to minimise the risk of bird-building collisions will be increasingly important.

Factors that influence visibility have long been discussed as affecting the navigational abilities of migrating birds and, consequently, interacting with the effects of light pollution (Allen, 1880; Cochran and Graber, 1958). Although birds are capable of maintaining their course even in thick clouds (Griffin, 1972), avoidance behaviour towards clouds and fog during migration has been observed (Panuccio *et al.*, 2019). Our results contribute to this discussion by showing a downward trend in MTR in response to increasing LCC in both light-polluted and dark settings. This effect may reflect the general tendency of birds to avoid migrating under adverse weather conditions involving thick clouds and fog.

Long-term observations have shown that birds accumulate at artificially illuminated structures under overcast conditions (Evans Ogden, 1996; Evans *et al.*, 2007). If this effect were strong in our study area, we might have expected higher MTR at the light-polluted site under high LCC; however, our model did not reveal such a pattern. An explanation could be that the absolute level of artificial illumination at our study site in Rovinj was too low to trigger additional accumulation of birds under overcast conditions. No clear interactive effect of light pollution and LCC was observed on migration intensity. However, flight altitudes at the light-polluted site decreased significantly by approximately 16 % for sea-crossing and 12 % for coastal migration under high LCC compared with clear-sky conditions. No such effect occurred at the dark site. This response adds to the main effect of light pollution, which already predicted lower flight altitudes at the light-polluted site regardless of LCC.

3.5.2 Conservation implications

The reaction of birds to light pollution demonstrated here has implications for the conservation of migratory birds. Our results suggest that migrating birds exhibit an in-flight response to artificial night-time lighting, even at low levels of illumination. This finding is consistent with previous research (Cabrera-Cruz *et al.*, 2021; Osterhaus *et al.*, 2025). Croatia is considered one of the most progressive countries in terms of light pollution regulation. Since 2008, the government has been working on measures to define, record, limit and prevent light pollution (Widmer, Marnane and Vounatsou, 2022). To this end, the first laws to prevent light pollution were introduced in 2019 (Hrvatski Sabor, 2019), followed by legislation establishing lighting zones with strict limits (Ministarstvo zaštite okoliša i energetike, 2020), including zones where only natural light is permitted. Nevertheless, local ecologists still view light pollution as a threat (Ječmenica *et al.*, 2020). With increasing tourism in the region, the anthropogenic influence on the Croatian coastal nightscape may grow further in the near future (Cho, Sung and Ki, 2014; Carić, 2018). Especially in coastal regions, we must be aware that night-time lighting could have far-reaching consequences.

Light-induced bird building collisions are believed to be one of the top contributors to avian mortality during migration. Estimates speak of up to a billion birds that are annually killed by collisions in the US alone (Loss, Will and Marra, 2015). The problem of light pollution has been recognised publicly, and first actions of collision mitigation are being implemented in several locations around the world (Evans Ogden, 2002; Loss *et al.*, 2023). Promising are large-scale actions such as the lights out initiative in Texas, USA (Saha, 2017; Convention on Migratory Species, 2024; Farnsworth, Horton and Marra, 2024), and the Bird Friendly Building Program (Evans Ogden, 2002).

Because bird migration is a highly dynamic phenomenon, it has been suggested that conservation measures can be so too (Horton *et al.*, 2021). Temporarily switching off non-essential illumination at nights where intense migration is expected can offer most birds safe passage. This, however, requires the implementation of accurate forecasting models on a large geographic scale (Kranstauber *et al.*, 2022). In the US, the free availability of continent-wide weather radar data has enabled scientists to implement such a model (Van Doren and Horton, 2018). However, in Europe, the restricted and heterogeneous availability of such data has prevented this so far (Desmet *et al.*, 2025). To implement this in the future, nations must work together to synchronise and distribute the data of their operational radar systems. Until then, it would be best to accompany infrastructural projects with an ornithological assessment, especially at potentially sensitive locations, where a lot of migrating birds might accumulate, and where the geographic and anthropogenic environment potentially creates fatal situations (Kirby *et al.*, 2008). Adapting the lighting schedules of buildings to migrating birds, especially during peak migration nights, could prevent millions of collisions annually.

3.6 Conclusion

Migratory birds responded differently to light pollution along the Croatian coast, depending on the direction of migration (sea-crossing or along the coast). We detected a significant response in the form of reduced airspeeds and markedly lower flight altitudes at the light-polluted site compared with the near-natural site. This is of concern because lower flight altitudes increase the risk of collisions with illuminated structures, particularly under conditions of reduced visibility. Our results warrant further research that includes more sites and potentially includes a lights-out program as an experimental evaluation. A deeper understanding of how birds are affected by night-time lighting is still urgently needed to understand how we can prevent unnecessary losses during migration. As this is a global phenomenon occurring across diverse geographical and anthropogenic contexts, such research could yield valuable insights.

4 Redistribution of sea-crossing bird migration in response to coastal artificial illumination

Simon Hirschhofer^{1,2}, Peter Ranacher¹, Robert Weibel¹, Barbara Helm², Barbara Vodarić Šurija³, Baptiste Schmid²

¹ University of Zurich, Department of Geography, Zurich, Switzerland

² Swiss Ornithological Institute, Department of Bird Migration, Sempach, Switzerland

³ Croatian Meteorological and Hydrological Service

Author contributions: **SH:** conceptualisation, data curation, formal analysis, investigation, methodology, project administration, software, validation, visualisation, writing—original draft, writing—review and editing. **PR:** conceptualisation, methodology, supervision, writing—review and editing. **RW:** conceptualisation, funding acquisition, supervision, writing—review and editing. **BH:** conceptualisation, funding acquisition, project administration, resources, supervision, writing—review and editing. **BV:** data curation, resources. **BS:** conceptualisation, data curation, funding acquisition, investigation, methodology, project administration, resources, software, supervision, validation, writing—original draft, writing—review and editing.

Submitted to:

Remote Sensing in Ecology and Conservation

Data and code:

Hirschhofer, S. et al. (2025). R scripts and data for the article 'Redistribution of sea-crossing bird migration in response to coastal artificial illumination'. Zenodo. <https://doi.org/10.5281/zenodo.17962319>.

Supporting Information in Appendix D.

4.1 Abstract

Artificial light at night is widely known to have an influence on avian broad-front migration. Extreme-intensity illumination attracts, confuses, and disorients birds, which can lead to lethal collisions with illuminated infrastructure. However, little is known about the in-flight redistribution of avian broad-front migration on a landscape scale, especially when the illumination is relatively dim. Furthermore, sea-crossing birds might be especially affected by coastal illumination due to the high contrast from the dark seascape to the illumination patterns on land. We investigated whether nighttime bird densities of sea-crossing migration exhibit differences over illuminated compared to the dark area over two consecutive spring migration seasons. Using coastal weather radar data from the Debeljak station in Croatia, we

compared vertically integrated bird densities between an illuminated (sky brightness increased by 53 %) and a dark (sky brightness increased by 14 %) sampling area using generalised linear mixed-effects modelling. Bird densities were consistently higher above the illuminated compared to the dark area, with the strongest effect noticeable two to three hours after civil dusk. These findings indicate an attraction and redistribution of migrating birds toward illuminated areas while approaching the coastline after crossing the Adriatic Sea, even with relatively low-intensity artificial light at night. Our research highlights the importance of reducing and controlling artificial light at night, particularly in coastal regions. We call for continued monitoring and adaptive management of artificial illumination to safeguard migratory species. Croatia's recent national legislation limiting light pollution represents an important step in that direction.

4.2 Introduction

Artificial light at night (ALAN) affects nocturnally migrating birds in-flight (Van Doren *et al.*, 2017; Cabrera-Cruz *et al.*, 2019; Weisshaupt *et al.*, 2022). Exposure to ALAN during migration can have cumulative consequences. Constant attraction and repulsion to and from ALAN can increase the total migration distance and thus, increase energetic costs of migration (Cabrera-Cruz *et al.*, 2021), draw birds toward suboptimal sites for stopover (McLaren *et al.*, 2018), and at the extreme end, lure birds toward illuminated buildings where millions end up in fatal collisions with human infrastructure each year (Evans Ogden, 1996; Korner, von Maravic and Haupt, 2022; Loss *et al.*, 2023).

The reaction to ALAN might be particularly high in a geographic setting where there is a high contrast between dark and illuminated areas. This is a particular problem during (Rebke *et al.*, 2019) or after the crossing of larger bodies of water (Van Doren *et al.*, 2021). Recently, the in-flight reactions of birds to ALAN were analysed separately for sea-crossing birds and birds following the coast by using ornithological radar at a light-polluted and a near-natural site in Istria, Croatia (Hirschhofer *et al.*, 2026). The study found that sea-crossing bird densities increased by 23 % from the near-natural site to the light-polluted site, though the difference was not statistically significant. The results suggested complex interactions between the effect of ALAN and migration direction, as well as with visibility.

Light pollution is often patchy and cannot be completely separated from other confounding variables, particularly from topography, which is known to strongly influence bird migration patterns (Aurbach *et al.*, 2018; Bruderer and Peter, 2022; Hirschhofer *et al.*, 2024). Broad-front bird migration upstream of a study area may already be influenced by topography or other ALAN patterns outside of the study area. One way to minimise these confounders is to study differences between areas of low and high ALAN along coastlines at landfall, immediately after birds have crossed the sea.

Weather radar has been shown to be an effective means of quantifying migratory behaviour over a large area. We analysed data from a coastal weather radar (Debeljak WR) near the city of Zadar, Croatia. During their spring migration, numerous birds migrate across the Adriatic Sea from Italy to Croatia at this location. Using ornithological radar capable of quantifying bird migration patterns from individual echoes, it has been demonstrated that the dominant migration direction is across the sea earlier in the season, from February to the end of March,

while by late April, nights characterised by sea-crossings had become much rarer (Hirschhofer *et al.*, 2025).

Most nocturnally migrating birds initiate flight shortly after dusk (Fortin, Liechti and Bruderer, 1999; Michev *et al.*, 2020). At Zadar, the Adriatic Sea is approximately 160 km wide (measured at a 75° azimuth course), and birds take roughly 3 to 5 hours to cross, depending on the wind, given estimated airspeeds between 10 and 13 m·s⁻¹. For birds that frequently cover 300 km within a single night (Tøttrup *et al.*, 2012), this stretch is not long enough to arrive exhausted, energy-depleted and in search of a stopover after the crossing and thus short enough to study the in-flight reaction of birds to ALAN.

In this study, we use integrated vertical profiles of bird densities derived from a coastal weather radar to compare areas with high and low levels of ALAN (here referred to as bright and dark areas). We expect attraction of sea-crossing birds to bright areas and hypothesise that there will be a generally higher density of birds over bright than over dark areas. However, we also anticipate shifts in this relationship over individual nights due to changes in flight behaviour from midnight to the early morning.

4.3 Methods

4.3.1 Study area and data

Our study area is located in Dalmatia, Croatia, along the eastern Adriatic coast. Here, the intensity of ALAN varies considerably, with notable contrasts between bright and dark areas.

To quantify bird migration across wide spatial scales, we analysed data from the Debeljak WR (44.0451°E, 15.3764°N, 208 m asl), which is located between the city of Zadar to the northwest and the Vransko Lake Nature Park to the southeast. We obtained single-polarisation polar volumes from the Croatian Meteorological and Hydrological Service, which were compiled according to the ODIM data centre standards (Michelson *et al.*, 2014). The data included three radar moments: logged horizontally polarised total (uncorrected) reflectivity factor (TV) [dBZ], logged horizontally polarised (corrected) reflectivity factor (DBZH) [dBZ] and horizontally polarised radial velocity (VRADH) [m·s⁻¹] (see Michelson *et al.*, 2014). Horizontally polarised radial velocity, too, was corrected and thus did not contain much biological information. We therefore only used TV, and applied our own filters to remove ground clutter, interference and precipitation (see below for details). Information on flight direction was obtained from a small-scale, vertically looking ornithological radar (BirdScan MR1) located in Zadar, which allowed us to distinguish nights dominated by bird migration across the Adriatic Sea from nights on which birds predominantly followed the coast in a north-northwest direction.

To investigate the effects of ALAN on sea-crossing birds, we: 1) selected nights between mid-February and late-April in 2023 and 2024 that were dominated by sea-crossing directions; 2) defined two sampling areas with a high contrast in ALAN levels perpendicular to the coastline; and 3) filtered the weather radar data and computed time series of vertically integrated bird density. Figure 4.1 provides an overview of the study area and the radar sites.

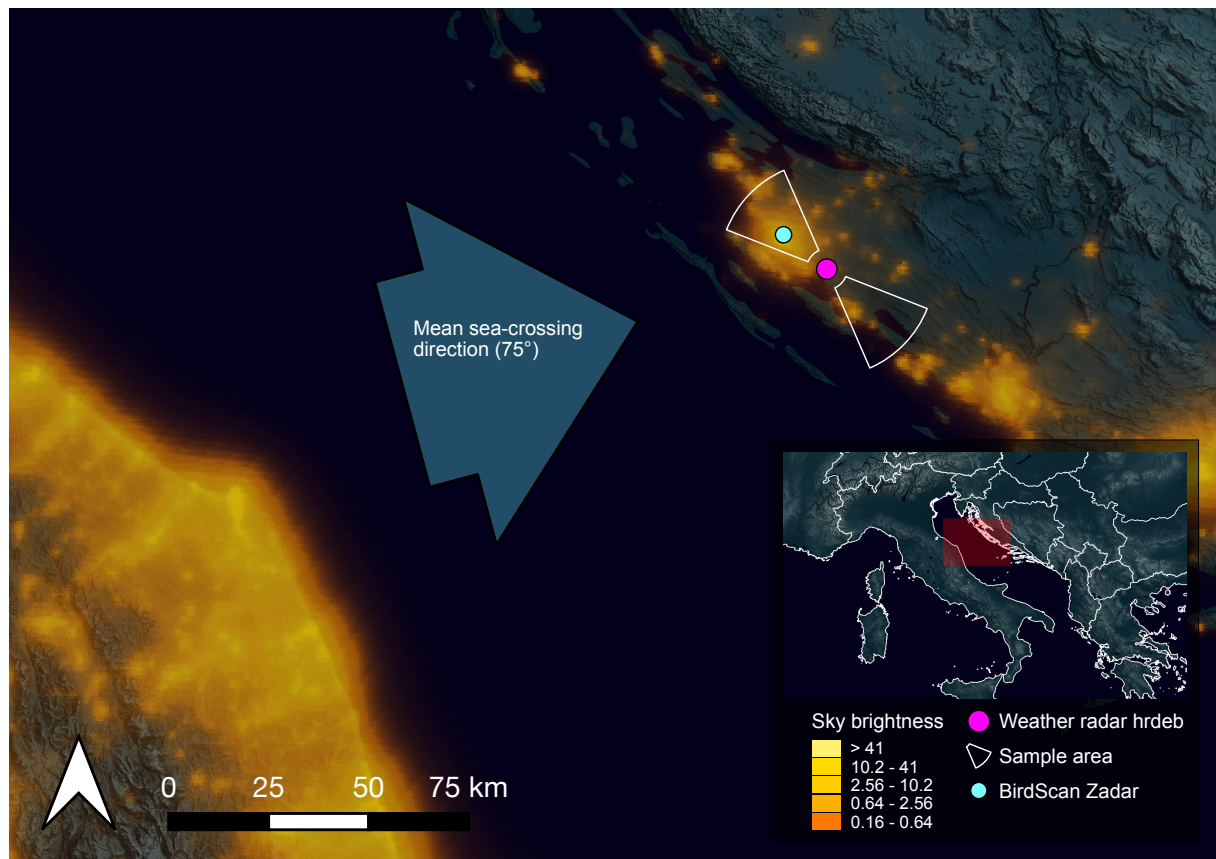


Figure 4.1. **Map overview of the study area at the east Adriatic coast**, showing topography, the extent of the sea, the location of the Debeljak weather surveillance radar, the position of the ornithological BirdScan MR1 radar from which we derived the mean migration direction of sea-crossing birds, and a visualization of ALAN. ALAN is shown as sky brightness, which we calculated from satellite-derived upward radiance (Elvidge *et al.*, 2021) using the simplified model of all-sky artificial sky glow (Duriscoe *et al.*, 2018).

4.3.2 Weather radar data processing

The Debeljak WR operates on the C-band and includes elevation angles ranging from 0.5° to 25° , with a total of nine elevation scans. During each rotation of the antenna, the radar records one scan at one elevation, then elevates the antenna before recording the next scan, repeating this process until the highest elevation angle is reached. These scans are aggregated to create a polar volume, which is typically completed every 15 minutes. The data is arranged on a polar grid, with volume pixels having an azimuthal resolution of 1° (azimuth gate) and a range resolution of 400 m (range gate).

Modern C-band weather radars routinely provide dual polarisation and Doppler velocity moments that facilitate echo classification (Stepanian *et al.*, 2016). Although the Debeljak weather radar was upgraded to dual polarisation in spring 2022, dual-polarisation products were not available to us due to a data infrastructure issue. Consequently, only horizontally polarised moments were accessible, and all biological signal extraction relied on single-polarisation reflectivity (TV).

To identify persistent non-biological echoes, we constructed a static clutter mask based on a visually selected clear-air day in March with minimal daytime bird- or insect activity. This day exhibited pronounced radio frequency interference (RFI), which typically affects fixed azimuths due to stationary electromagnetic emitters (Schaper *et al.*, 2022). For each elevation

scan separately, we averaged reflectivity across all polar volumes of that day to obtain an elevation-specific mean reflectivity field. Volume pixels with a mean reflectivity greater than -10 dBZ were classified as persistent clutter. Importantly, this threshold was applied to the averaged reflectivity field only, not to individual polar volumes. Thus, pixels exceeding -10 dBZ in the mean field were considered structurally contaminated and were masked in subsequent analyses by setting the corresponding volume pixel to NA. This approach follows the logic of Dokter et al. (2011) and was also successfully applied by Hoekstra et al. (2023). Because this threshold was derived from a temporal average rather than instantaneous reflectivity, it identifies volume pixels with consistently high reflectivity, while retaining transient biological signals in clean regions.

To account for terrain-induced blockage, we created an additional beam occultation mask. We therefore determined the beam width and height above the ground of the Debeljak WR. Ground elevation was derived from a digital elevation model of the region obtained from the Shuttle Radar Topography Mission (NASA JPL, 2013), and then applied to each volume pixel in the spatial grid of the Debeljak WR. Finally, for each affected elevation scan (0.5° and 1.3°), we simulated beam propagation along each azimuth gate, marking range gates as blocked where the estimated beam width intersected the topography. Subsequently, we removed volume pixels with partial or full blockage from the analysis. The method was described in Buler and Diehl (2009).

We created the final clutter mask by combining the static echo mask with the beam occultation mask. The mask was then used to clean the total reflectivity from static echoes and topographic clutter by setting affected volume pixels to NA.

We used QGIS (version 3.40.13) for mapmaking and to fit and analyse the bird density sampling area. We used R (version 4.3.1) to process the data, perform statistical analyses and visualise the results.

4.3.3 Weather radar sampling areas

We defined two sampling areas of equal size and distance from the Debeljak WR, both of which were located along the coastline within the surveyed volume (Figure 4.1). One sampling area, which is predominantly urbanised and characterised by relatively bright ALAN, is located in the northwest of the volume. The other sampling area, which is predominantly rural and relatively dark, is located in the southeast of the surveyed volume. The centres of the circular sampling areas were placed on a virtual line parallel to the estimated coastline. The sampling areas were then constructed as 45° ring sectors. Due to clutter contamination of weather radar data at close ranges and to avoid range-dependent biases (Dokter *et al.*, 2011), we set the minimum distance of the sampling areas to 5,000 m and the maximum distance to 27,000 m to exclude another urbanised area to the southeast of the dark sampling area. At these distances, the beam altitude of the lowest elevation angle (0.5°) is approximately 253 m ASL and 536 m ASL.

We quantified the contrast in ALAN between the two sampling areas by computing sky brightness from the 2023 annual cloud-free day-night band composite from VIIRS (Elvidge *et al.*, 2021), by following the simplified model of artificial sky glow (Duriscoe *et al.*, 2018), and summarising the value range within the sampling area polygons. Within the dark area, the artificial sky glow ratio was 0.14 ± 0.09 (14 % above natural sky brightness), ranging from

0.05 to 0.73. In the bright area, the ratio was 0.53 ± 0.52 (53 % above natural sky brightness). Nevertheless, these values represent relatively low levels of ALAN compared to other urbanised landscapes in southern Europe (Duriscoe *et al.*, 2018; Falchi *et al.*, 2019).

4.3.4 Filtering for sea-crossing nights

Ornithological radar data were collected from 1 March to 30 April 2023 and from 19 February to 30 April 2024 in the city centre of Zadar (44.1204° N, 15.2404° E; 19 m asl). The BirdScan MR1 ornithological radar records single bird echoes and classifies them into broad taxonomic groups based on echo intensity (related to scatterer size) and changes in intensity over time (related to wing-flapping patterns), using a random forest classifier (Schmid *et al.*, 2019). We used these data to define sea-crossing nights based on the mean nightly flight direction of bird echoes with intermittent wing flapping, corresponding to small- to medium-sized passerines, and continuous wing flapping echoes, corresponding to small- to medium-sized waders.

To distinguish between sea-crossing and coastal migration directions, we first visually identified a line along the coastline at our study site and measured its orientation (between 146° and 326°) using QGIS. We classified echoes with a flight direction of $56^\circ \pm 45^\circ$ as sea-crossing. We then calculated the migration traffic rate (MTR, in birds $\text{km}^{-1} \text{h}^{-1}$) for the sea-crossing migratory flux relative to the total migration volume. The MTR is a standard quantification for migrating birds which corrects for the altitude-dependent sampling bias of radar devices (Schmaljohann *et al.*, 2008). Finally, from a total of 133 nights with sufficient data for migration direction estimation, we selected 52 nights where sea-crossing MTR dominated the total avian movement aloft.

Furthermore, the BirdScan can distinguish between birds and insects, enabling insect contamination in the weather radar data to be assessed. All pre-selected nights showed a low proportion of insects, if dusk and dawn were excluded, which reflects the phenology of insect migration across Europe (Haest *et al.*, 2024).

4.3.5 Weather radar bird density time series

We quantified bird density over time for each sampling area by first computing vertical bird density profiles for nights dominated by sea-crossing migration, which were then integrated and merged into time series using the *bioRad* R package (Dokter *et al.*, 2019).

We divided the data into daytime and nighttime periods by estimating civil dusk and dawn, defined as the times at which the sun passes 6° below the horizon in the evening and morning, respectively. We used the *suncalc* R package (Thieurmél and Elmarhraoui, 2022) to make these estimations. Next, we focused on nighttime recordings of polar volumes only. For each night, we calculated the minutes after dusk for each polar volume and grouped them by hour after dusk. We then averaged the bird density for each sampling area within this grouping.

Finally, we excluded the first two hours of each night, as these correspond to the approximate minimum time required for sea-crossing birds to cross the Adriatic Sea, and to avoid insect contamination at dusk and dawn. Furthermore, we restricted the analysis to hours that were present in all sampled nights. Night length in Zadar varies substantially during the study period, from approximately 12 h 30 min in mid-February to about 8 h in late April. To ensure

comparable sampling effort across nights and avoid uneven representation of later hours, we excluded hours 9 to 12 after civil dusk.

4.3.6 Modelling bird densities

We analysed migratory bird density differences between bright and dark areas using a generalised linear mixed-effects modelling approach of hourly estimated bird densities, using the *glmmTMB* R package (Brooks *et al.*, 2017). We log-transformed the bird densities to meet the normality assumption of the residuals, correcting their right-skewed distribution. Fixed effects were specified for sampling area (factor, dark/bright, with dark as the reference level), hour after sunset (ordered factor, 2 to 8), and an interaction term between sampling area and hour after sunset. To account for within-night temporal dependencies of bird density measurements, our model employed a first-order autoregressive (AR1) correlation structure. We allowed the model to vary by hour of the night by estimating random slopes within the autocorrelation structure, and nested the structure within each night, allowing night-to-night variation in the strength of temporal autocorrelation. We fitted the model using restricted maximum likelihood (REML) estimation with Broyden-Fletcher-Goldfarb-Shanno (BFGS) optimisation to ensure reliable convergence regarding the complex model structure.

For statistical inference, we performed post-hoc analyses using the *emmeans* R package (Lenth, 2017) to compute estimated marginal means for each combination of sampling area and hour after dusk. We calculated pairwise contrasts between the bright and the dark area at each hour, with effect sizes reported as percentage differences and 95% confidence intervals. Doing so, we included a Bonferroni correction to compensate for multiple testing. We back-transformed the log-scale estimates to the response scale for biological interpretation. Significance was assessed using Wald tests. Finally, we visualised the results using point estimates and 95 % confidence intervals.

4.4 Results

Nighttime bird densities (Table 4.1) were on average 4.8 birds · km⁻² (Q1 = 1.6; Q3 = 7.9, max = 42.6) within the dark area, and 5.7 birds · km⁻² (Q1 = 1.4; Q3 = 9.9, max = 28.7) within the bright area. Measurements showed distinct changes within nights. The density peak within sea-crossing dominant nights was usually between 4 and 5 hours after civil dusk.

Table 4.1. **Vertically integrated bird density** from the Debeljak WR over the dark and bright areas during sea-crossing dominated nights in the spring migration seasons of 2023 and 2024 from mid-February to the end of April.

Hour after dusk	Dark mean ± sd	Dark max	Bright mean ± sd	Bright max
2	3.55 ± 2.10	18.42	5.12 ± 3.20	22.71
3	5.48 ± 4.74	23.98	7.01 ± 4.85	25.63
4	7.34 ± 5.87	33.74	7.83 ± 5.50	29.40
5	7.69 ± 6.00	55.60	8.24 ± 5.58	34.86
6	6.75 ± 4.74	31.66	7.40 ± 4.47	25.46
7	5.55 ± 3.13	14.97	6.37 ± 3.52	16.98
8	4.87 ± 2.59	17.01	5.75 ± 3.32	18.12

The linear mixed effects model showed significantly higher bird densities at the bright area, compared to the dark area, with distinct within-night dynamics in that relationship (Figure 4.2). The model explained 28.8 % of the variance in bird densities (marginal $R^2 = 0.288$, representing fixed effects only, as some of the random effects variances were close to zero), while all predictors showed a significant effect on bird densities.

The bright area exhibited significantly higher bird densities than the dark area for almost the whole night, although the effect varied throughout the night. Bird densities were higher in the bright area compared to the dark area during the early night (dark to bright, hour 2: + 30.5 %, $p < 0.05$; hour 3: + 27 %, $p < 0.05$), the difference decreased during the middle of the night (dark to bright, hour 4: + 7.2 %, $p < 0.05$; hour 5: + 9.4 %, $p < 0.05$), and the difference increased again towards the end of the night (dark to bright, hour 6: + 12.7 %, $p < 0.05$; hour 7: + 11.3 %, $p < 0.05$). Before sunrise, the difference from dark to bright was not statistically significant anymore (dark to bright, hour 8: + 11.3 %, $p = 0.43$).

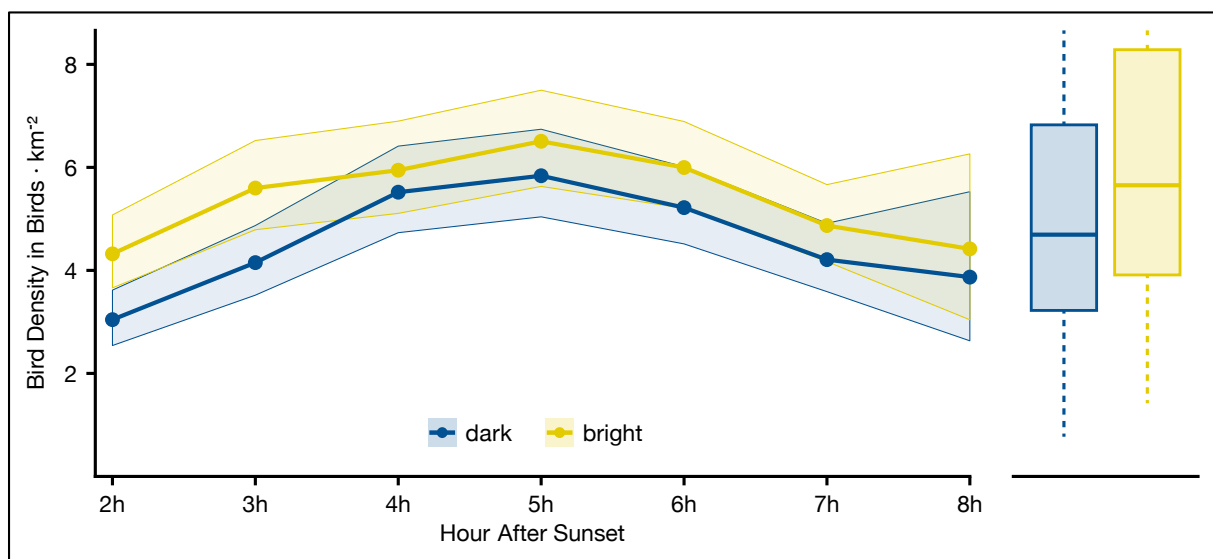


Figure 4.2. **Mean bird density in the dark and the bright sampling areas of the Debeljak WR.** The left-hand panel shows Bonferroni-corrected bird density estimates with 95 % confidence intervals. For reference, the right-hand panel shows the overall means and interquartile ranges of measured bird densities in dark and bright areas.

4.5 Discussion

4.5.1 Discussion of the results

We analysed data from a coastal weather radar at the eastern Adriatic coast to investigate vertically integrated bird densities during spring migration in a dark and a bright area. Measurements showed that throughout the night, bird densities in the bright area consistently exceeded bird densities in the dark area. We confirmed this difference with a generalised linear mixed model approach and have shown that there are distinct within-night differences in the correlation between dark and bright areas, suggesting a dynamic behavioural response of migrating birds to ALAN throughout the night.

In general, this result confirms our hypothesis that the density of migrating birds is higher over the bright area studied here than over the nearby near-natural area on nights when sea-crossings predominated. Although our modelling did not correct for the possible influence of additional effects on the difference in bird density between bright and dark areas, this result

strongly suggests that ALAN influences the redistribution of birds. Nocturnal bird migration across the Adriatic Sea occurs over a broad front (Bruderer and Liechti, 1999; Trösch et al., 2005). With no reasonable disturbance and deviation of over-sea broad-front migration by geographic features, a natural redistribution of birds during sea-crossing can only be explained by winds and rain (Erni et al., 2002; Erni, Liechti and Bruderer, 2005). However, there is no significant known heterogeneity in wind currents over the Adriatic Sea across a sufficiently small area to justify the significant differences observed between the two sampling areas (Pullen et al., 2007; Pasarić, Belušić and Chiggiato, 2009). Therefore, these variables should cancel each other out during modelling. Furthermore, due to the high level of simplification of the datasets, we attempted to keep the model as simple as possible to avoid introducing spurious correlations. Although it is reasonable to assume that the interaction between wind, visibility, and ALAN affects measured bird density, this effect was not observed in earlier regional studies (Hirschhofer et al., 2026). Although these were based on the BirdScan ornithological radar, which uses a vertical scanning mode with limited spatial extent, Nilsson et al. (2018) demonstrated that monitoring migration intensity with BirdScan correlates reasonably well with monitoring bird densities using weather radar (see also the Supporting Information for this article).

The influence of ALAN on migrating birds has long been recognised. Early observations already documented that illuminated structures such as lighthouses could attract and disorient migrating birds, often resulting in fatal collisions (Allen, 1880). Experimental studies have since shown that ALAN can disrupt orientation behaviour during migration, affecting both inexperienced and experienced migrants (Gauthreaux, 1982; Rebke *et al.*, 2019).

Our results suggest that even relatively dim coastal ALAN can redistribute sea-crossing bird migration. One plausible mechanism is the strong visual contrast between the dark seascape and illuminated coastal areas. Migrating birds approaching land after crossing open water may detect coastal illumination from considerable distances and respond to this high-contrast stimulus before reaching the coastline. A similar behavioural response to relatively low levels of ALAN has been observed in otherwise dark landscapes (Cabrera-Cruz *et al.*, 2021). In the present setting, where birds cross the Adriatic Sea without topographic obstacles shielding the distant coastline, the visual contrast between sea and illuminated land may amplify this response within the radar-surveyed volume (Åkesson *et al.*, 2021; Degen, Kolláth and Degen, 2022). An alternative explanation is the well-known tendency of birds to reorient toward land during sea crossings (Archibald *et al.*, 2017; Schekler, Levi and Sapir, 2024). However, the Adriatic crossing between Italy and Croatia is approximately 160 km wide, a distance that migrating birds regularly cover within a few hours and well below the typical nightly migration distance of several hundred kilometres (Tøttrup *et al.*, 2012). Consequently, land reorientation due to exhaustion alone seems unlikely to explain the redistribution towards illuminated coastal areas observed in this study. Either way, the higher vulnerability of sea-crossing birds to becoming victims of the influence of ALAN has been assumed previously by Van Doren et al. (2021) and confirmed by Hirschhofer et al. (2026). However, the mechanisms behind these findings remain unclear.

Besides ALAN alone, local geographical features may also influence the observed density patterns. Dalmatia is characterised by an extensive archipelago of more than 1200 offshore islands. Such island systems can affect migration behaviour during sea crossings (Barboutis *et al.*, 2022). Birds approaching the Croatian mainland may interact with illumination patterns on these islands before reaching the coast. In addition, stopovers on offshore islands could

generate short sea-crossing flights early in the night. Although we attempted to minimise this potential effect by excluding the first two hours after dusk, further studies in coastal regions without offshore island systems would help clarify the influence of archipelago stopovers on coastal migration patterns.

Besides the overall higher bird densities observed over the illuminated area, we also hypothesised that the strength of this difference might vary throughout the night. To our knowledge, such temporal dynamics have rarely been investigated. The biggest difference between bright and dark occurred during the early night (hours 2–3 after sunset), which likely corresponds to the arrival window of birds departing from the Italian mainland. Later in the night, density differences became smaller, possibly reflecting behavioural changes as birds approach stopover decisions closer to dawn. While late departures from offshore islands cannot be excluded, the temporal pattern broadly aligns with the expected timing of sea-crossing arrivals.

Attraction to illuminated areas may also have important ecological consequences. ALAN has been shown to influence stopover distributions across landscapes (Schekler *et al.*, 2022; Horton *et al.*, 2023). Although birds may still prefer darker habitats locally, stopover densities often increase in illuminated regions at larger spatial scales (McLaren *et al.*, 2018). Attraction towards illuminated urban areas can therefore increase exposure to anthropogenic hazards such as building collisions or predation by domestic cats (Erickson, Johnson and Young Jr., 2005; Borden *et al.*, 2010). In the present study region, birds were found to have redistributed towards the city of Zadar (the largest city in the region) and away from the well-known stopover area for migrating birds around Vransko Lake, which is to the south-east of the Debeljak WR (Tutiš and Radović, 2003).

Visibility conditions may further amplify the risks associated with ALAN. Higher collision rates near illuminated structures have been observed during foggy or cloudy nights when visual cues are impaired (Jones and Francis, 2003; Van Doren *et al.*, 2021; Chen *et al.*, 2024). However, at the landscape scale, previous work in the same region did not find strong interactions between ALAN and cloud cover in shaping migration passage rates (Hirschhofer *et al.*, 2026). This suggests that the observed increase in collision numbers in conditions of impaired visibility may be primarily due to local attraction and disorientation, rather than large-scale changes in migration intensity.

Our results show that even relatively dim coastal illumination can influence the in-flight behaviour of migrating birds. Some of the most striking documented ALAN effects involve high-intensity illumination (Van Doren *et al.*, 2017), but the present findings indicate that lower levels of coastal light pollution may also redistribute migration flows. Since artificial lighting is closely tied to human safety and infrastructure (Boyce, 2019), completely eliminating nighttime illumination is unrealistic. However, light pollution remains one of the few anthropogenic pollutants that can be effectively reduced through targeted management measures, including directing light downward, reducing brightness, limiting short wavelengths, and protecting sensitive habitats from illumination (Pothukuchi, 2021).

In this context, Croatia has recently implemented one of the most detailed national regulatory frameworks in Europe for managing light pollution. National legislation addressing light emissions was first introduced in 2008, followed by a comprehensive law in 2019 and binding illumination limits in 2020 (Hrvatski Sabor, 2019; Ministarstvo zaštite okoliša i energetike, 2020). These regulations include strict requirements for protected areas and zones with zero

illumination (Widmer, Marnane and Vounatsou, 2022). Given that even low-intensity coastal illumination can influence migrating birds, our results support continued efforts to reduce unnecessary nighttime lighting, particularly in ecologically sensitive coastal regions.

4.5.2 Limitations of this study

The geographical location and technical specifications of the Debeljak WR impose several limitations that must be considered when evaluating the significance of our results. The radar is positioned at 208 m ASL, and considering the beam propagation of the lowest elevation scan corresponds to 253 m ASL and 536 m ASL at the near and far boundaries of the sampling areas, respectively. Due to this elevation, the lowest atmospheric layers, which contain a significant proportion of the total migratory volume (Bruderer and Liechti, 2004; Bruderer et al., 2018; Kemp et al., 2013; Cabrera-Cruz et al., 2019), were largely unobserved. Examining the sea-crossing migration recorded simultaneously by BirdScan, approximately 40% of birds at the near boundary and around 80% of all birds at the far boundary pass below the weather radar.

Furthermore, the lowest two elevation scans (0.5° and 1.3°) of the Debeljak WR were affected by immense clutter from topographic obstacles and frequent RFI, which limited the reliability of high-resolution estimates across these scans. This high level of clutter contamination could also explain the relatively low bird densities overall. Similar studies typically document much higher bird densities, but most birds would be concentrated at lower altitudes, which were inaccessible in the current situation (Dokter *et al.*, 2011). As ecologically relevant interactions, such as bird-building collisions, primarily occur close to the ground, an analysis of altitude distributions and their ALAN-related changes would not have produced meaningful results and was therefore not included. As all coastal weather radars in Croatia are situated at higher elevations than the Debeljak WR, the Croatian coastline is not well-suited to studying altitudinal shifts in response to ALAN using weather radar. However, research using ornithological radar systems in Istria has revealed substantial altitude changes related to ALAN, prompting further research using more suitable instruments (Hirschhofer *et al.*, 2026).

Finally, during the study period, only single polarisation data products were available, and the spatial coverage of the radial velocity product was incomplete. This necessitated conservative data cleaning procedures and the reliance on aggregated densities within a sampling area, rather than analysing densities at a higher spatial resolution. Modern dual polarisation data would have enabled more efficient clutter removal using the *bioRad* R package (Dokter *et al.*, 2019), allowing higher-resolution spatial analyses of the redistribution of broad-front migration along the whole coastal region within the radar surveyed volume. The Croatian Meteorological and Hydrological Service has recently upgraded its radars to provide dual polarisation products (Barbara Vodarić Šurija, personal communication), which will enhance the quality of future aeroecological studies in the region. However, recent policy developments concerning the availability and applicability for biodiversity monitoring of meteorological data in Europe may jeopardise the long-term monitoring of avian movement in the aerosphere (Shamoun-Baranes *et al.*, 2022). As weather radar data have broad societal and scientific utility (Bauer *et al.*, 2017), it is essential that they are publicly available and harmonised in terms of content and structure across nations for comparative research. Our case study, therefore, also highlights the need for legislative support for such digital infrastructure.

4.6 Conclusion

Our analysis of weather radar data revealed higher bird densities above an illuminated area than above a nearby dark area. We argue that these differences were caused by relatively dim coastal ALAN, which redistributes the broad-front sea-crossing bird migration. Compared to other regions of southern Europe, large parts of Croatia still experience relatively low levels of nighttime illumination. In recent years, the Croatian government has also implemented a comprehensive national framework to regulate light pollution, including clearly defined, location-specific limits on outdoor lighting, particularly in protected areas. Our findings highlight the importance of such legislative measures and support efforts to reduce unnecessary nighttime illumination wherever possible.

Future research would benefit from exploring how temporary reductions in ALAN influence migration behaviour at broader spatial scales. Such dynamic mitigation measures could, for example, be implemented during nights with poor visibility or during periods of intense migration. However, the present study investigated the redistribution of migrants only and, due to the location of the Debeljak weather radar, focused on flight altitudes that are not yet directly relevant for bird–building collisions. Future studies should therefore investigate whether the redistribution of broad-front migration in response to dim coastal illumination also translates into increased collision risk.

5 Synthesis

5.1 Conclusion

This dissertation examined whether relatively dim coastal ALAN affects nocturnal bird migration across behavioural and spatial scales, and whether these effects depend on the migratory context, i.e. sea-crossing versus coastal-following routes. Three complementary studies revealed that low-intensity, patchy coastal illumination can alter migratory behaviour, particularly in sea-crossing birds, causing migration to shift towards illuminated areas on a regional scale.

The effect of artificial light at night on migrating birds is complex and dependent on various co-factors (Gaston *et al.*, 2013). The detrimental consequences of ALAN on birds were recognised more than 150 years ago, when early ornithologists first described large numbers of birds colliding with illuminated structures (Allen, 1880). Since then, technological progress and a much deeper understanding of the drivers of migration and the physiology of orientation have greatly expanded our knowledge of how ALAN influences nocturnal migrants (Hüppop *et al.*, 2019), the potential behavioural and demographic consequences (Burt *et al.*, 2023; Nemes *et al.*, 2023), and how the most severe effects can be mitigated (Farnsworth, Horton and Marra, 2024). Despite this progress, our understanding of how ALAN affects migrating birds across ecological and geographical contexts remains inconsistent.

Hölker *et al.* (2021) identified several pressing research gaps concerning the effects of ALAN on biodiversity. Three of these are addressed by the present research project. The first research gap concerns the lack of evidence for the thresholds at which ALAN becomes light pollution of ecological relevance. So far, research has only marginally studied ALAN at lower intensities, which are common in near-natural and rural landscapes. The second gap relates to the redistribution of animals in response to spatial patterns of ALAN. The third gap concerns the extent to which ecological and geographical context influence the impact of ALAN. Coastal regions represent ecological and geographic boundaries, because birds may undergo orientational adjustments in response to the changing landscape, in particular the emergence of new landmarks, and because the contrast between darkness at sea and heterogeneous illumination on land could amplify behavioural responses. Although Hölker *et al.* (2021) identified these gaps in relation to biodiversity in general, birds provide an excellent proxy for community-level research, as their movement aloft can be measured and quantified with increasing precision (Hoekstra *et al.*, 2023).

This dissertation comprises three research articles that address avian migration behaviour at the Croatian Adriatic coast and how it is influenced by ALAN at different geographic scales and behavioural levels. Chapter 2 quantified sea-crossing and coastal migratory fluxes to provide a contextual basis for the interpretation of behavioural reactions within a coastal landscape. Chapter 3 analysed BirdScan MR1 data to identify fine-scale behavioural responses to relatively low-intensity ALAN, taking into account expected differences in orientation between sea-crossing and coastal birds and the strong visual contrast between the dark sea and the patchy light pollution along the coastline. Chapter 4 adopted a broader spatial perspective, using weather radar to monitor bird accumulation over urban, illuminated, and near-natural areas during nights dominated by sea-crossing migration. This chapter brings these perspectives together by revisiting the research questions and evaluating how

the combined evidence advances our understanding of the spatiotemporal effects of ALAN on migrating birds.

5.1.1 Answering the research questions

The synthesis below revisits the three main gaps identified in Chapter 1: the quantification of migratory fluxes along the Croatian coast, the fine -scale behavioural effects of relatively low-intensity ALAN, and the regional redistribution of migration in response to dim coastal illumination.

A first radar-based quantification of bird migration at the coast of Croatia

RQ1.1: *What are the main migratory fluxes of nocturnally migrating birds at the Croatian Adriatic coast during spring migration?*

RQ1.2: *Do these migratory fluxes separate into distinct sea-crossing and coastal-following components, such that the two directions can be analysed separately in relation to ALAN?*

HP1: *Nocturnal migration activity at the Croatian Adriatic coast is dominated by two main components: sea-crossing and coastal migration. These components can be identified based on differences in the shape of within-night migration intensity profiles.*

Chapter 2 presents the first radar-based characterisation of nocturnal spring bird migration at the Croatian Adriatic coast, addressing a long-standing gap in the description of migration phenology and directionality in this region. Previous knowledge of migration in the eastern Adriatic has been derived primarily from ringing, field observations, biologging, and large-scale moonwatching, which together suggested that Croatia lies at the intersection of the eastern and central flyways (Bruderer and Liechti, 1999; Busse, Zaniewicz and Cofta, 2015). However, these approaches have not allowed a continuous, quantitative assessment of migratory fluxes, nor an evaluation of how migration intensity and direction vary within and between nights over the course of a full migration season.

The results demonstrate that nocturnal migration in this region is indeed dominated by two main directional components: a north-eastern migratory flux crossing the Adriatic Sea and a north-western flux along the Croatian coastline. Together, these two components account for most of the observed migratory activity and define the large-scale structure of spring migration at the Adriatic coast. In short, both sea-crossing and coastal movements were consistently present throughout the study area and period, albeit with varying contributions between Istria and Dalmatia. Overall, sea-crossing migration dominated the selected sites early in the season, but a shift in directionality occurred mid-season. Regional differences suggested that, while sea-crossing migration was dominant throughout the season in Istria, Dalmatia exhibited a stronger shift in dominance towards coastal movement between the end of March and late April. At a finer temporal scale, however, the within-night dynamics of directionality revealed that coastal movement often dominated the early evening, while sea-crossing migration took over during the early morning. Similar patterns have been observed by Weisshaupt et al. (2018) in a different coastal environment. Overall, migration intensity varied considerably between individual nights. These findings confirm previous patterns derived from limited temporal evidence and provide the first quantitative description of the

relative importance and temporal dynamics of spring migration fluxes across and along the Adriatic Sea.

Furthermore, the migratory activity can be meaningfully divided into sea-crossing and coastal components. These migratory fluxes were estimated using the BirdScan MR1 radar by combining the track direction of individual echoes with the proportional migration intensity within predefined directional corridors. This directional separation is essential for treating sea-crossing and coastal migration as distinct yet overlapping components of nocturnal migration along the Adriatic coast.

Within-night migration intensity profiles provided additional insight into the temporal structure of these migratory components. Nights dominated by sea-crossing migration tended to exhibit later peaks in migration intensity than nights with a higher coastal migration intensity. However, the relationship between within-night intensity profiles and migration direction was inconsistent across all regions. At the Istrian sites, profile shape alone was not a reliable indicator of the dominant flight direction but was probably more closely related to headwinds and tailwinds experienced during sea-crossing. By contrast, in Dalmatia, late-peaked profiles were more clearly associated with sea-crossing movements. Therefore, within-night profiles are best interpreted as complementary descriptors of migration dynamics rather than as a standalone classification tool.

Taken together, the results support HP1 in terms that nocturnal migratory activity at the Croatian Adriatic coast can be divided into two main components: sea-crossing and coastal migration. These two components exhibit distinct spatiotemporal patterns. However, the regional variability in within-night dynamics highlights the complexity of migration within the coastal area under study.

Beyond its descriptive contribution, Chapter 2 establishes the empirical foundation required for subsequent analyses of the effects of ALAN on bird migration across spatial scales. By quantifying the main migratory fluxes and demonstrating that sea-crossing and coastal migration can be analysed separately using directional radar data, Chapter 2 provides the necessary framework for examining how different migratory components respond to heterogeneous illumination along the coast. In this way, Chapter 2 stands as an independent contribution to the understanding of east Adriatic spring migration phenology and as a foundation for the ALAN-focused analyses presented in the following Chapters 3 and 4.

Local-scale reactions of birds to light pollution

RQ2.1: *How do airspeeds and flight altitudes of birds differ between light-polluted and near-natural sites?*

RQ2.2: *Do these reactions differ between birds that crossed the sea and birds that followed the shoreline?*

RQ2.3: *What is the interactive effect between ALAN and impaired visibility on airspeeds and altitudes?*

HP2: *Birds show lower airspeeds and reduced flight altitudes in response to ALAN for both, coastal and sea-crossing directions. Because the signs of confusion are similar in both directions, the reactions are similar. Impaired visibility amplifies these reactions.*

In Chapter 3, we explored the fine-scale behavioural reaction of migrating birds to ALAN in-flight. Behavioural reactions of birds to high-intensity illumination have been observed in experimental settings previously, and the reduction of airspeeds, besides circling around the light, or, less extreme, changing direction, have been related to signs of confusion and disorientation (Bruderer, Peter and Steuri, 1999; Van Doren *et al.*, 2017). Cabrera-Cruz *et al.* (2021) followed up on this research and provided a correlational case study using low-intensity and even bird-friendly lights in a relatively dark nightscape. Not only did they find that birds even react to these dim lights, but they were also able to observe an amplification of the reactions in intensity and frequency under poor visibility, such as low clouds and fog.

Chapter 3 provides a first insight into the behavioural responses that birds show in response to low-intensity ALAN while accounting for the total bird density aloft. It has been demonstrated that even the light pollution of a small town, which is around 32 times lower in brightness than the illumination in Europe's large cities (Falchi *et al.*, 2019), triggers a statistically significant reduction in airspeeds and significantly lower flight altitudes compared to a nearby near-natural site.

HP2 assumed that coastal and sea-crossing birds would show similar fine-scale behavioural reactions to ALAN when considering airspeeds and flight altitudes. However, the reductions in airspeed and altitude associated with ALAN were clearly stronger among sea-crossing migrants. Since both metrics have been interpreted as indicators of confusion or disorientation, which should intuitively affect both groups in a comparable way, the question arises as to why coastal migrants appear less influenced by ALAN at this behavioural scale.

To interpret this difference, it is necessary to revisit the navigational context of the two migratory pathways. Birds that approach land after crossing a wide water barrier do so in an environment that is largely devoid of terrestrial reference cues. Over water, migrants rely mainly on compass-based navigation (Alerstam, 1990; Gwinner, 1990), which may increase the relative salience of isolated light sources offshore or along the coast. Coastlines, in contrast, are well-established orientation landmarks for nocturnal migrants and can act as leading lines across spatial scales (Alerstam and Pettersson, 1977; Bruderer and Liechti, 1998; Diehl, Larkin and Black, 2003). For example, coastal birds have been shown to compensate for drift more strongly, thereby maintaining proximity to this guiding line (Horton *et al.*, 2016). In addition to their visual prominence, coastlines also provide a distinct acoustic signature through surf noise, which can be detected by birds even when visibility is poor (Arrowsmith and Hedlin, 2005). As Deutschlander and Beason (2014, p. 117) note, hearing a coast could be as effective as seeing it and may offer a more reliable cue during nocturnal

flights. Sea-crossing birds lack such clear landmarks, and lower-intensity ALAN near the shoreline may therefore act as a disproportionately strong stimulus, because it represents a conspicuous signal within an otherwise feature-poor seascape. Coastal birds, by contrast, move within a corridor that is rich in natural orientational information, which likely reduces the influence of weak ALAN on their behaviour. Nonetheless, both groups showed significant reactions to ALAN. Although the absolute magnitude of these changes, particularly in airspeed, was relatively small, any measurable behavioural deviation in response to an unnatural stimulus during active migration suggests a potentially detrimental interaction between migrants and light pollution.

The observed changes in flight altitude are more concerning than the changes in airspeed, because altitude is directly related to the likelihood of encountering human infrastructure. In Chapter 3, a mean flight altitude of almost 400 metres above sea level was measured for sea-crossing migration, which was around 40 metres higher than for coastal migrants. Over the light-polluted site, the height of sea-crossing migrants was reduced by around 50 metres and another almost 60 metres with reduced visibility. A mean flight altitude of around three hundred metres is not inherently dangerous, but it implies that a substantial proportion of individuals will fly below this height. For example, several studies on wind turbines use 200 metres above ground level as the critical flight altitude below which the risk of collision becomes significant (Bruderer and Liechti, 2004; Hoekstra *et al.*, 2025). When ALAN and reduced visibility co-occur, migrants are more likely to descend to lower altitudes and to enter this vertical zone where collisions with infrastructure become more likely. The altitude responses documented in Chapter 3 thus illustrate a plausible mechanistic link between low-intensity coastal light pollution, weather conditions, and collision risk for large numbers of nocturnal migrants.

In short, *HP2* can be confirmed partially. While relatively low-intensity ALAN induced a response in migrating birds that indicates confusion and disorientation, namely reduced airspeeds and lower flight altitudes, the response was not similarly strong for sea-crossing and coastal migrants. Sea-crossing birds expressed a stronger behavioural reaction to ALAN. Reduced visibility or the limited availability of visible orientation cues amplified the response to ALAN in both groups. However, the sea-crossing group was more severely affected.

Redistribution of sea-crossing birds in response to ALAN from a weather radar

RQ3.1: *Are there differences in bird density between an urban, light-polluted area and a nearby, near-natural area during nights dominated by sea-crossing migration?*

RQ3.2: *How does this difference between light-polluted and near-natural areas change over the course of a night, and could this reflect temporal dynamics in barrier crossing and the timing of landfall?*

RQ3.3: *How does visibility affect attraction by ALAN?*

HP3: *Bird densities and migration intensity are higher over light-polluted areas. This increase is more pronounced for sea-crossing migration than for coastal migration. The attraction is strongest during sunset reorientation and towards the end of the night, while searching for a suitable stopover site. Impaired visibility amplifies the attractive effect of ALAN on birds.*

In *HP3*, it was assumed that birds would be drawn to the ALAN. This meant that measured bird densities would be higher above urban areas than in nearby rural or near-natural areas. It was also assumed that this aggregating effect would be more pronounced for sea-crossing birds than for coastal birds, and that the timing of nights would matter in terms of sunset reorientation and stopover selection. Finally, it was assumed that impaired visibility would amplify the redistribution of birds in response to ALAN.

This posited effect has been tested twice throughout this dissertation, in different regions along the Croatian coast and with different radar systems. The original plan was to assess the same effect in Istria and Dalmatia twice, first with BirdScan MR1 and then with weather radar. However, things did not always go according to plan. A major technical issue affected the BirdScan MR1 at Vransko Lake, rendering the data unusable for accurate bird quantification. Conversely, the Goli weather radar, which overlooks the Istrian Peninsula, is positioned at too high an elevation and too far from the west coast of the peninsula, where sea-crossing birds would first make landfall after crossing the Adriatic Sea. Nevertheless, Chapters 3 and 4 were able to independently explore the effect of relatively low-level ALAN on sea-crossing birds, finding a very similar effect size both times.

In Istria, an increase of around 20% in MTR was estimated from the dark to its associated light-polluted site, and although this effect was not statistically significant, it is still noteworthy. Using the Debeljak weather radar, a similar range of increase was estimated from dark to bright areas. Considering within-night dynamics, roughly 10–30% more birds were detected over the bright area than the dark area. The results from the Debeljak WSR confirm the tendency observed in Istria using the BirdScan MR1, supporting the view that the wide confidence intervals around the estimated MTR in Istria may have obscured a clearer effect. Taken together, these findings reinforce the need for further research into the impact of dim ALAN.

Taken together, the results from Istria and Dalmatia suggest that even low-intensity ALAN can redistribute nocturnal migrants at a landscape level, although the extent of this effect varies regionally. This research further supports the idea that urban areas with low to medium intensity night-time illumination consistently attract more birds than nearby near-natural areas during nights dominated by sea-crossing migration. It is therefore necessary to investigate why this pattern emerges and what ecological mechanisms might underlie it.

One possible explanation may lie in the intensity of ALAN. When the two regions are compared, the difference in ALAN intensity is much greater in Dalmatia than in Istria. Rovinj is a small city of around 12,800 inhabitants with relatively dim night-time illumination, whereas Zadar is a larger city of around 70,100 inhabitants with a typical urban night-time environment (personal observation, Figure 1.11). Osterhauser *et al.* (2025) have demonstrated that birds exhibit minor behavioural responses under relatively low night-time illumination intensity that resemble natural migration patterns more than reactions to higher-intensity ALAN. Research on these low levels of ALAN is, however, scarce so far, and future studies need to focus more on these closer to natural levels of illumination (Hölker *et al.*, 2021).

A second explanation for the stronger aggregation effects observed in Dalmatia relates to geographical differences between the two regions. Assuming birds crossing the sea fly from southwest to northeast, the section between Italy and Dalmatia is 160 km wide. In contrast, the section between Italy and Istria is 20 km narrower. While the Adriatic barrier is not exceptionally wide, continuous over-water flight limits opportunities to rest or correct orientation. However, strong headwinds experienced during the crossing could quickly increase the distance travelled relative to the airflow (Liechti, 2006). The combination of exhaustion and the instinct to find land could make coastal light pollution disproportionately influential. In this case, ALAN could act as a landmark indicating safety (Archibald *et al.*, 2017; Heist *et al.*, 2018). The ability of birds to use landmarks has been widely discussed, e.g., by Alerstam (1990), while Weisshaupt *et al.* (2022) have provided evidence that birds can also use artificial illumination as landmarks. Wind patterns that create such strong drag frequently whip across the Adriatic Sea, especially in early spring (Pullen *et al.*, 2007; Pasarić, Belušić and Chiggiato, 2009). To test this theory, modelling avian flight trajectories and estimating the experienced wind field during the crossing of the Adriatic could provide valuable insights.

Another geographical distinction between the study regions is the presence of offshore islands along the Dalmatian coast. These islands could provide stopover habitats for birds crossing the sea before reaching the mainland and the radar sites (Stipčević, 1997; Kralj *et al.*, 2013). Such pre-landfall stopovers are common along archipelago coasts and have been well documented in passerines and other small migrants (Barboutis *et al.*, 2022). During departure, birds undergo a phase of reorientation in which they are particularly responsive to visual cues on the horizon, especially young and inexperienced individuals, a behaviour demonstrated in both experimental and field studies (Able and Able, 1997; Cochran, Mouritsen and Wikelski, 2004; Åkesson *et al.*, 2021). The within-night dynamics observed in Chapter 4 support this interpretation. Figure 4.2 illustrates that the strongest increases in bird density over illuminated areas occurred during the early night, when a substantial proportion of migrants measured by the radar are likely to originate from nearby islands rather than from the Italian mainland. Reorientation at sunset and the associated higher sensitivity to visual cues from ALAN from the mainland coast might explain this pattern. A 30% increase from the dark to the light-polluted area during the early night represents a substantial redistribution of birds from what is otherwise migration on a broad front. However, as the weather radar data from Debeljak were heavily affected by topographic and electromagnetic interference (see Chapter 4 for details), it is not possible to causally relate this density shift to sunset reorientation. Demonstrating this with radar would require high-quality and high-resolution weather radar data that allow the tracking of bird density shifts over time at a small spatial scale (Kranstauber *et al.*, 2020). Returning to the within-night dynamics of bird density differences between dark and light-polluted areas, we see a marked shift four hours past

sunset. This is the period when true sea-crossing migrants can be expected to complete the relatively longer over-water segment between the Italian and Croatian mainland. Although bird densities remained elevated over the light-polluted area compared to the dark, the difference was less pronounced. This could mean that, overall, migrating birds in-flight may be less susceptible to ALAN at non-extreme intensity. Late-night arrivals again showed slightly elevated redistribution compared to mid-night, which could indicate that birds post landfall begin searching for possible stopover sites at that time. At this stage, attraction to illuminated areas may redirect birds towards low-quality stopover sites (McLaren et al., 2018). Altogether, the findings from Chapter 4 demonstrate that the attraction of migrating birds to ALAN is a complex and temporally dynamic phenomenon, and although the explanations presented here seem plausible and are supported by known mechanisms, they remain tentative interpretations that require targeted testing in future work.

In general, an increase in the thickness of low-lying cloud cover has been shown to reduce the intensity of migration. Panuccio et al. (2019) demonstrated that migrating birds avoided flying through fog and low-lying clouds, assuming that they would either circumvent them or wait for better conditions on the ground. However, for birds that continued to fly, *HP3* assumed that cloud cover would interact additively with ALAN, and that the redistribution caused by coastal illumination would be stronger under impaired visibility than under clear skies. This expected interactive effect was not observed. Low cloud cover had no significant impact on migration intensity at either the bright or dark sites in Istria. One possible explanation for this observation is that thick, low-lying clouds and fog probably blocked most of the coastal ALAN for birds that were still offshore. This meant that broad-front sea-crossing migration continued relatively unaffected. This is consistent with evidence suggesting that birds migrating in clouds tend to maintain their course, relying primarily on compass navigation rather than landmarks (Griffin, 1972; Alerstam, 1990). As they approach the coastline, it takes birds much longer to perceive artificial visual cues from ALAN. The disturbance only becomes relevant when they are very close to the light source, which becomes visible through the cloud layer. At this point, impaired visibility and illumination combined to alter fine-scale behaviour by significantly reducing airspeeds and flight altitudes. This local additive interaction between ALAN and impaired visibility has ecologically relevant consequences. While fewer birds would migrate, ALAN could draw more birds closer to the ground, increasing the risk of collisions with buildings. Most studies that have focused on quantifying bird fatalities with illuminated infrastructure during cloudy and foggy nights confirm elevated numbers of dead birds in conditions of impaired visibility (Drewitt and Langston, 2008; Rebke *et al.*, 2019; Chen *et al.*, 2024). This suggests that the effects of visibility on migration intensity and on fine-scale behavioural responses to ALAN may operate through different mechanisms. This highlights the need for future work to disentangle these processes.

To summarise, *HP3* can be confirmed partially. While bird densities were elevated over bright areas for sea-crossing migration or during nights where sea-crossing dominated the whole migration volume, the timing within nights mattered substantially: birds seemed to be most attracted to light during the early night, less during late-night and least around midnight. Contrary to the hypothesis, impaired visibility in interaction with ALAN had no significant effect on bird densities.

5.1.2 Methodological implications and limitations

Methodological implications

This dissertation emphasises the importance of combining data from radar systems that monitor migratory behaviour across different spatial scales. The BirdScan MR1 detected fine-scale behavioural reactions calibrated to local passage rates, whereas the Debeljak WSR captured large-scale redistribution patterns. It was only by combining these two perspectives that an in-depth picture of how light pollution affects nocturnal migrants in-flight could be obtained.

However, further methodological perspectives are needed to infer causal relationships between the observed phenomena and their underlying mechanistic causes. This dissertation relied exclusively on the Eulerian approach of recording movement, which describes movement from fixed observation points. In contrast, a Lagrangian approach tracks the movement of individual organisms (Phillips *et al.*, 2019). The Eulerian perspective excels at quantifying the total mass of organisms in movement, in this case the biomass passing through the radar beams. The Lagrangian perspective, represented by biologging technologies such as light-level geolocators and GPS, instead provides a function of coordinates over time of individual birds that can be enriched with near-term atmospheric conditions and is therefore better suited for linking in-flight behavioural adaptations to environmental stressors, while also accounting for the bird's eye view. Degen *et al.* (2022) criticised that current research fails to acknowledge that the appearance and perceived influence of ALAN must depend on the flight altitude of single individuals. Over the sea, both radar systems used in this dissertation are unable to capture this perspective. As a result, it remains impossible to determine, for example, at what distance ALAN begins to affect birds when taking flight altitude, winds and visibility into account. Although weather radar can, in principle, offer a perspective out to sea, the offshore archipelago in Dalmatia prevented the retrieval of low elevation data because the radar beam intersected with islands. Even without topographic beam occultation, the radar will likely miss more than half of the migration volume after around 20 kilometres, as the beam height will be more than 400 metres above sea level at that distance. Achieving a similar perspective with BirdScan MR1 would require back simulation of bird trajectories, which is characterised by high uncertainty, as especially the movement of more experienced birds is not always predictable based on atmospheric conditions alone. Although the gross movement of bird masses can be predicted with relatively high accuracy (Aurbach, 2021; Horton *et al.*, 2021; Bradarić *et al.*, 2024), predicting individual behaviour remains challenging because relevant variables often remain unknown (Hedenström, 2008), and because individuals differ in timing and route choice (Moore, 1985; López-López, García-Ripollés and Urios, 2014).

Methodological limitations

Several methodological limitations affected all three chapters of this dissertation. The most consequential was the loss of the near-natural site due to the technical malfunction of the receiver of the Vransko Lake BirdScan MR1, which removed the possibility of replicating the fine-scale analyses in Chapters 3 and 4. Although Nillson *et al.* (2018) concluded that radar-derived migratory fluxes are comparable across systems, the weather radar in Dalmatia lacked a valid replicate for low altitude migration because of its elevation above sea level and

the strong influence of radio frequency interferences, further explained below. As a result, the ecologically and conservation-relevant portion of the migration flow in Dalmatia could not be fully quantified.

The evaluation of the weather radar data was further constrained by the geography and the quality of the available data. The coastal topography strongly limited the choice of suitable weather radars, particularly regarding elevation above sea level and distance to relevant coastline sections. In addition, the amount of radio frequency interference (RFI) present in the radar data, particularly in the lowest two to three elevation scans, was unexpectedly high and initially discouraging. RFI in the C-band occurs when weather radars share frequencies with other devices operating at 5600 to 5650 MHz (Schaper *et al.*, 2022). These signals most commonly originate from WiFi networks (Huuskonen, Saltikoff and Holleman, 2014). As no procedure currently exists to clean compromised polar volumes from RFI, shutting down RFI sources remains the only effective mitigation (Schaper *et al.*, 2022). A further limitation was that only single polarisation data were available at the time the analysis associated with Chapter 4 was conducted, and except for the uncorrected reflectivity factor TH, all products had already been filtered for meteorological use. This prevented automated removal of hydrometeors, topographic interference and anthropogenic scatterers such as vessels, aircraft and wind turbines. It also made it impossible to derive migration traffic rates instead of bird densities, as for that, volume covering radial velocities is required. Ultimately, the heavy clutter in the two to three lowest elevation scans meant that fine-resolution spatial analyses of bird densities were not feasible, which necessitated restricting the analyses to two predefined sampling areas, one over the city of Zadar and one over the Nature Park Vransko Lake.

Finally, although the BirdScan MR1 can categorise biological scatterers into rough taxonomic groups based on size and wing-flapping patterns, it is currently not possible to identify different species using radar. Taxonomic information is not currently available for weather radar either, although Matthews *et al.* (2025) explain that the data does contain information on rough taxonomic classes and that this could be retrieved by machine learning algorithms in the future. Research into bird-building collisions has demonstrated that certain bird species are overrepresented among the victims (Loss *et al.*, 2014, 2019). Even when considering total abundance, some species appear to be more vulnerable to collisions; most of these are migratory (Colling *et al.*, 2022), accounting for over 90% of all birds collected during migration seasons (Borden *et al.*, 2010). Adopting a taxonomic approach to avian redistribution during migration in response to light could reveal further mechanistic drivers behind collisions. Meanwhile, parallel acoustic monitoring could overcome this limitation. During their nighttime flights, migratory birds emit specific calls. These flight calls can be used to determine species composition and vulnerability to ALAN (Winger, Weeks, *et al.*, 2019). However, as call rates cannot reflect bird densities in-flight (Gillings and Scott, 2021), call-rate monitoring could complement radar data by providing fine-scale behavioural information (Osterhaus *et al.*, 2025).

5.1.3 ALAN vs. light pollution

ALAN has become a defining characteristic of the Anthropocene and anthropogenically modified landscapes (Rodrigo-Comino *et al.*, 2023). For us humans, nighttime illumination makes us feel safer outside while walking and driving, and supports commercial, industrial and recreational activity (Boyce, 2019). In this sense, ALAN fulfils a legitimate social function. However, not all illumination serves essential needs. It is hard to imagine that decorative façade lighting, illuminated advertisements, upward-directed architectural lighting and large-scale commercial installations have any important purpose besides crying for our attention. In other cases, our careless use of lighting that is actually justified leads to unnecessary emissions (Korner, von Maravic and Haupt, 2022). Such excessive illumination is often not only unnecessary but also negatively affects our own health (Hölker *et al.*, 2010). Oftentimes, ALAN can be reduced without compromising functionality or human well-being (Lyytimäki, 2025). When illumination exceeds what is required for safety, when our footprint impacts the well-being of other organismic communities, that ALAN becomes light pollution (Longcore and Rich, 2004).

Regarding the research gaps identified by Holker *et al.* (2021), the current research provided new insight regarding the ALAN intensity that triggers a response, the redistribution of species, and the landscape context that interacts with the effect of ALAN. Migrating birds are a particularly good model to study, as their in-flight response can be easily measured by quantitative methods (Hoekstra *et al.*, 2023). This research has shown that birds react even to relatively low illumination intensities and that these reactions can be interpreted as a negative response. The results have shown that in this context, there is a redistribution of nocturnal broad-front migration, but that in the case discussed here, this depends on the direction of migration and thus on the geographical context. Furthermore, the results suggest that coastal regions or, in general, ecological barriers could play a special role in relation to light pollution. Above all else, especially Chapter 3 suggests that ecologically relevant light pollution does not require bright floodlights and huge fronts of illuminated windows but begins smoothly with relatively dim illumination. These conclusions align with a recent series of studies on low-level light pollutions and bird migration (Cabrera-Cruz *et al.*, 2021; Osterhaus *et al.*, 2025).

Regarding these three ecological issues, future research must focus more on low-intensity light pollution to find out how the subtle behavioural changes it causes accumulate, interact with other stressors, and, if necessary, add up to ultimately have a possible effect on populations and ecological communities. Furthermore, the question arises as to what extent the redistribution from broad-front migration observed here affects the number of bird collisions, and thus direct mortality, and how such relatively low light pollution can influence the search for suitable resting places, which also raises the question of possible indirect consequences. Thirdly, the question arises as to what effect light pollution has in coastal regions, where birds must cross a much wider water barrier. The associated exhaustion could have previously unimagined consequences. With the expansion of offshore energy production, it is also necessary to find out how such spots of relatively strong light sources affect an otherwise completely dark environment, especially in areas known to be flown over by millions of birds.

In order to reduce light pollution, the public must be made aware of the complex of problems associated with this phenomenon (Falcón *et al.*, 2020; Farnsworth, Horton and Marra, 2024).

In urban areas, the main obstacles to protecting nocturnal animals include a lack of public awareness, the priority given to energy efficiency in political decisions, and the association of more light with greater safety (Pothukuchi, 2021). Furthermore, it is difficult to define, measure, and quantify light pollution, which often plays a key role in political matters (Hölker *et al.*, 2010; Convention on Migratory Species, 2024). In practical terms, night-time illumination becomes an environmental nuisance when it serves no purpose, when it is not directed where it is needed, when its intensity is too high, when it is not tailored to the time of day, and when its spectrum contains excessively short wavelengths (Hartley and Liebel, 2020).

This dissertation contributes to the discourse on artificial light at night and light pollution by demonstrating that ecologically relevant light pollution begins at much lower illumination levels than commonly assumed and does not require bright or visually conspicuous lighting. Migrating birds responded behaviourally to relatively dim artificial light at night, indicating that light pollution emerges along a smooth gradient rather than at a distinct threshold. Furthermore, the results reveal that artificial light at night causes a redistribution of nocturnal broad-front migration, which depends on migration direction and geographical context. Coastal regions and other ecological barriers play a particularly significant role in this process. Together, these findings emphasise that even low-intensity lighting can have a disproportionate ecological impact in sensitive landscapes. This refines our understanding of how light pollution should be conceptualised and assessed in ecological research and conservation.

5.1.4 Consequences for conservation

Birds matter to people, both emotionally and culturally. As highlighted by Cox and Gaston (2015) and echoed in my own experience, many people feel a deep affection for birds, enjoy watching and listening to them, and value their presence in their surroundings (Belaire *et al.*, 2015). Ironically, despite this connection, bird populations are declining globally due to agricultural intensification, habitat degradation and fragmentation, climate change, hunting, noise and light pollution. These stressors interact and accumulate, creating a complex conservation challenge. Protecting migratory species is particularly difficult because it requires coordinated action across entire flyways that transcend national borders, seasons and ecosystems (Bairlein, 2016; Convention on Migratory Species, 2024).

Research plays a central role in addressing this dilemma. Evidence on skyglow propagation, species-specific sensitivity to illumination, behavioural responses and redistribution are the basis for informing conservationists and policymakers to identify where illumination reductions are required and most effective. Furthermore, effective conservation research must create instruments that overcome the bridge between scientists and policymakers (Cook *et al.*, 2013), while some of these will have to be highly specialised to develop local mitigation strategies (Williams, Balmford and Wilcove, 2020).

Within the Croatian context, such behavioural sensitivity has direct implications for conservation planning. Croatia is currently undergoing an intensified transition to sustainable energy production, including offshore wind farms (Blecich, Petrić and Franković, 2016). While this remains essential for global decarbonisation (Dincer, 2000), the planning of such infrastructure must be ecologically responsible and sensitive to migratory movements.

Windfarms are oftentimes accompanied by offshore illumination, which can exacerbate the impact wind farms can already have on migrating birds (Drewitt and Langston, 2006). One effective strategy is to identify high-risk zones for bird strikes and exclude them from the set of potentially suitable sites (Liechti, Guélat and Komenda-Zehnder, 2013). Croatia has made strong progress in this respect, protecting key coastal areas for resident and migratory birds, including the regions examined in this study (Lučin *et al.*, 2024). Nonetheless, wind energy is just one way humans invade offshore areas. Thus, the increasing anthropogenic alteration of the seascape highlights the need to integrate ALAN-related behavioural shifts into environmental impact assessments. In particular, the findings here suggest that a mix between static and temporally dynamic conservation measures is advised. On the one hand, bird migration is spatiotemporally dynamic and undergoes wide fluctuations within and between nights. Temporally reducing infrastructural illumination provides a first step in the right direction (Saha, 2017). On the other hand, ecosystem boundary zones, such as coastlines, usually host a very rich biodiversity and are especially sensitive to ecological light pollution (Manfrin *et al.*, 2017; Hirt *et al.*, 2023), which promotes static conservation implementations via protected zones.

Although this dissertation's empirical work focuses on the Croatian Adriatic, its findings are relevant to other coastal migration systems in which birds abruptly transition from dark water to patchily illuminated shorelines. The observed reductions in flight altitude and redistribution towards illuminated areas suggest a plausible pathway by which even dim ALAN may increase collision risk, especially under impaired visibility. However, direct mortality was not measured here.

Nonetheless, the findings of this dissertation collectively suggest that ecological harm does not require strong illumination. Chapter 3 showed that the dim lighting of a small coastal town reduced airspeeds and flight altitudes in migrating birds, particularly sea-crossing individuals, with stronger effects under low visibility. Chapters 3 and 4 demonstrated that low to medium intensity urban lighting redistributed ten to thirty per cent more migrants into illuminated airspace compared to nearby darker areas. These patterns emerged across radar systems and regions, highlighting that ALAN shapes migration behaviour across geographic and biological scales, from local to regional and from individuals to communities. Although these behavioural responses to low-intensity ALAN were subtle, they were consistent. Ultimately, any measurable behavioural change in response to an unnatural stimulus represents a potentially harmful stressor. During migration, such disruptions can accumulate into energetic costs, reduced navigational efficiency, increased collision risk and altered stopover decisions. Unlike many other anthropogenic pollutants, however, light pollution is unusually easy to address. When not in use, light can simply and instantly be switched off. It is up to us to unite our own needs with what is best for birds.

Conservation ultimately depends not only on scientific knowledge but also on public commitment. Many people feel emotionally invested in birds, and these emotions can be powerful drivers of conservation actions (Castillo-Huitrón *et al.*, 2020). Thus, when we as researchers really want to make an impact, we must raise awareness among the public.

5.2 Outlook

During my research, I came across several phenomena in my data or in the literature that sparked my curiosity. However, these were either outside the scope of this dissertation, technically infeasible or required tools or data that were unavailable to me. In this section, I will discuss three questions linked to the geographical setting of the study area along the Croatian coast, which would expand our understanding of the ecologically relevant responses of individual birds and of broad-front migration to ALAN. My focus will be on questions relevant to bird conservation that also have a scientifically interesting bearing. Furthermore, I will emphasise radar-based research.

Some of the questions presented below will be reserved for the future as the necessary technology simply does not yet exist, but others are perfectly feasible with the right tools.

How do birds respond to ALAN while out at sea?

Imagine a bird departing from the Italian mainland and flying northeast across the sea towards Croatia. Out at sea, it would probably follow a fairly straight course (Lopez-Ricaurte *et al.*, 2021). Depending on its altitude and visibility, it would eventually see patches of artificial light in the distance (Degen, Kolláth and Degen, 2022). Studying the distance at which ALAN from the coast has an impact on birds would surely be interesting, but given that weather radar has a strong range limitation for high-resolution monitoring of avian movement of 5 to 25 km (Hoekstra *et al.*, 2023), and that the minimum altitude is increasing with distance, the relevant airspace for these reactions might be hard to survey.

However, it is not only light from the coastline that influences birds during sea crossings; countless objects emit artificial light at night across the sea. Offshore oil platforms and wind farms, for example, are a known source of light pollution (Hüppop *et al.*, 2016). In this dissertation, I focus on the response of birds to ALAN over land as measured from land. To my knowledge, the redistribution of broad-front migration offshore in response to ALAN has never been studied before. In the discussion, I also hypothesised that coastal ALAN could have an amplified impact on migrating birds due to the visual contrast between the dark seascape and the illuminated coastline. How much worse could this effect be when birds are surrounded by darkness at first, and within that darkness, there is a patch of isolated light?

As part of its transition to renewable energies, Croatia is planning to increase its offshore wind capacity (Blecich, Petrić and Franković, 2016). While much of Croatia's coastline is protected under Natura 2000 (Lučin *et al.*, 2024) and is therefore excluded from wind farm planning, the vast majority of the Adriatic Sea remains available for offshore energy development. This expansion of offshore wind infrastructure is not unique to the Adriatic but reflects a broader trend across the Mediterranean Basin, where suitable sites for offshore wind farms often overlap with frequently used migratory passage corridors or lie adjacent to important stopover regions (Bray *et al.*, 2016). The consequences of disorientation, especially during barrier crossing, might go far beyond direct lethality at the light sources themselves. Disorientation at sea is likely to be much worse than on land, raising the question of the extent to which offshore infrastructure attracts migrating birds, causing redistribution of birds towards ALAN and possibly leading to increased mortality.

Deshlom and Kahlert (2005) showed that migrating waterbirds mostly avoid offshore wind farms, and those that enter these areas avoid flying near the turbines. In contrast, Hüppop

et al. (2016) observed hundreds of bird collisions at a single offshore platform and estimated that there were hundreds of thousands of collisions in the entire North Sea each year. These contradictory conclusions have sparked scientific debate and call for an assessment of movement patterns related to collisions and sublethal behavioural alterations that could lead to increased mortality later during the crossing.

To study avian movement out at sea, Casement (1966) used ship-borne radar to quantify migration intensity across the Mediterranean, while Desholm and Kahlert (2005) used tracking radar to resolve movement close to the wind farm on a fine scale. Such a combined study setup could possibly help resolve discussions around the harm caused to migrating birds by offshore ALAN beyond lethality. This is crucial for better coordinating the transition to renewable energies and migratory bird conservation.

How does the response of birds to ALAN at the coast translate into collision risk?

Although numerous studies have demonstrated that ALAN alters the migratory behaviour of nocturnal birds (Van Doren *et al.*, 2017, 2021), the mechanisms linking these behavioural changes to collision risk remain poorly understood. Furthermore, while this dissertation revealed a redistribution of broad-front migration in response to coastal ALAN under clear-sky conditions, there was no amplification of this effect when visibility was low. However, it is precisely at this time that collisions are reported to occur most frequently, when clouds and fog hinder landmark orientation, and the effect of ALAN is possibly amplified on a very local scale (Jones and Francis, 2003; Chen *et al.*, 2024). This discrepancy raises a key question: if large-scale redistribution is limited, what movement processes lead to elevated collision rates during fog and low cloud cover?

Based on the assumptions developed in this dissertation, behavioural responses to ALAN under impaired visibility are largely restricted to the near-coastal zone and the immediate vicinity of illuminated structures. When clouds or fog obscure distant light sources, birds are unlikely to respond to coastal illumination until they are close enough for the artificial light to pass through the water vapour. Consequently, responses to ALAN are spatially compressed and occur over much shorter distances than under clear-sky conditions. While these near-field reactions may not produce detectable redistribution at the scale of broad-front migration, they may nonetheless have severe ecological consequences.

This dissertation identifies a reduction in flight altitude in illuminated areas under impaired visibility as a potential key mechanism for the increased number of collisions in the absence of redistribution. Bowlin et al. (2015) corroborate the observations made in this dissertation, having identified unexpected altitude drops in their biologging data, which they have assumed to be vertical responses to ALAN. Intuitively, lower flight altitudes pose a risk when birds enter airspace low enough to bring them close to buildings. In the geographical context of this dissertation, these behavioural changes occur at spatial scales that are largely invisible to weather radar analyses of migratory biomass. This is either because they are below the minimum range claimed to be safe for analysis by comparative studies, since weather radar at close ranges is often affected by clutter, or because they occur at altitudes that cannot be monitored by the coastal weather radars used here.

Studying these near-field responses requires observation systems that can resolve fine-scale movement in low visibility conditions at close ranges, while still having a wide enough range

to monitor broad-front migration as it approaches. High-resolution avian radar systems, such as the Robin MAX Avian Radar (Robin Radar Systems, 2025), can track thousands of birds simultaneously at short ranges of presumably up to 4 km,⁴ and thus offer a promising new perspective on changes in flight altitude, speed, and horizontal movement near illuminated coastlines, while accounting for a large proportion of the biomass in motion. Nonetheless, the applicability of radar depends strongly on the surrounding environment, as terrain and built structures constrain radar performance. In an urban environment, the fine-scale movement of birds would only be possible from the coast until the first row of buildings, provided that other ground clutter could be taken care of. As birds enter urban environments, radar coverage is obstructed by buildings.

Resolving movement within these radar shadows requires complementary Lagrangian approaches (e.g., Phillips *et al.*, 2019), such as biologging, to capture individual behaviour in urban environments. Combining high-resolution radar observations with individual tracking would enable movement patterns in the air to be directly linked to collision risk on the ground. This would represent a significant step forward, moving beyond post-hoc carcass counts towards a mechanistic understanding of how ALAN influences bird behaviour in conditions of impaired visibility. For now, movement within the urban environment remains hidden because biologging with a high enough spatial accuracy to allow monitoring such fine-scale behaviour is restrained by the size and weight of GPS tags and thus limited to larger birds, a limitation that could be overcome in the future.

Taken together, this perspective suggests that the apparent contradiction between weak large-scale redistribution and high collision rates can be resolved by focusing on near-range behavioural responses in conditions of poor visibility. Shifting the focus from broad-front migration to fine-scale movement in illuminated coastal and urban environments will enable future research to better identify the processes that translate ALAN exposure into direct mortality risk, thereby informing more effective mitigation strategies.

In what ways does ALAN affect birds at different stages of their migratory flights and in different geographic settings?

One suspicious phenomenon that I have discussed in this dissertation is that a substantial proportion of the overall redistribution of birds towards ALAN occurs early at night, just two hours after sunset. However, within-night migration intensity profiles from Zadar suggested that most sea-crossing migrants arrived later, around midnight. Although the first two hours of the night were excluded from the analysis to account for birds that may have departed from offshore islands before reaching the Croatian mainland, this time window is likely insufficient for most migrants. Given typical flight speeds, the majority of birds would require three hours or more to cover the full distance between the Italian Marche region and the Dalmatian coast. This raises the question of where these birds originate from, given that they account for the approximately 30% higher bird densities observed over Zadar compared to the Vransko Lake Nature Park, only two hours after sunset.

One plausible explanation is that a significant number of the birds contributing to these early-night dynamics had stopped over on the islands of the Dalmatian archipelago despite efforts to exclude them from the analysis. This assumption is fuelled by the fact that migrating birds

⁴ 3.3 km for “micro” birds and 4 km for “small” birds (<https://www.robinradar.com>).

use polarised light cues at the horizon during dawn and dusk for orientation (Muheim, Moore and Phillips, 2006; McLaren, Schmaljohann and Blasius, 2022). Furthermore, Moore (1982) demonstrated that the artificial manipulation of the sunset cue can alter the departure directions of migratory birds. While Moore explains that birds could use polarised light at the zenith of the sky to determine the position of the sun, clouds would obstruct this celestial cue. This would create an additional interactive effect between clouds and ALAN during sunset reorientation. In the study region, illumination from the city of Zadar could be reflected off the sea surface between the archipelago and the mainland, potentially creating polarised light pollution. Such reflections are assumed to be particularly effective in influencing avian orientation (Horváth *et al.*, 2009). Consequently, birds departing from island stopover sites may be especially susceptible to artificial light cues from the mainland, leading to stronger-than-expected attraction to coastal illumination. At the scale of migratory flux, this process could plausibly explain the elevated bird densities detected by coastal weather radar during the early evening.

However, the proposed link between island stopovers and the significant increase in bird densities remains purely hypothetical. Testing this theory would require the quantitative monitoring of avian movement between the islands and the mainland coast at a high spatial resolution, to determine whether and to what extent these movement patterns are shaped by coastal ALAN. We recall the Robin Avian Radar, which was designed to record three-dimensional avian flight tracks with high spatial accuracy. However, the distance between the closest island and the mainland is approximately 4.5 km, exceeding the Robin Radar's maximum detection range for small to medium-sized passerines. Following a suggestion by Gauthreaux *et al.* (2019), an alternative promising approach could be to use a specialised L-band radar system, originally developed for monitoring avian movement for aviation safety at airports. With an operating wavelength of around 23 cm, the BSTARTM avian surveillance and warning system can track the location of small birds (0.1 kg) in three dimensions over a range of 10 km. Furthermore, existing evidence suggests that L-band radar is comparatively insensitive to water surface clutter (Mengen, Marre and Dhar, 2009), which otherwise is a substantial limitation to radar-based bird migration monitoring near water surfaces.

In short, while the approach used in this dissertation was effective in capturing broad-scale migration patterns, it inevitably smoothed out fine-scale spatial features. This makes it difficult to conclude whether the birds that contributed to the high difference in bird densities from dark to bright areas were sea-crossing migrants or stopped over on the archipelago islands. During their departure from these islands, birds could be more vulnerable to false orientation cues from ALAN. This would make these islands highly sensitive areas during the migration seasons. Future work should combine large-scale weather radar analyses with targeted, high-resolution radar observations in coastal and island settings to resolve these fine-scale dynamics. Such an integrative approach would enable researchers to identify the periods during the migratory journey when birds are most susceptible to ALAN and pinpoint sensitive ecosystems where stricter regulation would be most effective.

What can high-temporal-resolution weather surveillance radar reveal about the arrival of sea-crossing migration fronts along heterogeneously illuminated coasts?

In Chapter 4 of this dissertation, the integration of ornithological data and weather surveillance radar enabled the identification of fine-scale behavioural patterns of sea-crossing migrants, while accounting for broad-scale redistribution in response to ALAN. However, important fine-scale patterns in the weather radar data remained unresolved due to limitations in quality, which made it difficult to isolate and extract these signals from the remaining clutter from various sources. Personally, I found one phenomenon in the weather radar data incredibly fascinating. Visual inspection of consecutive maps of vertically integrated bird densities revealed that sea-crossing migrants arrived at the Dalmatian coast in broad fronts with clearly defined spatial structures. These formed wave-like patterns that propagated towards the shoreline. However, these waves were not approaching the coastline uniformly. It appeared as if they were drawn towards the illuminated regions in the north-west of the radar, prompting me to wonder what insights we could gain from these single-front arrivals of sea-crossing birds.

Most studies that analyse such broad-scale patterns do so by averaging movement. This results in a loss of much of the variability inherent to migration dynamics. The original plan for Chapter 4 was therefore to resolve these individual fronts. Unfortunately, this was not possible because the data quality was insufficient to reliably separate the observed signals from remaining clutter and RFI.

With access to a coastal weather radar providing consistently high-quality, high-resolution data, it would be possible to examine sea-crossing migration at a much finer spatial and temporal scale. Such a system could capture how incoming migratory fronts deform, fragment, or concentrate as they approach coastlines with heterogeneous illumination, while birds are still over the sea. Preserving the temporal structure of migration within single nights would allow researchers to study dynamic responses to spatial gradients in ALAN, rather than relying on nightly or seasonal averages, while considering current atmospheric conditions. Ultimately, such an approach could bridge the gap between fine-scale behavioural responses and large-scale patterns of collision risk, offering a powerful new perspective on the ecological consequences of coastal light pollution.

Bibliography

- Able, K.P. and Able, M.A. (1997) 'Development of sunset orientation in a migratory bird: no calibration by the magnetic field', *Animal Behaviour*, 53(2), pp. 363–368. Available at: <https://doi.org/10.1006/anbe.1996.0394>.
- Adamík, P. *et al.* (2016) 'Barrier crossing in small avian migrants: individual tracking reveals prolonged nocturnal flights into the day as a common migratory strategy', *Scientific Reports*, 6(1), p. 21560. Available at: <https://doi.org/10.1038/srep21560>.
- Åkesson, S. *et al.* (2021) 'Migratory orientation in inexperienced and experienced avian migrants', *Ethology Ecology & Evolution*, 33(3), pp. 206–229. Available at: <https://doi.org/10.1080/03949370.2021.1905076>.
- Akesson, S., Alerstam, T. and Hedenstrom, A. (1996) 'Flight Initiation of Nocturnal Passerine Migrants in Relation to Celestial Orientation Conditions at Twilight', *Journal of Avian Biology*, 27(2), p. 95. Available at: <https://doi.org/10.2307/3677138>.
- Åkesson, S. and Hedenström, A. (2000) 'Wind selectivity of migratory flight departures in birds', *Behavioral Ecology and Sociobiology*, 47(3), pp. 140–144. Available at: <https://doi.org/10.1007/s002650050004>.
- Åkesson, S. and Helm, B. (2020) 'Endogenous Programs and Flexibility in Bird Migration', *Frontiers in Ecology and Evolution*, 8, p. 78. Available at: <https://doi.org/10.3389/fevo.2020.00078>.
- Alerstam, T. (1990) 'Ecological causes and consequences of bird orientation', *Experientia*, 46.
- Alerstam, T. (2006) 'Strategies for the transition to breeding in time-selected bird migration'. *Ardea*, pp. 347–357. Available at: <https://www.scopus.com/inward/record.uri?eid=2-s2.0-33645832693&partnerID=40&md5=dc58df54532ee3e9c195a9df2bcd9bca>.
- Alerstam, T. (2009) 'Flight by night or day? Optimal daily timing of bird migration', *Journal of Theoretical Biology*, 258(4), pp. 530–536. Available at: <https://doi.org/10.1016/j.jtbi.2009.01.020>.
- Alerstam, T., Hedenström, A. and Åkesson, S. (2003) 'Long-distance migration: evolution and determinants', *Oikos*, 103(2), pp. 247–260. Available at: <https://doi.org/10.1034/j.1600-0706.2003.12559.x>.
- Alerstam, T. and Pettersson, S.-G. (1977) 'Why do migrating birds fly along coastlines?', *Journal of Theoretical Biology*, 65(4), pp. 699–712. Available at: [https://doi.org/10.1016/0022-5193\(77\)90016-9](https://doi.org/10.1016/0022-5193(77)90016-9).
- Allen, J.A. (1880) 'Destruction of birds by light-houses', *Bulletin of the Nuttall Ornithological Club*, 5(3), pp. 131–138.
- Anderson, G.Q.A. and Green, R.E. (2009) 'The value of ringing for bird conservation', *Ringling & Migration*, 24(3), pp. 205–212. Available at: <https://doi.org/10.1080/03078698.2009.9674393>.

Archibald, K.M. *et al.* (2017) 'Migrating birds reorient toward land at dawn over the Great Lakes, USA', *The Auk*, 134(1), pp. 193–201. Available at: <https://doi.org/10.1642/AUK-16-123.1>.

Arrowsmith, S.J. and Hedlin, M.A.H. (2005) 'Observations of infrasound from surf in southern California', *Geophysical Research Letters*, 32(9), p. 2005GL022761. Available at: <https://doi.org/10.1029/2005GL022761>.

Assunção, R.V. *et al.* (2020) '3D characterisation of the thermohaline structure in the southwestern tropical Atlantic derived from functional data analysis of in situ profiles', *Progress in Oceanography*, 187, p. 102399. Available at: <https://doi.org/10.1016/j.pocean.2020.102399>.

Aurbach, A. *et al.* (2018) 'Complex behaviour in complex terrain - Modelling bird migration in a high resolution wind field across mountainous terrain to simulate observed patterns', *Journal of Theoretical Biology*, 454, pp. 126–138. Available at: <https://doi.org/10.1016/j.jtbi.2018.05.039>.

Aurbach, A. (2021) *Spatially and temporal explicit forecast model of broad front bird migration across Europe using radar surveillance data*. ETH Zurich. Available at: [10.3929/ethz-b-000510665](https://doi.org/10.3929/ethz-b-000510665).

Bairlein, F. (2016) 'Migratory birds under threat', *Science*, 354(6312), pp. 547–548. Available at: <https://doi.org/10.1126/science.aah6647>.

Barboutis, C. *et al.* (2022) 'Arriving depleted after crossing of the Mediterranean: obligatory stopover patterns underline the importance of Mediterranean islands for migrating birds', *Animal Migration*, 9(1), pp. 14–23. Available at: <https://doi.org/10.1515/ami-2022-0117>.

Bauer, S. *et al.* (2017) 'From Agricultural Benefits to Aviation Safety: Realizing the Potential of Continent-Wide Radar Networks', *BioScience*, 67(10), pp. 912–918. Available at: <https://doi.org/10.1093/biosci/bix074>.

Bauer, S. and Hoyer, B.J. (2014) 'Migratory Animals Couple Biodiversity and Ecosystem Functioning Worldwide', *Science*, 344(6179), p. 1242552. Available at: <https://doi.org/10.1126/science.1242552>.

Bauer, S., McNamara, J.M. and Barta, Z. (2020) 'Environmental variability, reliability of information and the timing of migration', *Proceedings of the Royal Society B: Biological Sciences*, 287(1926), p. 20200622. Available at: <https://doi.org/10.1098/rspb.2020.0622>.

Belaire, J.A. *et al.* (2015) 'Urban residents' perceptions of birds in the neighborhood: Biodiversity, cultural ecosystem services, and disservices', *The Condor*, 117(2), pp. 192–202. Available at: <https://doi.org/10.1650/CONDOR-14-128.1>.

Blackburn, E. *et al.* (2019) 'Spring migration strategies of Whinchat *Saxicola rubetra* when successfully crossing potential barriers of the Sahara and the Mediterranean Sea', *Ibis*, 161(1), pp. 131–146. Available at: <https://doi.org/10.1111/ibi.12610>.

Blecich, P., Petrić, M. and Franković, B. (2016) 'Renewable Energy in Croatia: a Review of Present State and Future Development', *Proceedings of EuroSun2016*. EuroSun2016, Palma de Mallorca, Spain: International Solar Energy Society, pp. 1–8. Available at: <https://doi.org/10.18086/eurosun.2016.11.02>.

Blondel, J. and Mourer-Chauviré, C. (1998) 'Evolution and history of the western Palaearctic avifauna', *Trends in Ecology & Evolution*, 13(12), pp. 488–492. Available at: [https://doi.org/10.1016/S0169-5347\(98\)01461-X](https://doi.org/10.1016/S0169-5347(98)01461-X).

Borden, W.C. *et al.* (2010) 'Seasonal, Taxonomic, and Local Habitat Components of Bird-window Collisions on an Urban University Campus in Cleveland, OH', *Ohio Journal of Science*, 3(110), pp. 44–52.

Bornemann, A. *et al.* (2016) 'The demise of the early Eocene greenhouse – Decoupled deep and surface water cooling in the eastern North Atlantic', *Global and Planetary Change*, 145, pp. 130–140. Available at: <https://doi.org/10.1016/j.gloplacha.2016.08.010>.

Both, C. *et al.* (2006) 'Climate change and population declines in a long-distance migratory bird', *Nature*, 441(7089), pp. 81–83. Available at: <https://doi.org/10.1038/nature04539>.

Both, C. and Visser, M.E. (2001) 'Adjustment to climate change is constrained by arrival date in a long-distance migrant bird', *Nature*, 411(6835), pp. 296–298. Available at: <https://doi.org/10.1038/35077063>.

Bowlin, M.S. *et al.* (2015) 'Unexplained altitude changes in a migrating thrush: Long-flight altitude data from radio-telemetry', *The Auk*, 132(4), pp. 808–816. Available at: <https://doi.org/10.1642/AUK-15-33.1>.

Boyce, P.R. (2019) 'The benefits of light at night', *Building and Environment*, 151, pp. 356–367. Available at: <https://doi.org/10.1016/j.buildenv.2019.01.020>.

Bradarić, M. *et al.* (2020) 'Winds at departure shape seasonal patterns of nocturnal bird migration over the North Sea', *Journal of Avian Biology*, 51(10), p. jav.02562. Available at: <https://doi.org/10.1111/jav.02562>.

Bradarić, M. *et al.* (2024) 'Forecasting nocturnal bird migration for dynamic aeroconservation: The value of short-term datasets', *Journal of Applied Ecology*, pp. 1365–2664.14651. Available at: <https://doi.org/10.1111/1365-2664.14651>.

Bray, L. *et al.* (2016) 'Expected Effects of Offshore Wind Farms on Mediterranean Marine Life', *Journal of Marine Science and Engineering*, 4(1), p. 18. Available at: <https://doi.org/10.3390/jmse4010018>.

Bridge, E.S. *et al.* (2011) 'Technology on the Move: Recent and Forthcoming Innovations for Tracking Migratory Birds', *BioScience*, 61(9), pp. 689–698. Available at: <https://doi.org/10.1525/bio.2011.61.9.7>.

Briedis, M. *et al.* (2020) 'Broad-scale patterns of the Afro-Palaeartic landbird migration', *Global Ecology and Biogeography*. Edited by B. McGill, 29(4), pp. 722–735. Available at: <https://doi.org/10.1111/geb.13063>.

Brooks, M. *et al.* (2017) 'glmmTMB: Generalized Linear Mixed Models using Template Model Builder'. Available at: <https://doi.org/10.32614/CRAN.package.glmmTMB>.

Bruderer, B. (1997) 'The Study of Bird Migration by Radar Part 1: The Technical Basis', *Naturwissenschaften*, 84, pp. 1–8. Available at: <https://doi.org/10.1007/s001140050338>.

Bruderer, B. *et al.* (2010) 'Wing-beat characteristics of birds recorded with tracking radar and cine camera', *Ibis*, 152(2), pp. 272–291. Available at: <https://doi.org/10.1111/j.1474-919X.2010.01014.x>.

Bruderer, B. and Boldt, A. (2001) 'Flight characteristics of birds: I. radar measurements of speeds', *Ibis*, 143, pp. 178–204. Available at: <https://doi.org/10.1111/j.1474-919X.2001.tb04475.x>.

Bruderer, B. and Liechti, F. (1998) 'Flight Behaviour of Nocturnally Migrating Birds in Coastal Areas: Crossing or Coasting', *Journal of Avian Biology*, 29(4), p. 499. Available at: <https://doi.org/10.2307/3677169>.

Bruderer, B. and Liechti, F. (1999) 'Bird migration across the Mediterranean'. *Proc Int Ornithol Congr, Durban. Johannesburg: BirdLife South Africa*, pp. 1983–1999.

Bruderer, B. and Liechti, F. (2004) 'Welcher Anteil ziehender Vögel fliegt im Höhenbereich von Windturbinen?', *Ornithologischer Beobachter*, 101, pp. 327–335.

Bruderer, B. and Peter, D. (2022) 'Topography and wind moulding directions of autumn migration between Europe and the West African savannas', *Journal of Ornithology*, 163(2), pp. 357–371. Available at: <https://doi.org/10.1007/s10336-022-01971-8>.

Bruderer, B., Peter, D. and Korner-Nievergelt, F. (2018) 'Vertical distribution of bird migration between the Baltic Sea and the Sahara', *Journal of Ornithology*, 159(2), pp. 315–336. Available at: <https://doi.org/10.1007/s10336-017-1506-z>.

Bruderer, B., Peter, D. and Steuri, T. (1999) 'Behaviour of migrating birds exposed to X-band radar and a bright light beam', *The Journal of Experimental Biology*, 202, pp. 1015–1022. Available at: <https://doi.org/10.1242/jeb.202.9.1015>.

Bruderer, B. and Salewski, V. (2008) 'Evolution of bird migration in a biogeographical context', *Journal of Biogeography*, 35(11), pp. 1951–1959. Available at: <https://doi.org/10.1111/j.1365-2699.2008.01992.x>.

Bruderer, B., Underhill, L.G. and Liechti, F. (1995) 'Altitude choice by night migrants in a desert area predicted by meteorological factors', *Ibis*, 137, pp. 44–55. Available at: <https://doi.org/10.1111/j.1474-919X.1995.tb03218.x>.

Brusatte, S.L. (2015) 'The Origin and Diversification of Birds', *Current Biology*, 25, pp. 888–898. Available at: <http://dx.doi.org/10.1016/j.cub.2015.08.003>.

Buckland, J. (1915) 'The Value of Birds to Man', *Journal of the Royal Society of Arts*, 63(3265), pp. 701–711.

Buler, J.J. and Diehl, R.H. (2009) 'Quantifying Bird Density During Migratory Stopover Using Weather Surveillance Radar', *IEEE Transactions on Geoscience and Remote Sensing*, 47(8), pp. 2741–2751. Available at: <https://doi.org/10.1109/TGRS.2009.2014463>.

Burt, C.S. *et al.* (2023) 'The effects of light pollution on migratory animal behavior', *Trends in Ecology & Evolution*, p. 14. Available at: <https://doi.org/10.1016/j.tree.2022.12.006>.

Busse, P., Zaniwicz, G. and Cofta, T. (2015) 'Evolution of the Western Palaearctic Passerine Migration Pattern Presentation Style', *The Ring*, 36(1), pp. 3–21. Available at: <https://doi.org/10.2478/ring-2014-0001>.

Cabrera-Cruz, S.A. *et al.* (2019) 'Urban areas affect flight altitudes of nocturnally migrating birds', *Journal of Animal Ecology*. Edited by J. Chapman, 88(12), pp. 1873–1887. Available at: <https://doi.org/10.1111/1365-2656.13075>.

Cabrera-Cruz, S.A. *et al.* (2020) 'Artificial Light at Night is Related to Broad-Scale Stopover Distributions of Nocturnally Migrating Landbirds along the Yucatan Peninsula, Mexico', *Remote Sensing*, 12(3), p. 395. Available at: <https://doi.org/10.3390/rs12030395>.

Cabrera-Cruz, S.A. *et al.* (2021) 'Potential Effect of Low-Rise, Downcast Artificial Lights on Nocturnally Migrating Land Birds', *Integrative and Comparative Biology*, 61(3), pp. 1216–1236. Available at: <https://doi.org/10.1093/icb/icab154>.

Cabrera-Cruz, S.A., Smolinsky, J.A. and Buler, J.J. (2018) 'Light pollution is greatest within migration passage areas for nocturnally-migrating birds around the world', *Scientific Reports*, 8(1), p. 3261. Available at: <https://doi.org/10.1038/s41598-018-21577-6>.

Campión, D. *et al.* (2020) 'A method for capturing and GPS tracking breeding White-backed Woodpeckers *Dendrocopos leucotos*', *Bird Study*, 67(2), pp. 239–244. Available at: <https://doi.org/10.1080/00063657.2020.1811202>.

Carić, H. (2018) 'Perspectives of greening tourism development – the concepts, the policies, the implementation', 66(1).

Casement, M.B. (1966) 'Migration across the Mediterranean observed by radar', *Ibis*, 108(4), pp. 461–491. Available at: <https://doi.org/10.1111/j.1474-919X.1966.tb07205.x>.

Cassone, V.M. (2014) 'Avian circadian organization: A chorus of clocks', *Frontiers in Neuroendocrinology*, 35(1), pp. 76–88. Available at: <https://doi.org/10.1016/j.yfrne.2013.10.002>.

Castillo-Huitrón, N.M. *et al.* (2020) 'The Importance of Human Emotions for Wildlife Conservation', *Frontiers in Psychology*, 11, p. 1277. Available at: <https://doi.org/10.3389/fpsyg.2020.01277>.

Chen, K. *et al.* (2024) 'Heavy migration traffic and bad weather are a dangerous combination: Bird collisions in New York City', *Journal of Applied Ecology*, pp. 1365–2664.14590. Available at: <https://doi.org/10.1111/1365-2664.14590>.

Cho, W., Sung, C.-Y. and Ki, K.-S. (2014) 'Characterizing light pollution in national parks during peak and off-peak tourist seasons using nighttime satellite images', *Korean Journal of Environment and Ecology*, 28(4), pp. 484–489. Available at: <https://doi.org/10.13047/KJEE.2014.28.4.484>.

Clark, J.A., Thorup, K. and Stroud, D.A. (2009) 'Quantifying the movement patterns of birds from ring recoveries', *Ringed & Migration*, 24(3), pp. 180–188. Available at: <https://doi.org/10.1080/03078698.2009.9674390>.

Claussen, M. (2003) 'Die Rolle der Vegetation im Klimasystem', *promet*, 29(1–4), pp. 80–89.

Cochran, W.W. and Graber, R.R. (1958) 'Attraction of Nocturnal Migrants by Lights on a Television Tower', *The Wilson Bulletin*, 70(4), pp. 378–380.

Cochran, W.W., Mouritsen, H. and Wikelski, M. (2004) 'Migrating Songbirds Recalibrate Their Magnetic Compass Daily from Twilight Cues', *Science*, 304(5669), pp. 405–408. Available at: <https://doi.org/10.1126/science.1095844>.

Colling, O.M. *et al.* (2022) 'Migratory songbirds and urban window collision mortality: vulnerability depends on species, diel timing of migration, and age class', *Avian Conservation and Ecology*, 17(1), p. 17. Available at: <https://doi.org/10.5751/ACE-02107-170122>.

Convention on Migratory Species (2024) *CMS International Light Pollution Guidelines for Migratory Species*, p. 144.

Cook, C.N. *et al.* (2013) 'Achieving Conservation Science that Bridges the Knowledge–Action Boundary', *Conservation Biology*, 27(4), pp. 669–678. Available at: <https://doi.org/10.1111/cobi.12050>.

Cooper, A. and Penny, D. (1997) 'Mass Survival of Birds Across the Cretaceous-Tertiary Boundary: Molecular Evidence', *Science*, 275(5303), pp. 1109–1113. Available at: <https://doi.org/10.1126/science.275.5303.1109>.

Coppack, T., Becker, S.F. and Becker, P.J.J. (2008) 'Circadian flight schedules in night-migrating birds caught on migration', *Biology Letters*, 4(6), pp. 619–622. Available at: <https://doi.org/10.1098/rsbl.2008.0388>.

Cox, D.T.C. and Gaston, K.J. (2015) 'Likeability of Garden Birds: Importance of Species Knowledge & Richness in Connecting People to Nature', *PLOS ONE*. Edited by D.N. Bonter, 10(11), p. e0141505. Available at: <https://doi.org/10.1371/journal.pone.0141505>.

Cox, G.W. (1968) 'The Role of Competition in the Evolution of Bird Migration', *Evolution*, 22(1), pp. 181–192. Available at: <https://doi.org/10.2307/2406662>.

Degen, T., Kolláth, Z. and Degen, J. (2022) 'X,Y, and Z: A bird's eye view on light pollution', *Ecology and Evolution*, 12(12), p. e9608. Available at: <https://doi.org/10.1002/ece3.9608>.

- Deng, Y. *et al.* (2023) 'Quantifying long-term phenological patterns of aerial insectivores roosting in the Great Lakes region using weather surveillance radar', *Global Change Biology*, 29(5), pp. 1407–1419. Available at: <https://doi.org/10.1111/gcb.16509>.
- Desholm, M. and Kahlert, J. (2005) 'Avian collision risk at an offshore wind farm', *Biology Letters*, 1(3), pp. 296–298. Available at: <https://doi.org/10.1098/rsbl.2005.0336>.
- Desmet, P. *et al.* (2025) 'Biological data derived from European weather radars', *Scientific Data*, 12(1), p. 361. Available at: <https://doi.org/10.1038/s41597-025-04641-5>.
- Deutschlander, M.E. and Beason, R.C. (2014) 'Avian Navigation and Geographic Positioning', *Journal of Field Ornithology*, 85(2), pp. 111–133. Available at: <https://doi.org/10.1111/jofo.12055>.
- Diehl, R.H., Larkin, R.P. and Black, J.E. (2003) 'Radar Observations of Bird Migration Over The Great Lakes', *The Auk*, 120(2), pp. 278–290. Available at: <https://doi.org/10.1093/auk/120.2.278>.
- Dincer, I. (2000) 'Renewable energy and sustainable development: a crucial review', *Renewable and Sustainable Energy Reviews*, 4(2), pp. 157–175. Available at: [https://doi.org/10.1016/S1364-0321\(99\)00011-8](https://doi.org/10.1016/S1364-0321(99)00011-8).
- Dingle, H. (2014) *Migration: The Biology of Life on the Move*. Oxford University Press. Available at: <https://doi.org/10.1093/acprof:oso/9780199640386.001.0001>.
- Dokter, A.M. *et al.* (2011) 'Bird migration flight altitudes studied by a network of operational weather radars', *Journal of The Royal Society Interface*, 8(54), pp. 30–43. Available at: <https://doi.org/10.1098/rsif.2010.0116>.
- Dokter, A.M. *et al.* (2013) 'High Altitude Bird Migration at Temperate Latitudes: A Synoptic Perspective on Wind Assistance', *PLoS ONE*. Edited by N. Saino, 8(1), p. e52300. Available at: <https://doi.org/10.1371/journal.pone.0052300>.
- Dokter, A.M. *et al.* (2019) 'bioRad: biological analysis and visualization of weather radar data', *Ecography*, 42(5), pp. 852–860. Available at: <https://doi.org/10.1111/ecog.04028>.
- Dominoni, D. *et al.* (2014) 'Individual-based measurements of light intensity provide new insights into the effects of artificial light at night on daily rhythms of urban-dwelling songbirds', *Journal of Animal Ecology*. Edited by S. Verhulst, 83(3), pp. 681–692. Available at: <https://doi.org/10.1111/1365-2656.12150>.
- Dominoni, D., Quetting, M. and Partecke, J. (2013a) 'Artificial light at night advances avian reproductive physiology', *Proceedings of the Royal Society B: Biological Sciences*, 280(1756), p. 20123017. Available at: <https://doi.org/10.1098/rspb.2012.3017>.
- Dominoni, D., Quetting, M. and Partecke, J. (2013b) 'Long-Term Effects of Chronic Light Pollution on Seasonal Functions of European Blackbirds (*Turdus merula*)', *PLoS ONE*. Edited by C. Wicker-Thomas, 8(12), p. e85069. Available at: <https://doi.org/10.1371/journal.pone.0085069>.

Dominoni, D.M. *et al.* (2013) 'Urban-like night illumination reduces melatonin release in European blackbirds (*Turdus merula*): implications of city life for biological time-keeping of songbirds', *Frontiers in Zoology*, 10(1), p. 60. Available at: <https://doi.org/10.1186/1742-9994-10-60>.

Dominoni, D.M. and Partecke, J. (2015) 'Does light pollution alter daylength? A test using light loggers on free-ranging European blackbirds (*Turdus merula*)', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1667), p. 20140118. Available at: <https://doi.org/10.1098/rstb.2014.0118>.

Douglas, D.J.T. *et al.* (2023) 'A global review identifies agriculture as the main threat to declining grassland birds', *Ibis*, 165(4), pp. 1107–1128. Available at: <https://doi.org/10.1111/ibi.13223>.

Drewitt, A.L. and Langston, R.H.W. (2006) 'Assessing the impacts of wind farms on birds', *Ibis*, 148, pp. 29–42. Available at: <https://doi.org/10.1111/j.1474-919X.2006.00516.x>.

Drewitt, A.L. and Langston, R.H.W. (2008) 'Collision Effects of Wind-power Generators and Other Obstacles on Birds', *Annals of the New York Academy of Sciences*, 1134(1), pp. 233–266. Available at: <https://doi.org/10.1196/annals.1439.015>.

Duriscoe, D.M. *et al.* (2018) 'A simplified model of all-sky artificial sky glow derived from VIIRS Day/Night band data', *Journal of Quantitative Spectroscopy and Radiative Transfer*, 214, pp. 133–145. Available at: <https://doi.org/10.1016/j.jqsrt.2018.04.028>.

Elvidge, C.D. *et al.* (2021) 'Annual Time Series of Global VIIRS Nighttime Lights Derived from Monthly Averages: 2012 to 2019', *Remote Sensing*, 13(5), p. 922. Available at: <https://doi.org/10.3390/rs13050922>.

Elvidge, C.D. *et al.* (2022) 'Fifty years of nightly global low-light imaging satellite observations', *Frontiers in Remote Sensing*, 3, p. 16. Available at: <https://doi.org/10.3389/frsen.2022.919937>.

Erickson, W.P., Johnson, G.D. and Young Jr., D.P. (2005) 'A Summary and Comparison of Bird Mortality from Anthropogenic Causes with an Emphasis on Collisions', *Department of Agriculture Forest Service General Technical Report*, 191, pp. 1029–1042.

Ericson, P.G.P. *et al.* (2006) 'Diversification of Neoaves: integration of molecular sequence data and fossils', *Biology Letters*, p. 5.

Ericson, P.G.P., Irestedt, M. and Johansson, U.S. (2003) 'Evolution, biogeography, and patterns of diversification in passerine birds', *Journal of Avian Biology*, 34(1), pp. 3–15. Available at: <https://doi.org/10.1034/j.1600-048X.2003.03121.x>.

Erni, B. *et al.* (2002) 'Wind and rain govern the intensity of nocturnal bird migration in central Europe – a log-linear regression analysis', *Ardea*, 90(1), pp. 155–166.

Erni, B., Liechti, F. and Bruderer, B. (2005) 'The role of wind in passerine autumn migration between Europe and Africa', *Behavioral Ecology*, 16(4), pp. 732–740. Available at: <https://doi.org/10.1093/beheco/ari046>.

EUMETNET (2025) *A network of 33 European National Meteorological & Hydrological Services*. Available at: <https://eumetnet.eu>.

Evans Ogden, L.J. (1996) *Collision Course: The Hazards of Lighted Structures and Windows to Migrating Birds*. 3.

Evans Ogden, L.J. (2002) *Summary Report on the Bird Friendly Building Program: Effect of Light Reduction on Collision of Migratory Birds*. Paper 5. Lincoln: University of Nebraska, p. 29.

Evans, W.R. *et al.* (2007) 'Response of Night-migrating Songbirds in Cloud to Colored and Flashing Light', *North American Birds*, 60(4), pp. 476–488.

Falchi, F. *et al.* (2016) 'The new world atlas of artificial night sky brightness', *Science Advances*, 2(6), p. e1600377. Available at: <https://doi.org/10.1126/sciadv.1600377>.

Falchi, F. *et al.* (2019) 'Light pollution in USA and Europe: The good, the bad and the ugly', *Journal of Environmental Management*, 248, p. 109227. Available at: <https://doi.org/10.1016/j.jenvman.2019.06.128>.

Falcón, J. *et al.* (2020) 'Exposure to Artificial Light at Night and the Consequences for Flora, Fauna, and Ecosystems', *Frontiers in Neuroscience*, 14, p. 602796. Available at: <https://doi.org/10.3389/fnins.2020.602796>.

Farnsworth, A., Horton, K.G. and Marra, P.P. (2024) 'To mitigate bird collisions, enforce the Migratory Bird Treaty Act', *Proceedings of the National Academy of Sciences*, 121(9), p. e2320411121. Available at: <https://doi.org/10.1073/pnas.2320411121>.

Fisher, N.I. (1993) *Statistical analysis of circular data*. Cambridge [England]; New York, NY, USA: Cambridge University Press.

Fortin, D., Liechti, F. and Bruderer, B. (1999) 'Variation in the nocturnal flight behaviour of migratory birds along the northwest coast of the Mediterranean Sea', *Ibis*, 141(3), pp. 480–488. Available at: <https://doi.org/10.1111/j.1474-919X.1999.tb04417.x>.

Gargallo, G. *et al.* (2011) *Spring migration in the western Mediterranean and NW Africa: the results of 16 years of the Piccole Isole project*. 6. Barcelona: Museu de Ciències Naturals, Institut de Cultura, Ajuntament de Barcelona.

Garrett, J.K., Donald, P.F. and Gaston, K.J. (2020) 'Skyglow extends into the world's Key Biodiversity Areas', *Animal Conservation*, 23(2), pp. 153–159. Available at: <https://doi.org/10.1111/acv.12480>.

Gaston, K.J. *et al.* (2013) 'The ecological impacts of nighttime light pollution: a mechanistic appraisal: Nighttime light pollution', *Biological Reviews*, 88(4), pp. 912–927. Available at: <https://doi.org/10.1111/brv.12036>.

Gaston, K.J. and de Miguel, A.S. (2022) 'Environmental Impacts of Artificial Light at Night', *Annual Review of Environment and Resources*, 47(1), p. annurev-environ-112420-014438. Available at: <https://doi.org/10.1146/annurev-environ-112420-014438>.

Gauthreaux, S. and Diehl, R. (2020) 'Discrimination of Biological Scatterers in Polarimetric Weather Radar Data: Opportunities and Challenges', *Remote Sensing*, 12(3), p. 545. Available at: <https://doi.org/10.3390/rs12030545>.

Gauthreaux, S.A. (1982) 'Age-Dependent Orientation in Migratory Birds', in F. Papi and H.G. Wallraff (eds) *Avian Navigation*. Berlin, Heidelberg: Springer Berlin Heidelberg, pp. 68–74.

Gauthreaux, S.A. (1996) 'Bird Migration: Methodologies and Major Research Trajectories (1945-1995)', *The Condor*, 98(2), pp. 442–453. Available at: <https://doi.org/10.2307/1369168>.

Gauthreaux, S.A. et al. (2019) 'Detecting bird movements with L-band avian radar and S-band dual-polarization Doppler weather radar', *Remote Sensing in Ecology and Conservation*. Edited by N. Horning and M. Van Den Broeke, 5(3), pp. 237–246. Available at: <https://doi.org/10.1002/rse2.101>.

Gauthreaux, S.A. and Belser, C.G. (2003) 'Bird Movements on Doppler Weather Surveillance Radar', *Birding*, pp. 616–628.

Gauthreaux, S.A., Belser, C.G. and van Blaricom, D. (2003) 'Using a Network of WSR-88D Weather Surveillance Radars to Define Patterns of Bird Migration at Large Spatial Scales', *Avian Migration*. Springer, Berlin, Heidelberg, pp. 335–346.

Gelb, Y. and Delacretaz, N. (2009) 'Windows and Vegetation: Primary Factors in Manhattan Bird Collisions', *Northeastern Naturalist*, 16(3), pp. 455–470. Available at: <https://doi.org/10.1656/045.016.n312>.

Gillings, S. and Scott, C. (2021) 'Nocturnal flight calling behaviour of thrushes in relation to artificial light at night', *Ibis*, 163(4), pp. 1379–1393. Available at: <https://doi.org/10.1111/ibi.12955>.

Godard, M. et al. (2020) 'Diving Behavior of *Mirounga leonina*: A Functional Data Analysis Approach', *Frontiers in Marine Science*, 7, p. 595. Available at: <https://doi.org/10.3389/fmars.2020.00595>.

Gordo, O. (2007) 'Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology', *Climate Research*, 35, pp. 37–58. Available at: <https://doi.org/10.3354/cr00713>.

Griffin, D.R. (1972) 'Nocturnal bird migration in Opaque Clouds', in S.R. Galler et al. (eds) *Animal Orientation and Navigation*. Washington D.C.: National Aeronautics and Space Administration SP-262, Washington D.C. , U.S. Government Printing Office, pp. 169–188.

Gu, J.-Y. et al. (2011) 'Polarimetric Attenuation Correction in Heavy Rain at C Band', *Journal of Applied Meteorology and Climatology*, 50(1), pp. 39–58. Available at: <https://doi.org/10.1175/2010JAMC2258.1>.

- Gwinner, E. (1990) *Bird migration: physiology and ecophysiology*. Berlin: Springer.
- Gwinner, E. and Brandstätter, R. (2001) 'Complex bird clocks', *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 356(1415), pp. 1801–1810. Available at: <https://doi.org/10.1098/rstb.2001.0959>.
- Haest, B. et al. (2019) 'Autumn bird migration phenology: A potpourri of wind, precipitation and temperature effects', *Global Change Biology*, (25), pp. 4064–4080. Available at: <https://doi.org/10.1111/gcb.14746>.
- Haest, B. et al. (2024) 'Continental-scale patterns in diel flight timing of high-altitude migratory insects', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 379(1904), p. 20230116. Available at: <https://doi.org/10.1098/rstb.2023.0116>.
- Haest, B., Hüppop, O. and Bairlein, F. (2018) 'The influence of weather on avian spring migration phenology: What, where and when?', *Global Change Biology*, 24(12), pp. 5769–5788. Available at: <https://doi.org/10.1111/gcb.14450>.
- Hahn, S. et al. (2014) 'Variable detours in long-distance migration across ecological barriers and their relation to habitat availability at ground', *Ecology and Evolution*, 4(21), pp. 4150–4160. Available at: <https://doi.org/10.1002/ece3.1279>.
- Hahn, S., Bauer, S. and Liechti, F. (2009) 'The natural link between Europe and Africa - 2.1 billion birds on migration', *Oikos*, 118(4), pp. 624–626. Available at: <https://doi.org/10.1111/j.1600-0706.2008.17309.x>.
- Halupka, L. et al. (2017) 'Conditions at autumn stopover sites affect survival of a migratory passerine', *Journal of Ornithology*, 158(4), pp. 979–988. Available at: <https://doi.org/10.1007/s10336-017-1472-5>.
- Hardegree, S.P. et al. (2008) 'Evaluation of NEXRAD Radar Precipitation Products for Natural Resource Applications', *Rangeland Ecology & Management*, 61(3), pp. 346–353. Available at: <https://doi.org/10.2111/07-036.1>.
- Harman, I.T. and Drake, V.A. (2004) 'Insect monitoring radar: analytical time-domain algorithm for retrieving trajectory and target parameters', *Computers and Electronics in Agriculture*, 43(1), pp. 23–41. Available at: <https://doi.org/10.1016/j.compag.2003.08.005>.
- Harper, W.G. (1958) 'Detection of bird migration by centimetric radar—a cause of radar “angels”', *Proceedings of the Royal Society B: Biological Sciences*, 149(937), pp. 484–502. Available at: <https://doi.org/10.1098/rspb.1958.0088>.
- Hartley, R. and Liebel, B. (2020) *IDA and IES announce strategic collaboration to advance quality lighting to reduce light pollution*. Available at: <https://darksky.org/news/joining-forces-to-protect-the-night-from-light-pollution/?eType=EmailBlastContent&eld=ac9ec4ff-250f-4545-85fe-791cea66d6c3> (Accessed: 28 November 2025).

Haupt, H. (2009) 'Der Letzte macht das Licht an! – Zu den Auswirkungen leuchtender Hochhäuser auf den nächtlichen Vogelzug am Beispiel des „Post-Towers“ in Bonn', *Charadrius*, 45(1), pp. 1–19.

Hedenström, A. *et al.* (2007) 'Migration speed and scheduling of annual events by migrating birds in relation to climate change', *Climate Research*, 35, pp. 79–91. Available at: <https://doi.org/10.3354/cr00715>.

Hedenström, A. (2008) 'Adaptations to migration in birds: behavioural strategies, morphology and scaling effects', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1490), pp. 287–299. Available at: <https://doi.org/10.1098/rstb.2007.2140>.

Hedenström, A. and Åkesson, S. (2017) 'Flight speed adjustment by three wader species in relation to winds and flock size', *Animal Behaviour*, 134, pp. 209–215. Available at: <https://doi.org/10.1016/j.anbehav.2017.10.022>.

Heist, K.W. *et al.* (2018) 'Radar quantifies migrant concentration and Dawn reorientation at a Great Lakes shoreline', *Movement Ecology*, 6(1), p. 15. Available at: <https://doi.org/10.1186/s40462-018-0135-3>.

Helbig, A.J. (1992) 'Population differentiation of migratory directions in birds: comparison between ringing results and orientation behaviour of hand-raised migrants', *Oecologia*, 90(4), pp. 483–488. Available at: <https://doi.org/10.1007/BF01875441>.

Hersbach, H. *et al.* (2020) 'The ERA5 global reanalysis', *Quarterly Journal of the Royal Meteorological Society*, 146(730), pp. 1999–2049. Available at: <https://doi.org/10.1002/qj.3803>.

Hewitt, G. (2000) 'The genetic legacy of the Quaternary ice ages', *Nature*, 405(6789), pp. 907–913. Available at: <https://doi.org/10.1038/35016000>.

Hirschhofer, S. *et al.* (2025) 'Avian spring migration at the east Adriatic coast: coastal and sea-crossing dynamics of intensity, timing, and flight directions', *Movement Ecology*, 13(1), p. 44. Available at: <https://doi.org/10.1186/s40462-025-00572-3>.

Hirschhofer, S. *et al.* (2026) 'When nocturnally migrating birds encounter low-level light pollution patches: a case study from the Croatian coast', *Biological Conservation*, 313, p. 111620. Available at: <https://doi.org/10.1016/j.biocon.2025.111620>.

Hirschhofer, S.J. *et al.* (2024) 'High-intensity bird migration along Alpine valleys calls for protective measures against anthropogenically induced avian mortality', *Remote Sensing in Ecology and Conservation*, 10(3), pp. 360–373. Available at: <https://doi.org/10.1002/rse2.377>.

Hirt, M.R. *et al.* (2023) 'Light pollution in complex ecological systems', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 378(1892), p. 20220351. Available at: <https://doi.org/10.1098/rstb.2022.0351>.

Hoekstra, B. *et al.* (2023) 'Fireworks disturbance across bird communities', *Frontiers in Ecology and the Environment*, p. fee.2694. Available at: <https://doi.org/10.1002/fee.2694>.

Hoekstra, B. *et al.* (2025) 'Large-scale mapping of nocturnal bird migration to accelerate a nature-inclusive energy transition', *Journal of Environmental Management*, 395, p. 127753. Available at: <https://doi.org/10.1016/j.jenvman.2025.127753>.

Hölker, F. *et al.* (2010) 'The Dark Side of Light: A Transdisciplinary Research Agenda for Light Pollution Policy', *Ecology and Society*, 15(4), p. art13. Available at: <https://doi.org/10.5751/ES-03685-150413>.

Hölker, F. *et al.* (2021) '11 Pressing Research Questions on How Light Pollution Affects Biodiversity', *Frontiers in Ecology and Evolution*, 9, p. 767177. Available at: <https://doi.org/10.3389/fevo.2021.767177>.

Horton, K.G. *et al.* (2016) 'Nocturnally migrating songbirds drift when they can and compensate when they must', *Scientific Reports*, 6(1), p. 21249. Available at: <https://doi.org/10.1038/srep21249>.

Horton, K.G. *et al.* (2021) 'Near-term ecological forecasting for dynamic aeroconservation of migratory birds', *Conservation Biology*, 35(6), pp. 1777–1786. Available at: <https://doi.org/10.1111/cobi.13740>.

Horton, K.G. *et al.* (2023) 'Artificial light at night is a top predictor of bird migration stopover density', *Nature Communications*, 14(1), p. 7446. Available at: <https://doi.org/10.1038/s41467-023-43046-z>.

Horváth, G. *et al.* (2009) 'Polarized light pollution: a new kind of ecological photopollution', *Frontiers in Ecology and the Environment*, 7(6), pp. 317–325. Available at: <https://doi.org/10.1890/080129>.

Hrvatski Sabor (2019) *Zakon o zaštiti od svjetlosnog onečišćenja*. Available at: https://narodne-novine.nn.hr/clanci/sluzbeni/2019_02_14_271.html.

Hull, P. (2015) 'Life in the Aftermath of Mass Extinctions', *Current Biology*, 25(19), pp. R941–R952. Available at: <https://doi.org/10.1016/j.cub.2015.08.053>.

Hüppop, O. *et al.* (2016) 'Bird collisions at an offshore platform in the North Sea', *Bird Study*, 63(1), pp. 73–82. Available at: <https://doi.org/10.1080/00063657.2015.1134440>.

Hüppop, O. *et al.* (2019) 'Perspectives and challenges for the use of radar in biological conservation', *Ecography*, 42(5), pp. 912–930. Available at: <https://doi.org/10.1111/ecog.04063>.

Hutchinson, D.K. *et al.* (2021) 'The Eocene–Oligocene transition: a review of marine and terrestrial proxy data, models and model–data comparisons', *Climate of the Past*, 17(1), pp. 269–315. Available at: <https://doi.org/10.5194/cp-17-269-2021>.

Huuskonen, A., Saltikoff, E. and Holleman, I. (2014) 'The Operational Weather Radar Network in Europe', *Bulletin of the American Meteorological Society*, 95(6), pp. 897–907. Available at: <https://doi.org/10.1175/BAMS-D-12-00216.1>.

Ječmenica, B. *et al.* (2020) *Site assessment report of threats and recreational activities in the Lastovo Archipelago*. Association Biom (BirdLife Croatia), p. 17.

Jenni, L. and Kéry, M. (2003) 'Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants', *Proceedings of the Royal Society B: Biological Sciences*, 270(1523), pp. 1467–1471. Available at: <https://doi.org/10.1098/rspb.2003.2394>.

Jetz, W., Wilcove, D.S. and Dobson, A.P. (2007) 'Projected Impacts of Climate and Land-Use Change on the Global Diversity of Birds', *PLoS Biology*. Edited by G.M. Mace, 5(6), p. e157. Available at: <https://doi.org/10.1371/journal.pbio.0050157>.

Johnson, M.D., Kellermann, J.L. and Stercho, A.M. (2010) 'Pest reduction services by birds in shade and sun coffee in Jamaica', *Animal Conservation*, 13(2), pp. 140–147. Available at: <https://doi.org/10.1111/j.1469-1795.2009.00310.x>.

Jones, J. and Francis, C.M. (2003) 'The effects of light characteristics on avian mortality at lighthouses', *Journal of Avian Biology*, 34(4), pp. 328–333. Available at: <https://doi.org/10.1111/j.0908-8857.2003.03183.x>.

Kanerva, A.-M. *et al.* (2020) 'The impact of tree crops and temperature on the timing of frugivorous bird migration', *Oecologia*, 193(4), pp. 1021–1026. Available at: <https://doi.org/10.1007/s00442-020-04726-5>.

Kelly, J.F. *et al.* (2012) 'Quantifying animal phenology in the aerosphere at a continental scale using NEXRAD weather radars', *Ecosphere*, 3(2), p. art16. Available at: <https://doi.org/10.1890/ES11-00257.1>.

Kemp, M.U. *et al.* (2013) 'The influence of weather on the flight altitude of nocturnal migrants in mid-latitudes', *Ibis*. Edited by R. Norris, 155(4), pp. 734–749. Available at: <https://doi.org/10.1111/ibi.12064>.

Kiepenheuer, J. and Linsenmair, E. (1965) 'Vogelzug an der nordafrikanischen Küste von Tunesien bis Rotes Meer nach Tag- und Nachtbeobachtungen 1963 und 1964', *Die Vogelwarte*, 23(1), pp. 80–94.

Kirby, J.S. *et al.* (2008) 'Key conservation issues for migratory land- and waterbird species on the world's major flyways', *Bird Conservation International*, 18(S1), pp. S49–S73. Available at: <https://doi.org/10.1017/S0959270908000439>.

Klein, H., Berthold, P. and Gwinner, E. (1973) 'Der Zug europäischer Garten- und Mönchsgrasmücken (*Sylvia borin* und *S. atricapilla*)', *Die Vogelwarte*, 27(2), pp. 73–134.

Koistinen, J. (2000) 'Bird migration patterns on weather radars', *Physics and Chemistry of the Earth, Part B: Hydrology, Oceans and Atmosphere*, 25(10–12), pp. 1185–1193. Available at: [https://doi.org/10.1016/S1464-1909\(00\)00176-3](https://doi.org/10.1016/S1464-1909(00)00176-3).

Kokko, H. (1999) 'Competition for early arrival in migratory birds', *Journal of Animal Ecology*, 68(5), pp. 940–950. Available at: <https://doi.org/10.1046/j.1365-2656.1999.00343.x>.

Komenda-Zehnder, S. *et al.* (2001) 'Gibt es topographie-unabhängigen Nachtzug über den Alpen?', *Der Ornithologische Beobachter*, 98, pp. 215–222.

Korner, P., von Maravic, I. and Haupt, H. (2022) 'Birds and the "Post Tower" in Bonn: a case study of light pollution', *Journal of Ornithology*, 163(3), pp. 827–841. Available at: <https://doi.org/10.1007/s10336-022-01985-2>.

Korner-Nievergelt, F. *et al.* (2010) 'Improving the analysis of movement data from marked individuals through explicit estimation of observer heterogeneity', *Journal of Avian Biology*, 41(1), pp. 8–17. Available at: <https://doi.org/10.1111/j.1600-048X.2009.04907.x>.

Korpach, A.M. *et al.* (2022) 'Urbanization and artificial light at night reduce the functional connectivity of migratory aerial habitat', *Ecography* [Preprint]. Available at: <https://doi.org/10.1111/ecog.05581>.

Kralj, J. *et al.* (eds) (2013) *Croatian bird migration atlas*. Zagreb: Hrvatska akademija znanosti i umjetnosti.

Kralj, J. *et al.* (2020) 'Geolocator study reveals east African migration route of Central European Common Terns', *Avian Research*, 11(1), p. 6. Available at: <https://doi.org/10.1186/s40657-020-00191-z>.

Kralj, J. and Dolenec, Z. (2008) 'First arrival dates of the Nightingale (*Luscinia megarhynchos*) to Central Croatia in the early 20th century and at the turn of the 21st century', *Open Life Sciences*, 3(3), pp. 295–298. Available at: <https://doi.org/10.2478/s11535-008-0024-7>.

Kranstauber, B. *et al.* (2022) 'Ensemble predictions are essential for accurate bird migration forecasts for conservation and flight safety', *Ecological Solutions and Evidence*, 3(3). Available at: <https://doi.org/10.1002/2688-8319.12158>.

Kranstauber, B., Bauer, S. and Shamoun-Baranes, J. (2023) 'Geographic barriers and season shape the nightly timing of avian migration', *Global Ecology and Biogeography*, p. geb.13742. Available at: <https://doi.org/10.1111/geb.13742>.

Kunz, T.H. *et al.* (2007) 'Aeroecology: probing and modeling the aerosphere', *Integrative and Comparative Biology*, 48(1), pp. 1–11. Available at: <https://doi.org/10.1093/icb/icn037>.

Kyba, C.C.M. *et al.* (2011) 'Cloud Coverage Acts as an Amplifier for Ecological Light Pollution in Urban Ecosystems', *PLoS ONE*. Edited by J. Añel, 6(3), p. e17307. Available at: <https://doi.org/10.1371/journal.pone.0017307>.

Kyba, C.C.M. *et al.* (2017) 'Artificially lit surface of Earth at night increasing in radiance and extent', *Science Advances*, 3(11), p. e1701528. Available at: <https://doi.org/10.1126/sciadv.1701528>.

La Sorte, F.A. *et al.* (2016) 'Convergence of broad-scale migration strategies in terrestrial birds', *Proceedings of the Royal Society B: Biological Sciences*, 283(1823), p. 20152588. Available at: <https://doi.org/10.1098/rspb.2015.2588>.

La Sorte, F.A. *et al.* (2022) 'Seasonal associations with light pollution trends for nocturnally migrating bird populations', *Ecosphere*, 13(3). Available at: <https://doi.org/10.1002/ecs2.3994>.

Lack, D. and Varley, G.C. (1945) 'Detection of birds by Radar', *Nature*, 156, p. 446.

Lai, J. *et al.* (2024) 'Evaluating the relative importance of predictors in Generalized Additive Models using the gam.hp R package', *Plant Diversity*, 46(4), pp. 542–546. Available at: <https://doi.org/10.1016/j.pld.2024.06.002>.

Lao, S. *et al.* (2020) 'The influence of artificial light at night and polarized light on bird-building collisions', *Biological Conservation*, 241, p. 108358. Available at: <https://doi.org/10.1016/j.biocon.2019.108358>.

Latham, R.E. and Ricklefs, R.E. (1993) 'Continental Comparisons of Temperate-Zone Tree Species Diversity', *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. University of Chicago Press.

Lehikoinen, A. *et al.* (2019) 'Phenology of the avian spring migratory passage in Europe and North America: Asymmetric advancement in time and increase in duration', *Ecological Indicators*, 101, pp. 985–991. Available at: <https://doi.org/10.1016/j.ecolind.2019.01.083>.

Lenth, R.V. (2017) 'emmeans: Estimated Marginal Means, aka Least-Squares Means'. Available at: <https://doi.org/10.32614/CRAN.package.emmeans>.

Liechti, F. *et al.* (1996) 'Die Alpen, ein Hindernis im nächtlichen Breitfrontzug - eine großräumige Übersicht nach Mondbeobachtungen', *Journal für Ornithologie*, 137, pp. 337–356.

Liechti, F. (2006) 'Birds: blowin' by the wind?', *Journal of Ornithology*, 147(2), pp. 202–211. Available at: <https://doi.org/10.1007/s10336-006-0061-9>.

Liechti, F., Bruderer, B. and Paproth, H. (1995) 'Quantification of nocturnal bird migration by moonwatching: comparison with radar and infrared observations', *Journal of Field Ornithology*, 66(4), pp. 457–652.

Liechti, F., Guélat, J. and Komenda-Zehnder, S. (2013) 'Modelling the spatial concentrations of bird migration to assess conflicts with wind turbines', *Biological Conservation*, 162, pp. 24–32. Available at: <https://doi.org/10.1016/j.biocon.2013.03.018>.

Lindström, Å., Alerstam, T. and Hedenström, A. (2019) 'Faster fuelling is the key to faster migration', *Nature Climate Change*, 9(4), pp. 288–289. Available at: <https://doi.org/10.1038/s41558-019-0443-7>.

Literák, I. *et al.* (2021) 'Weather-influenced water-crossing behaviour of black kites (*Milvus migrans*) during migration', *Biologia*, 76(4), pp. 1267–1273. Available at: <https://doi.org/10.2478/s11756-020-00643-3>.

Longcore, T. and Rich, C. (2004) 'Ecological light pollution', *Frontiers in Ecology and the Environment*, 2(4), pp. 191–198. Available at: [https://doi.org/10.1890/1540-9295\(2004\)002%255B0191:ELP%255D2.0.CO;2](https://doi.org/10.1890/1540-9295(2004)002%255B0191:ELP%255D2.0.CO;2).

Longrich, N.R., Tokaryk, T. and Field, D.J. (2011) 'Mass extinction of birds at the Cretaceous–Paleogene (K–Pg) boundary', *Proceedings of the National Academy of Sciences*, 108(37), pp. 15253–15257. Available at: <https://doi.org/10.1073/pnas.1110395108>.

López-López, P., García-Ripollés, C. and Urios, V. (2014) 'Individual repeatability in timing and spatial flexibility of migration routes of trans-Saharan migratory raptors', *Current Zoology*, 60(5), pp. 642–652. Available at: <https://doi.org/10.1093/czoolo/60.5.642>.

Lopez-Ricaurte, L. *et al.* (2021) 'Barrier crossings and winds shape daily travel schedules and speeds of a flight generalist', *Scientific Reports*, 11(1), p. 12044. Available at: <https://doi.org/10.1038/s41598-021-91378-x>.

Loss, S.R. *et al.* (2014) 'Bird–building collisions in the United States: Estimates of annual mortality and species vulnerability', *The Condor*, 116(1), pp. 8–23. Available at: <https://doi.org/10.1650/CONDOR-13-090.1>.

Loss, S.R. *et al.* (2019) 'Factors influencing bird-building collisions in the downtown area of a major North American city', *PLoS ONE*. Edited by C.A. Lepczyk, 14(11), p. e0224164. Available at: <https://doi.org/10.1371/journal.pone.0224164>.

Loss, S.R. *et al.* (2023) 'Citizen science to address the global issue of bird–window collisions', *Frontiers in Ecology and the Environment*, 21(9), pp. 418–427. Available at: <https://doi.org/10.1002/fee.2614>.

Loss, S.R., Will, T. and Marra, P.P. (2012) 'Direct human-caused mortality of birds: improving quantification of magnitude and assessment of population impact', *Frontiers in Ecology and the Environment*, 10(7), pp. 357–364. Available at: <https://doi.org/10.1890/110251>.

Loss, S.R., Will, T. and Marra, P.P. (2015) 'Direct Mortality of Birds from Anthropogenic Causes', *Annual Review of Ecology, Evolution, and Systematics*, 46(1), pp. 99–120. Available at: <https://doi.org/10.1146/annurev-ecolsys-112414-054133>.

Lowery, G.H. (1951) 'A Quantitative Study of the Nocturnal Migration of Birds', *University of Kansas Publications*, 3(2), pp. 361–472. Available at: <https://doi.org/10.2307/4510313>.

Lučin, I. *et al.* (2024) 'Transnational experience exchange between countries towards speeding up EU renewable transition: example of Norway-Croatia', *Journal of Physics: Conference Series*, 2875(1), p. 012049. Available at: <https://doi.org/10.1088/1742-6596/2875/1/012049>.

Lüdecke, D. (2018) 'ggeffects: Tidy Data Frames of Marginal Effects from Regression Models', *Journal of Open Source Software*, 3(26), p. 772. Available at: <https://doi.org/10.21105/joss.00772>.

Lukač, G., Stipčević, M. and Tvrtković, N. (1997) 'The status and distribution of Eleonora's falcon (*Falco eleonora* Gene 1834) in Croatia', *Natura Croatica*, 6(3), pp. 323–333.

Lyytimäki, J. (2025) 'Sustainable Development Goals relighted: light pollution management as a novel lens to SDG achievement', *Discover Sustainability*, 6(1), p. 197. Available at: <https://doi.org/10.1007/s43621-025-00991-7>.

Manfrin, A. *et al.* (2017) 'Artificial Light at Night Affects Organism Flux across Ecosystem Boundaries and Drives Community Structure in the Recipient Ecosystem', *Frontiers in Environmental Science*, 5, p. 61. Available at: <https://doi.org/10.3389/fenvs.2017.00061>.

Manola, I. *et al.* (2020) 'Associations of Synoptic Weather Conditions With Nocturnal Bird Migration Over the North Sea', *Frontiers in Ecology and Evolution*, 8, p. 542438. Available at: <https://doi.org/10.3389/fevo.2020.542438>.

Matthews, T. *et al.* (2025) 'Taxonomic resolution in dual-polarization weather radar observations of biological scatterers: A systematic review', *Ecosphere*, 16(10), p. e70419. Available at: <https://doi.org/10.1002/ecs2.70419>.

McKinnon, E.A., Fraser, K.C. and Stutchbury, B.J.M. (2013) 'New discoveries in landbird migration using geolocators, and a flight plan for the future', *The Auk*, 130(2), pp. 211–222. Available at: <https://doi.org/10.1525/auk.2013.12226>.

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

McLaren, J.D. *et al.* (2018) 'Artificial light at night confounds broad-scale habitat use by migrating birds', *Ecology Letters*. Edited by R. Norris, 21(3), pp. 356–364. Available at: <https://doi.org/10.1111/ele.12902>.

McLaren, J.D., Schmaljohann, H. and Blasius, B. (2022) 'Predicting performance of naïve migratory animals, from many wrongs to self-correction', *Communications Biology*, 5(1), p. 1058. Available at: <https://doi.org/10.1038/s42003-022-03995-5>.

Mellone, U. *et al.* (2013) 'The trans-equatorial loop migration system of Eleonora's falcon: differences in migration patterns between age classes, regions and seasons', *Journal of Avian Biology*, 44(5), pp. 417–426. Available at: <https://doi.org/10.1111/j.1600-048X.2013.00139.x>.

Mengen, C., Marre, F. and Dhar, T. (2009) 'Sea-clutter analysis at multiple wavelengths (L, C, X) for target-clutter contrast assessment in littoral waters', *2009 IEEE International Geoscience and Remote Sensing Symposium. 2009 IEEE International Geoscience and Remote Sensing Symposium (IGARSS 2009)*, Cape Town: IEEE, p. IV-713–IV-716. Available at: <https://doi.org/10.1109/IGARSS.2009.5417476>.

Mettke-Hofmann, C. and Gwinner, E. (2003) 'Long-term memory for a life on the move', *PNAS*, 100(10), pp. 5863–5866. Available at: <https://doi.org/www.pnas.org/cgi/doi/10.1073/pnas.1037505100>.

Michalik, A. *et al.* (2014) 'Star compass learning: how long does it take?', *Journal of Ornithology*, 155(1), pp. 225–234. Available at: <https://doi.org/10.1007/s10336-013-1004-x>.

Michelson, D.B. *et al.* (2014) 'EUMETNET OPERA weather radar information model for implementation with the HDF5 file format, version 2.2', *EUMETNET OPERA Document* [Preprint].

Michev, B. *et al.* (2020) 'Patterns of Bird Migration Defined by a Weather Radar at Part of the East European Flyway (Via Pontica)', *Acta Zoologica Bulgaria*, 72(2), pp. 263–277.

Mills, A.M. *et al.* (2011) 'Passerines Use Nocturnal Flights for Landscape-Scale Movements during Migration Stopover', *The Condor*, 113(3), pp. 597–607. Available at: <https://doi.org/10.1525/cond.2011.100186>.

Ministarstvo zaštite okoliša i energetike (2020) *Pravilnik o zonama rasvijetljenosti, dopuštenim vrijednostima rasvjetljavanja i načinima upravljanja rasvjetnim sustavima*. Available at: https://narodne-novine.nn.hr/clanci/sluzbeni/2020_11_128_2442.html.

Møller, A.P. (1994) 'Phenotype-dependent arrival time and its consequences in a migratory bird', *Behavioral Ecology and Sociobiology*, 35, pp. 115–122. Available at: <https://doi.org/10.1007/BF00171501>.

Mols, C.M.M. and Visser, M.E. (2002) 'Great tits can reduce caterpillar damage in apple orchards', *Journal of Applied Ecology*, 39(6), pp. 888–899. Available at: <https://doi.org/10.1046/j.1365-2664.2002.00761.x>.

Monti, F. *et al.* (2024) 'Spatio-temporal migratory patterns, habitat crossing and within-individual movement repeatability of Central Mediterranean European Rollers *Coracias garrulus*', *Behavioral Ecology and Sociobiology*, 78(8), p. 83. Available at: <https://doi.org/10.1007/s00265-024-03501-3>.

Moore, F.R. (1982) 'Sunset and the orientation of a nocturnal bird migrant: A mirror experiment', *Behavioral Ecology and Sociobiology*, 10(2), pp. 153–155. Available at: <https://doi.org/10.1007/BF00300176>.

Moore, F.R. (1985) 'Individual Variability in the Migratory Orientation of the Savannah Sparrow, *Passerculus sandwichensis*', *Zeitschrift für Tierpsychologie*, 67(1–4), pp. 144–153. Available at: <https://doi.org/10.1111/j.1439-0310.1985.tb01383.x>.

Morelli, F. *et al.* (2023) 'Effects of light and noise pollution on avian communities of European cities are correlated with the species' diet', *Scientific Reports*, 13(1), p. 4361. Available at: <https://doi.org/10.1038/s41598-023-31337-w>.

Morrison, C.A. *et al.* (2013) 'Recent population declines in Afro-Palaeartic migratory birds: the influence of breeding and non-breeding seasons', *Diversity and Distributions*. Edited by R. Duncan, 19(8), pp. 1051–1058. Available at: <https://doi.org/10.1111/ddi.12084>.

Mourer-Chauviré, C. (1995) 'Dynamics of the avifauna during the Paleogene and the Early Neogene of France. Settling of the recent fauna', *Acta Zoologica Cracoviensia*, 38(3), pp. 325–342.

Mouritsen, H. (2018) 'Long-distance navigation and magnetoreception in migratory animals', *Nature*, 558(7708), pp. 50–59. Available at: <https://doi.org/10.1038/s41586-018-0176-1>.

Mouritsen, H., Heyers, D. and Güntürkün, O. (2016) 'The Neural Basis of Long-Distance Navigation in Birds', *Annual Review of Physiology*, 78(1), pp. 133–154. Available at: <https://doi.org/10.1146/annurev-physiol-021115-105054>.

Muheim, R., Moore, F.R. and Phillips, J.B. (2006) 'Calibration of magnetic and celestial compass cues in migratory birds - a review of cue-conflict experiments', *Journal of Experimental Biology*, 209(1), pp. 2–17. Available at: <https://doi.org/10.1242/jeb.01960>.

NASA JPL (2013) 'NASA Shuttle Radar Topography Mission Global 1 arc second'. NASA Land Processes Distributed Active Archive Center. Available at: <https://doi.org/10.5067/MEASURES/SRTM/SRTMGL1.003>.

Nemes, C.E. *et al.* (2023) 'More than mortality: Consequences of human activity on migrating birds extend beyond direct mortality', *Ornithological Applications*, 125(3). Available at: <https://doi.org/10.1093/ornithapp/duad020>.

Newton, I. (2004) 'Population limitation in migrants', *Ibis*, 146(2), pp. 197–226. Available at: <https://doi.org/10.1111/j.1474-919X.2004.00293.x>.

Newton, I. (2006) 'Can conditions experienced during migration limit the population levels of birds?', *Journal of Ornithology*, 147(2), pp. 146–166. Available at: <https://doi.org/10.1007/s10336-006-0058-4>.

Newton, I. (2007) 'Weather-related mass-mortality events in migrants', *Ibis*, 149, pp. 453–467.

Newton, I. (2008) *The Migration Ecology of Birds*. First edition. Cambridgeshire, UK: Elsevier.

Newton, I. (2024) 'Migration mortality in birds', *Ibis*, p. ibi.13316. Available at: <https://doi.org/10.1111/ibi.13316>.

Nilsson, C. *et al.* (2018) 'Field validation of radar systems for monitoring bird migration', *Journal of Applied Ecology*. Edited by G. Siriwardena, 55(6), pp. 2552–2564. Available at: <https://doi.org/10.1111/1365-2664.13174>.

Nilsson, C. *et al.* (2019) 'Revealing patterns of nocturnal migration using the European weather radar network', *Ecography*, 42(5), pp. 876–886. Available at: <https://doi.org/10.1111/ecog.04003>.

Nilsson, C., Bäckman, J. and Alerstam, T. (2014) 'Seasonal modulation of flight speed among nocturnal passerine migrants: differences between short- and long-distance migrants', *Behavioral Ecology and Sociobiology*, 68(11), pp. 1799–1807. Available at: <https://doi.org/10.1007/s00265-014-1789-5>.

Nussbaumer, R. *et al.* (2021) 'Quantifying year-round nocturnal bird migration with a fluid dynamics model', *Journal of The Royal Society Interface*, 18, p. 8. Available at: <https://doi.org/10.1098/rsif.2021.0194>.

Osterhaus, D.M. *et al.* (2025) 'Nocturnal flight call monitoring reveals in-flight behavioral alteration by avian migrants in response to artificial light at night', *Biological Conservation*, 311, p. 111441. Available at: <https://doi.org/10.1016/j.biocon.2025.111441>.

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

Packmor, F. *et al.* (2020) 'Stopover departure decisions in songbirds: do long-distance migrants depart earlier and more independently of weather conditions than medium-distance migrants?', *Movement Ecology*, 8(1), p. 6. Available at: <https://doi.org/10.1186/s40462-020-0193-1>.

Panuccio, M. *et al.* (2019) 'Migrating birds avoid flying through fog and low clouds', *International Journal of Biometeorology*, 63(2), pp. 231–239. Available at: <https://doi.org/10.1007/s00484-018-01656-z>.

Papachristou, C.S. (2019) 'Aristotle's Explanations of Bird Migration', in D. Sphendonē-Mentzou (ed.) *Proceedings of the World Congress "Aristotle 2400 Years"*. Thessaloniki: Aristotle University of Thessaloniki, pp. 135–146.

Parkins, K.L., Elbin, S.B. and Barnes, E. (2015) 'Light, Glass, and Bird—Building Collisions in an Urban Park', *Northeastern Naturalist*, 22(1), pp. 84–94. Available at: <https://doi.org/10.1656/045.022.0113>.

Pasarić, Z., Belušić, D. and Chiggiato, J. (2009) 'Orographic effects on meteorological fields over the Adriatic from different models', *Journal of Marine Systems*, 78, pp. S90–S100. Available at: <https://doi.org/10.1016/j.jmarsys.2009.01.019>.

Petras, T. and Vrezec, A. (2022) 'Long-Term Ringing Data on Migrating Passerines Reveal Overall Avian Decline in Europe', *Diversity*, 14(905). Available at: <https://doi.org/10.3390/d14110905>.

Phillips, E.M. *et al.* (2019) 'Does perspective matter? A case study comparing Eulerian and Lagrangian estimates of common murre (*Uria aalge*) distributions', *Ecology and Evolution*, 9(8), pp. 4805–4819. Available at: <https://doi.org/10.1002/ece3.5083>.

Pilastro, A. *et al.* (1998) 'Spring migratory routes of eight trans-Saharan passerines through the central and western Mediterranean; results from a network of insular and coastal ringing sites', *Ibis*, 140(4), pp. 591–598. Available at: <https://doi.org/10.1111/j.1474-919X.1998.tb04704.x>.

Pothukuchi, K. (2021) 'City Light or Star Bright: A Review of Urban Light Pollution, Impacts, and Planning Implications', *Journal of Planning Literature*, 36(2), pp. 155–169. Available at: <https://doi.org/10.1177/0885412220986421>.

Procházka, P. *et al.* (2018) 'Across a migratory divide: divergent migration directions and non-breeding grounds of Eurasian reed warblers revealed by geolocators and stable isotopes', *Journal of Avian Biology*, 49(6), p. jav-012516. Available at: <https://doi.org/10.1111/jav.01769>.

Pullen, J. *et al.* (2007) 'Bora event variability and the role of air-sea feedback', *Journal of Geophysical Research: Oceans*, 112(C3), p. 2006JC003726. Available at: <https://doi.org/10.1029/2006JC003726>.

R Core Team (2013) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at: <http://www.R-project.org/>.

Radović, D. *et al.* (2008) 'Results and population estimates from the 1997/98 Non-Estuarine Coastal Waterbird Survey in Croatia', *International Wader Studies*, 18, pp. 13–17.

Radović, D., Kralj, J. and Tutiš, V. (1999) 'Migration pattern and seasonal activity of waders at Draganic fishponds in NW Croatia', *Wader Study Group Bulletin*, 90, pp. 35–41.

Rappole, J.H. and Jones, P. (2002) 'Evolution of old and new world migration systems', *Ardea*, 90(3), pp. 525–537.

Rebke, M. *et al.* (2019) 'Attraction of nocturnally migrating birds to artificial light: The influence of colour, intensity and blinking mode under different cloud cover conditions', *Biological Conservation*, 233, pp. 220–227. Available at: <https://doi.org/10.1016/j.biocon.2019.02.029>.

Rhyne, G.S. *et al.* (2024) 'Barometric geolocators can reveal unprecedented details about the migratory ecology of small birds', *Ornithology*, 141(3), p. ukae010. Available at: <https://doi.org/10.1093/ornithology/ukae010>.

Richardson, W.J. (1978) 'Timing and Amount of Bird Migration in Relation to Weather: A Review', *Oikos*, 30(2), p. 224. Available at: <https://doi.org/10.2307/3543482>.

Rigal, S. *et al.* (2023) 'Farmland practices are driving bird population decline across Europe', *Proceedings of the National Academy of Sciences*, 120(21), p. e2216573120. Available at: <https://doi.org/10.1073/pnas.2216573120>.

Robin Radar Systems (2025) *MAX Avian Radar*. Available at: <https://www.robinradar.com> (Accessed: 13 December 2025).

Rodgers, C.T. and Hore, P.J. (2009) 'Chemical magnetoreception in birds: The radical pair mechanism', *Proceedings of the National Academy of Sciences*, 106(2), pp. 353–360. Available at: <https://doi.org/10.1073/pnas.0711968106>.

Rodrigo-Comino, J. *et al.* (2023) 'Light pollution: A review of the scientific literature', *The Anthropocene Review*, 10(2), pp. 367–392. Available at: <https://doi.org/10.1177/20530196211051209>.

Rodríguez, A. *et al.* (2022) 'Tracking Flights to Investigate Seabird Mortality Induced by Artificial Lights', *Frontiers in Ecology and Evolution*, 9, p. 786557. Available at: <https://doi.org/10.3389/fevo.2021.786557>.

Rössler, M. and Schauer, C. (2014) 'Flugrichtungen und räumliche Verteilung des nächtlichen Vogelzuges über den Ostalpen: Mondbeobachtungen 2005–2007', *Ornithologischer Beobachter*, 111(3), pp. 173–186.

Rubolini, D. *et al.* (2007) 'Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among European bird species', *Climate Research*, 35, pp. 135–146. Available at: <https://doi.org/10.3354/cr00720>.

Runge, C.A. *et al.* (2014) 'Conserving mobile species', *Frontiers in Ecology and the Environment*, 12(7), pp. 395–402. Available at: <https://doi.org/10.1890/130237>.

Runge, C.A. *et al.* (2015) 'Protected areas and global conservation of migratory birds', *Science*, 350(6265), pp. 1255–1258. Available at: <https://doi.org/10.1126/science.aac9180>.

Rushing, C.S., Ryder, T.B. and Marra, P.P. (2016) 'Quantifying drivers of population dynamics for a migratory bird throughout the annual cycle', *Proceedings of the Royal Society B: Biological Sciences*, 283(1823), p. 20152846. Available at: <https://doi.org/10.1098/rspb.2015.2846>.

Saha, P. (2017) *Lights out for the Texas skyscraper that caused hundreds of songbird deaths*, *Audubon*. Available at: <https://www.audubon.org/news/lights-out-texas-skyscraper-caused-hundreds-songbird-deaths> (Accessed: 22 April 2025).

Saino, N. *et al.* (2010) 'Spring migration decisions in relation to weather are predicted by wing morphology among trans-Mediterranean migratory birds', *Functional Ecology*, 24(3), pp. 658–669. Available at: <https://doi.org/10.1111/j.1365-2435.2009.01659.x>.

Salewski, V. and Bruderer, B. (2007) 'The evolution of bird migration - a synthesis', *Naturwissenschaften*, 94(4), pp. 268–279. Available at: <https://doi.org/10.1007/s00114-006-0186-y>.

Saltikoff, E. *et al.* (2019) 'OPERA the Radar Project', *Atmosphere*, 10(6), p. 320. Available at: <https://doi.org/10.3390/atmos10060320>.

Sanderson, F.J. *et al.* (2006) 'Long-term population declines in Afro-Palearctic migrant birds', *Biological Conservation*, 131(1), pp. 93–105. Available at: <https://doi.org/10.1016/j.biocon.2006.02.008>.

Schaper, M. *et al.* (2022) 'Radio frequency interference detection and mitigation in the DWD C-band weather radar network', *Atmospheric Measurement Techniques*, 15(22), pp. 6625–6642. Available at: <https://doi.org/10.5194/amt-15-6625-2022>.

Schaub, M. and Jenni, L. (2000a) 'Body mass of six long-distance migrant passerine species along the autumn migration route', *Journal für Ornithologie*, 141, pp. 441–460.

Schaub, M. and Jenni, L. (2000b) 'Fuel deposition of three passerine bird species along the migration route', *Oecologia*, 122(3), pp. 306–317. Available at: <https://doi.org/10.1007/s004420050036>.

Schaub, M., Liechti, F. and Jenni, L. (2004) 'Departure of migrating European robins, *Erithacus rubecula*, from a stopover site in relation to wind and rain', *Animal Behaviour*, 67(2), pp. 229–237. Available at: <https://doi.org/10.1016/j.anbehav.2003.03.011>.

Schekler, I. *et al.* (2022) 'Bird Migration at the Edge – Geographic and Anthropogenic Factors but Not Habitat Properties Drive Season-Specific Spatial Stopover Distributions Near Wide Ecological Barriers', *Frontiers in Ecology and Evolution*, 10, p. 822220. Available at: <https://doi.org/10.3389/fevo.2022.822220>.

Schekler, I., Levi, Y. and Sapir, N. (2024) 'Contrasting seasonal responses to wind in migrating songbirds on a globally important flyway', *Proceedings of the Royal Society B: Biological Sciences*, 291(2027), p. 20240875. Available at: <https://doi.org/10.1098/rspb.2024.0875>.

Schmaljohann, H. *et al.* (2008) 'Quantification of bird migration by radar - a detection probability problem', *Ibis*, 150(2), pp. 342–355. Available at: <https://doi.org/10.1111/j.1474-919X.2007.00797.x>.

Schmaljohann, H. and Both, C. (2017) 'The limits of modifying migration speed to adjust to climate change', *Nature Climate Change*, 7(8), pp. 573–576. Available at: <https://doi.org/10.1038/nclimate3336>.

Schmaljohann, H. and Eikenaar, C. (2017) 'How do energy stores and changes in these affect departure decisions by migratory birds? A critical view on stopover ecology studies and some future perspectives', *Journal of Comparative Physiology A*, 203(6–7), pp. 411–429. Available at: <https://doi.org/10.1007/s00359-017-1166-8>.

Schmaljohann, H., Eikenaar, C. and Sapir, N. (2022) 'Understanding the ecological and evolutionary function of stopover in migrating birds', *Biological Reviews*, p. brv.12839. Available at: <https://doi.org/10.1111/brv.12839>.

Schmid, B. *et al.* (2019) 'Size matters in quantitative radar monitoring of animal migration: estimating monitored volume from wingbeat frequency', *Ecography*, 42(5), pp. 931–941. Available at: <https://doi.org/10.1111/ecog.04025>.

Schulte, P. *et al.* (2010) 'The Chicxulub Asteroid Impact and Mass Extinction at the Cretaceous-Paleogene Boundary', *Science*, 327(5970), pp. 1214–1218. Available at: <https://doi.org/10.1126/science.1177265>.

Schwilch, R. *et al.* (2002) 'Do migratory birds need a nap after a long non-stop flight?', *Ardea*, 90(1), pp. 149–154.

Shamoun-Baranes, J. *et al.* (2010) 'Stochastic atmospheric assistance and the use of emergency staging sites by migrants', *Proceedings of the Royal Society B: Biological Sciences*, 277(1687), pp. 1505–1511. Available at: <https://doi.org/10.1098/rspb.2009.2112>.

Shamoun-Baranes, J. *et al.* (2019) 'Taking radar aeroecology into the 21st century', *Ecography*, 42(5), pp. 847–851. Available at: <https://doi.org/10.1111/ecog.04582>.

Shamoun-Baranes, J. *et al.* (2022) 'Meteorological Data Policies Needed to Support Biodiversity Monitoring with Weather Radar', *Bulletin of the American Meteorological Society*, 103(4), pp. E1234–E1242. Available at: <https://doi.org/10.1175/BAMS-D-21-0196.1>.

Shamoun-Baranes, J., Liechti, F. and Vansteelant, W.M.G. (2017) 'Atmospheric conditions create freeways, detours and tailbacks for migrating birds', *Journal of Comparative Physiology A*, 203(6–7), pp. 509–529. Available at: <https://doi.org/10.1007/s00359-017-1181-9>.

Shi, X. *et al.* (2021) 'Seasonal Trends in Movement Patterns of Birds and Insects Aloft Simultaneously Recorded by Radar', *Remote Sensing*, 13(9), p. 1839. Available at: <https://doi.org/10.3390/rs13091839>.

Skip, M.M. *et al.* (2015) 'Migrating songbirds on stopover prepare for, and recover from, oxidative challenges posed by long-distance flight', *Ecology and Evolution*, 5(15), pp. 3198–3209. Available at: <https://doi.org/10.1002/ece3.1601>.

Smith, R.J. and Moore, F.R. (2005) 'Arrival timing and seasonal reproductive performance in a long-distance migratory landbird', *Behavioral Ecology and Sociobiology*, 57(3), pp. 231–239. Available at: <https://doi.org/10.1007/s00265-004-0855-9>.

Somveille, M., Rodrigues, A.S.L. and Manica, A. (2015) 'Why do birds migrate? A macroecological perspective', *Global Ecology and Biogeography*, 24(6), pp. 664–674. Available at: <https://doi.org/10.1111/geb.12298>.

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

Stach, R. *et al.* (2015) 'Wide ranging stopover movements and substantial fuelling in first year garden warblers at a northern stopover site', *Journal of Avian Biology*, 46(3), pp. 315–322. Available at: <https://doi.org/10.1111/jav.00492>.

Stepanian, P.M. *et al.* (2016) 'Dual-polarization radar products for biological applications', *Ecosphere*, 7(11). Available at: <https://doi.org/10.1002/ecs2.1539>.

Stipčević, M. (1997) 'A survey of spring wader migration on the wetlands of the island of Pag, Croatia (March-May 1990-1991)', *Wader Study Group Bulletin*, 84, pp. 26–32.

Taylor, P.D. *et al.* (2011) 'Landscape Movements of Migratory Birds and Bats Reveal an Expanded Scale of Stopover', *PLoS ONE*. Edited by T. Mappes, 6(11), p. e27054. Available at: <https://doi.org/10.1371/journal.pone.0027054>.

Thieurmél, B. and Elmarhraoui, A. (2022) '_suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase_'. Available at: <https://CRAN.R-project.org/package=suncalc>.

Thorup, K. *et al.* (2013) 'Timing of songbird migration: individual consistency within and between seasons', *Journal of Avian Biology*, 44(5), pp. 486–494. Available at: <https://doi.org/10.1111/j.1600-048X.2013.05871.x>.

Thorup, K. *et al.* (2014) 'Large-scale spatial analysis of ringing and re-encounter data to infer movement patterns: A review including methodological perspectives', *Methods in Ecology and Evolution*. Edited by C. Francis, 5(12), pp. 1337–1350. Available at: <https://doi.org/10.1111/2041-210X.12258>.

Thorup, K. and Rabøl, J. (2001) 'The orientation system and migration pattern of long-distance migrants: conflict between model predictions and observed patterns', *Journal of Avian Biology*, 32(2), pp. 111–119. Available at: <https://doi.org/10.1034/j.1600-048X.2001.320203.x>.

Tikkanen, H. *et al.* (2024) 'Survival estimates of GPS-tagged adult Golden Eagles (*Aquila chrysaetos*) breeding in Finland', *Ornis Fennica*, pp. 00–00. Available at: <https://doi.org/10.51812/of.144459>.

Tøttrup, A.P. *et al.* (2012) 'The annual cycle of a trans-equatorial Eurasian–African passerine migrant: different spatio-temporal strategies for autumn and spring migration', *Proceedings of the Royal Society B: Biological Sciences*, 279(1730), pp. 1008–1016. Available at: <https://doi.org/10.1098/rspb.2011.1323>.

Trösch, B. *et al.* (2005) 'Spatial and seasonal variation in nocturnal autumn and spring migration patterns in the western Mediterranean area: a moon-watching survey', *Avocetta*, 29, pp. 63–73.

Tschanz, P. *et al.* (2019) 'Consistency of spatio-temporal patterns of avian migration across the Swiss lowlands', *Remote Sensing in Ecology and Conservation*, pp. 1–14. Available at: <https://doi.org/10.1002/rse2.143>.

Tutiš, V. and Radović, D. (2003) 'Ornithological value of Vransko jezero Nature Park and the influence of proposed hydrological stabilization on it', *Hydrological stabilization and conservation of biodiversity of the Vransko jezero Nature Park catchment area. Round Table*, Biograd, Croatia: Public Institution Nature Park Vransko Jezero, p. 77 ff.

Tyagi, T. and Bhardwaj, S.K. (2021) 'Orientation cues and mechanisms used during avian navigation: A review', *Journal of Applied and Natural Science*, 13(2), pp. 627–640. Available at: <https://doi.org/10.31018/JANS.V13I2.2684>.

Van Doren, B.M. *et al.* (2017) 'High-intensity urban light installation dramatically alters nocturnal bird migration', *Proceedings of the National Academy of Sciences*, 114(42), pp. 11175–11180. Available at: <https://doi.org/10.1073/pnas.1708574114>.

Van Doren, B.M. *et al.* (2021) 'Drivers of fatal bird collisions in an urban center', *Proceedings of the National Academy of Sciences*, 118(24), p. e2101666118. Available at: <https://doi.org/10.1073/pnas.2101666118>.

- Van Doren, B.M. and Horton, K.G. (2018) 'A continental system for forecasting bird migration', *Science*, 361(6407), pp. 1115–1118. Available at: <https://doi.org/10.1126/science.aat7526>.
- Végvári, Z. *et al.* (2010) 'Life history predicts advancement of avian spring migration in response to climate change', *Global Change Biology*, 16(1), pp. 1–11. Available at: <https://doi.org/10.1111/j.1365-2486.2009.01876.x>.
- Wallraff, H.G. (2005) *Avian Navigation: Pigeon Homing as a Paradigm*. Berlin/Heidelberg: Springer-Verlag. Available at: <http://link.springer.com/10.1007/b137573>.
- Weisshaupt, N. *et al.* (2018) 'Effects of a sea barrier on large-scale migration patterns studied by a network of weather radars', *Bird Study*, 65(2), pp. 232–240. Available at: <https://doi.org/10.1080/00063657.2018.1476457>.
- Weisshaupt, N. *et al.* (2022) 'Anthropogenic Illumination as Guiding Light for Nocturnal Bird Migrants Identified by Remote Sensing', *Remote Sensing*, 14(7), p. 1616. Available at: <https://doi.org/10.3390/rs14071616>.
- Werber, Y. and Sapir, N. (2025) 'Radar-measured passerine vertical speeds reveal a migratory switch near a major barrier', *iScience*, 28(2), p. 111892. Available at: <https://doi.org/10.1016/j.isci.2025.111892>.
- Werfeli, M., Ranacher, P. and Liechti, F. (2022) 'Gone with the wind: Inferring bird migration with light-level geolocation, wind and activity measurements', *Methods in Ecology and Evolution*, 13(6), pp. 1265–1274. Available at: <https://doi.org/10.1111/2041-210X.13837>.
- Whelan, C.J., Şekercioğlu, Ç.H. and Wenny, D.G. (2015) 'Why birds matter: from economic ornithology to ecosystem services', *Journal of Ornithology*, 156(S1), pp. 227–238. Available at: <https://doi.org/10.1007/s10336-015-1229-y>.
- Whelan, C.J., Wenny, D.G. and Marquis, R.J. (2008) 'Ecosystem Services Provided by Birds', *Annals of the New York Academy of Sciences*, 1134(1), pp. 25–60. Available at: <https://doi.org/10.1196/annals.1439.003>.
- Widmer, K., Marnane, I. and Vounatsou, P. (2022) *Review and Assessment of Available Information on Light Pollution in Europe*. Kjeller, Norway.
- Williams, D.R., Balmford, A. and Wilcove, D.S. (2020) 'The past and future role of conservation science in saving biodiversity', *Conservation Letters*, 13(4), p. e12720. Available at: <https://doi.org/10.1111/conl.12720>.
- Wiltschko, R. (2017) 'Navigation', *Journal of Comparative Physiology A*, 203(6–7), pp. 455–463. Available at: <https://doi.org/10.1007/s00359-017-1160-1>.
- Wiltschko, W. and Wiltschko, R. (2001) 'Light-dependent magnetoreception in *Erithacus rubecula*', *The Journal of Experimental Biology*, 204, pp. 3295–3302.
- Wiltschko, W. and Wiltschko, R. (2012) 'Global navigation in migratory birds: tracks, strategies, and interactions between mechanisms', *Current Opinion in Neurobiology*, 22(2), pp. 328–335. Available at: <https://doi.org/10.1016/j.conb.2011.12.012>.

Winger, B.M., Auteri, G.G., *et al.* (2019) 'A long winter for the Red Queen: rethinking the evolution of seasonal migration', *Biological Reviews*, 94(3), pp. 737–752. Available at: <https://doi.org/10.1111/brv.12476>.

Winger, B.M., Weeks, B.C., *et al.* (2019) 'Nocturnal flight-calling behaviour predicts vulnerability to artificial light in migratory birds', *Proceedings of the Royal Society B: Biological Sciences*, 286(1900), p. 20190364. Available at: <https://doi.org/10.1098/rspb.2019.0364>.

Wood, S.N. (2023) 'Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models', *Journal of the Royal Statistical Society (B)*, 73(1), pp. 3–36.

Zachos, J. *et al.* (2001) 'Trends, Rhythms, and Aberrations in Global Climate 65 Ma to Present', *Science*, 292(5517), pp. 686–693. Available at: <https://doi.org/10.1126/science.1059412>.

Zaugg, S. *et al.* (2008) 'Automatic identification of bird targets with radar via patterns produced by wing flapping', *Journal of The Royal Society Interface*, 5(26), pp. 1041–1053. Available at: <https://doi.org/10.1098/rsif.2007.1349>.

Zhang, Z. *et al.* (2014) 'Aridification of the Sahara desert caused by Tethys Sea shrinkage during the Late Miocene', *Nature*, 513, pp. 401–405. Available at: <https://doi.org/doi:10.1038/nature13705>.

Zhou, Y. *et al.* (2022) *fdapace: Functional Data Analysis and Empirical Dynamics*. Available at: <https://CRAN.R-project.org/package=fdapace>.

Zúñiga, D. *et al.* (2016) 'Abrupt switch to migratory night flight in a wild migratory songbird', *Scientific Reports*, 6(1), p. 34207. Available at: <https://doi.org/10.1038/srep34207>.

Appendix A: Correction to Hirschhofer et al. (2025), “Avian spring migration at the east Adriatic coast: coastal and sea crossing dynamics of intensity, timing, and flight directions”

Abstract

We provide a correction to the publication by Hirschhofer et al., published in this journal in 2025. Data from Vransko Lake were found to be erroneous and were therefore removed from the analyses. The results and figures of the original publication have been updated accordingly, and we detail herein the analyses that led to this decision. Despite the partial retraction of data, the overall results and conclusions of the study remain unchanged.

Erroneous radar data from Vransko Lake

In Hirschhofer et al. (2025), we reported low migration intensity and scattered flight directions at Vransko Lake. We discussed the results only briefly, acknowledging our inability to rule out technical malfunctions of the radar, and emphasizing the need to confirm the migration pattern shown by the radar data by collecting and analysing further data.

New insights from subsequent cross-calibration revealed that the data from Vransko Lake (radar ID : BS223) in 2023 was affected by a major hardware failure of the radar receiver. We therefore decided to remove the data from Vransko Lake from the analyses. Despite the partial retraction of data, the general results and conclusions of the study remain unchanged.

The authors apologise to the publisher and the readers for the erroneous data from Vransko Lake. We first present a correction of the figures and results. We then detail new results that led to the conclusion of partial data retraction.

I. Corrected results

We fully removed the data collected at Vransko Lake in 2023 from the analysis and accordingly updated the related figures (Figure-corrected 1 to 5) and associated text by removing any mention of Vransko Lake in this erratum. In the original publication, most of the data from Vransko Lake were discussed independently. However, removing the data from Vransko lake changed the results of the functional principal component analyses (FPCA) and the unsupervised cluster analyses, as detailed below.

Migration intensity

We delete the following sentence:

The lowest migration intensities were measured at Vrana, where recording only started in mid-April (see radar monitoring methods and discussion; mean MTR = 191; max MTR = 529 on May 16; IQR = 171):

We corrected the associated figure as follows:

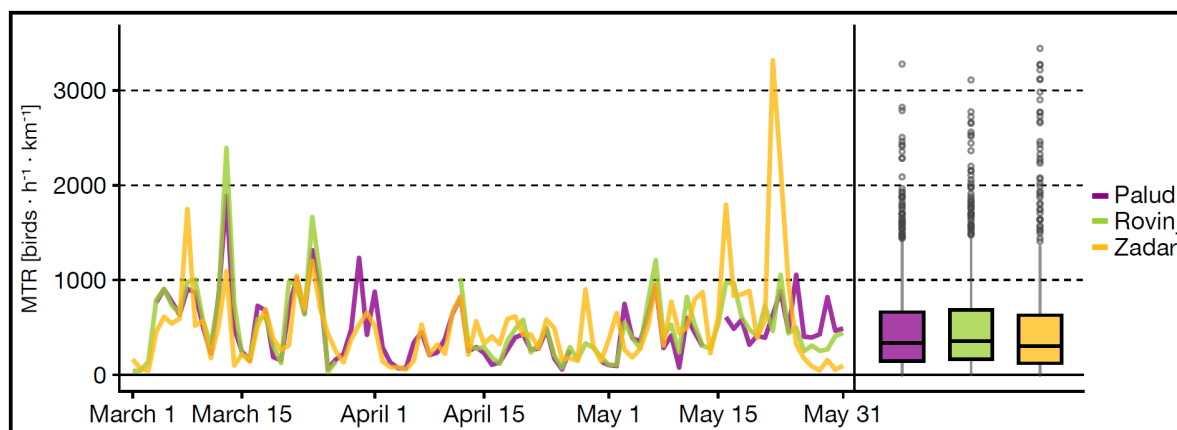


Figure-corrected 1. Left: Timeline plot of the nightly mean migration intensity for the three sites in the 2023 spring season. Right: Summary of migration intensities at each site shown as boxplots, including the median, interquartile range, and outliers.

Flight directions

We edited the sentence as follows:

We found flight directions to be similar between the Istrian sites of Palud and Rovinj (Palud: mean direction = 5.2° (N), MRL = 0.72; Rovinj: mean direction = 2.9° (N), MRL = 0.72). Compared to these Istrian sites, flight directions in Zadar were more aligned to the coast (Zadar: mean direction = 339° (NNW), MRL = 0.68).

We corrected the associated figures as follows:

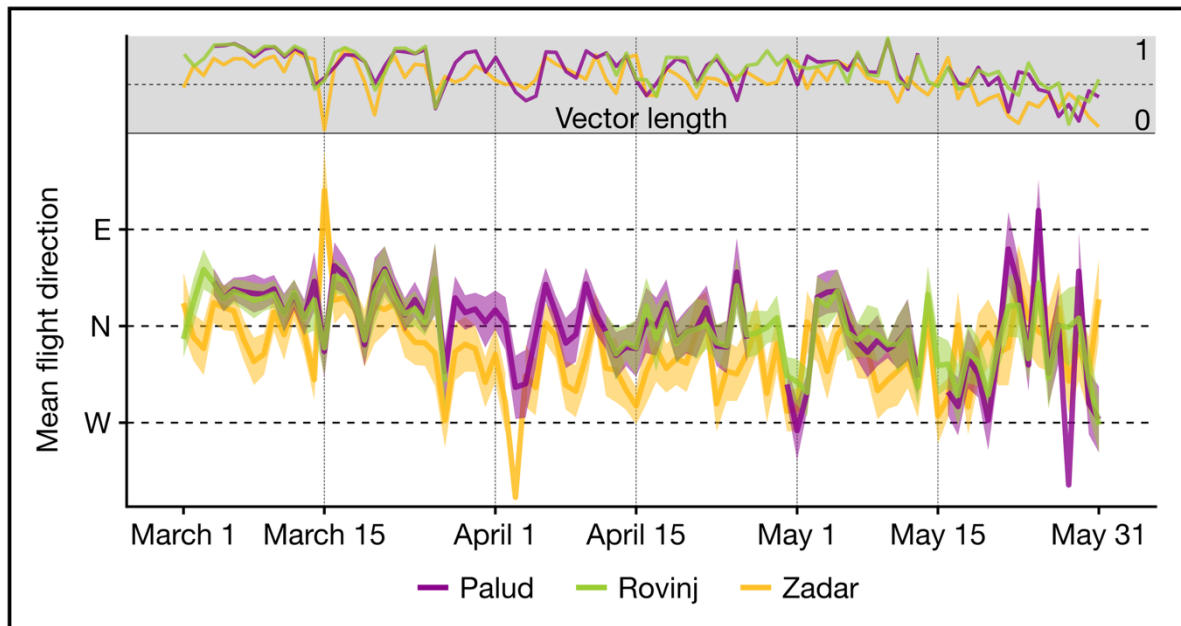


Figure-corrected 2. Nightly flight direction means and interquartile ranges for each radar site during the spring migration season 2023. Inset plot shows the concentration of flight direction as the mean resultant vector length (MRL).

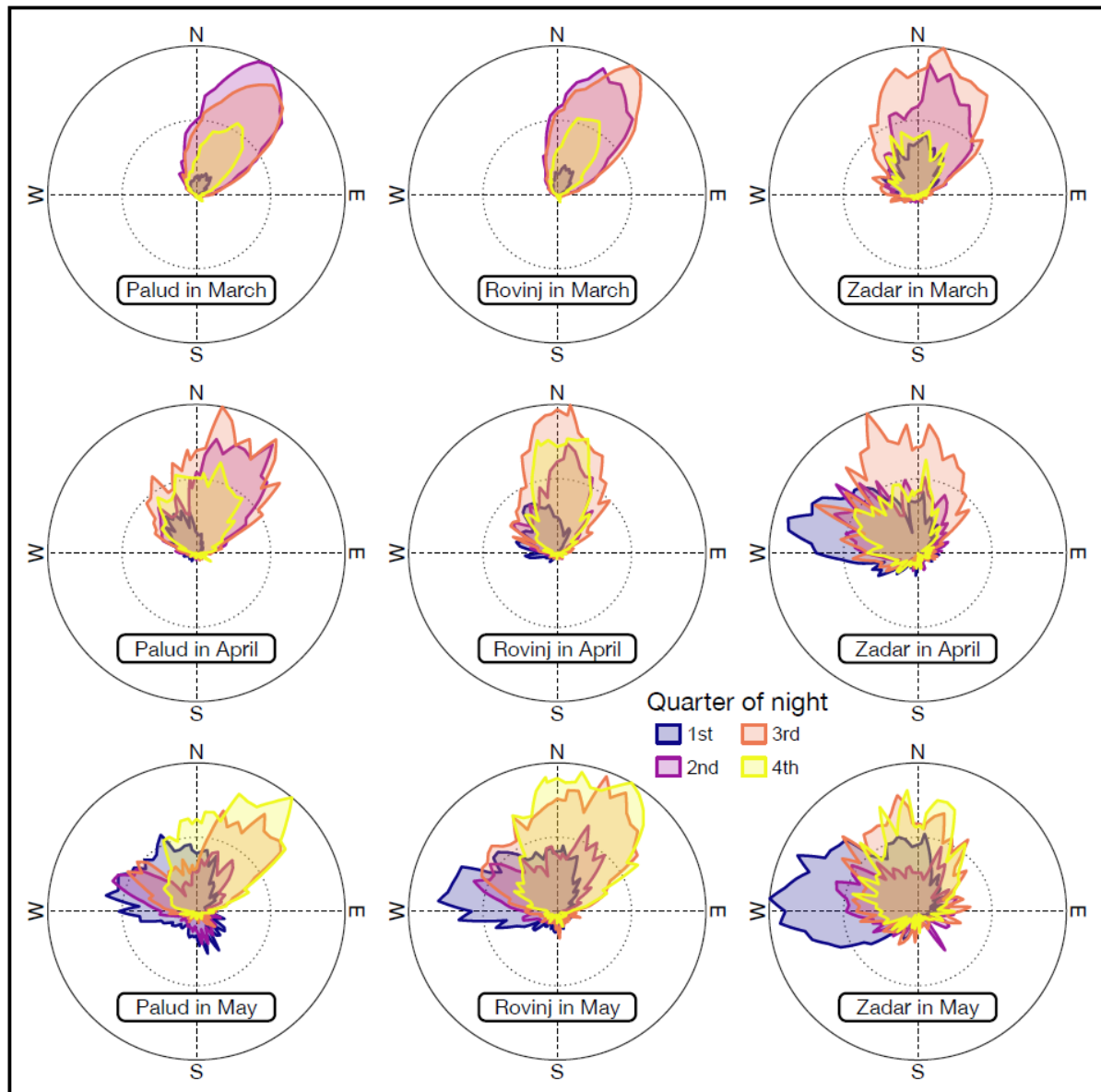


Figure-corrected 3. Distribution of recorded flight directions per site and month. Bird echoes have been quantified per 5-degree segment of the circle and standardised for comparability. Colours represent quarters of the night with blue just after sunset, purple before midnight, orange just after midnight, and yellow before sunrise.

FPCA and clustering

Removing the data from Vransko Lake changed the results of the FPCA and cluster analyses. The first two component of the FPCA now explain 83.6 % of the variation (compared to 84.5 % in the original manuscript). Based on these two first components, we now identified three clusters (compared to four clusters in the original manuscript): i) low migration intensity, ii) early peak and medium to high migration intensity, iii) late peak and medium to high migration intensity. In line with the previous results, the cluster analyses based on functional principal component analysis (FPCA) allowed to characterise the dynamics of the migratory flyway at the Croatian Adriatic coast, with early peaks of nightly migration intensity profiles denoting a dominance of migration fluxes along the coast from the South-East, and late peaks relating to a higher volume of migration across the Adriatic sea from the South-West.

We summarised the performance and clustering outputs of the revised FPCA as follows:

Functional Components	Principal	Explained variability	Interpretation
1		73.6	variations in amplitude: low eigenvalues correspond to low migration intensity, high eigenvalues correspond to high migration intensity
2		10.2	peak migration timing: low eigenvalues correspond to early peak, high eigenvalues to late peak

Clusters	Mean MTR	Timing of peak – percentage of night's time passed since sunset
1	263	47%
2	684	46%
3	810	64%

We corrected the associated figures as follows:

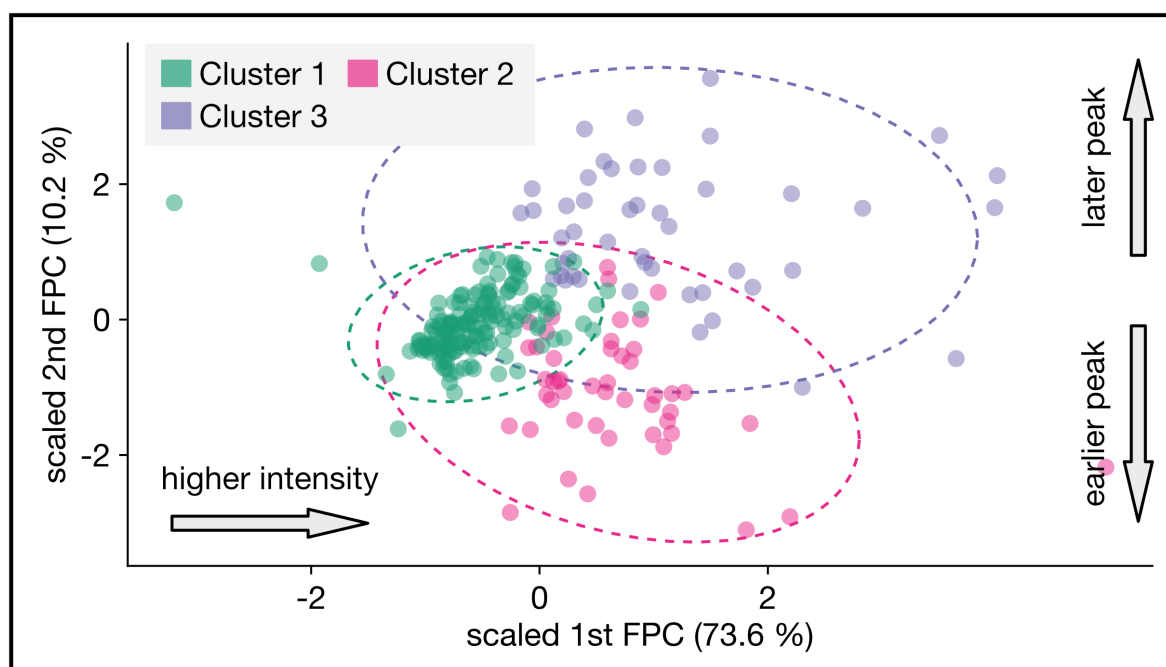


Figure-corrected 4. Cluster-specific density distribution of the scaled first and second FPC eigenvalues of radar nights. The first FPC represents the amplitude of the migration intensity profiles, the second FPC represents a shift in the timing of the peak intensity during the night.

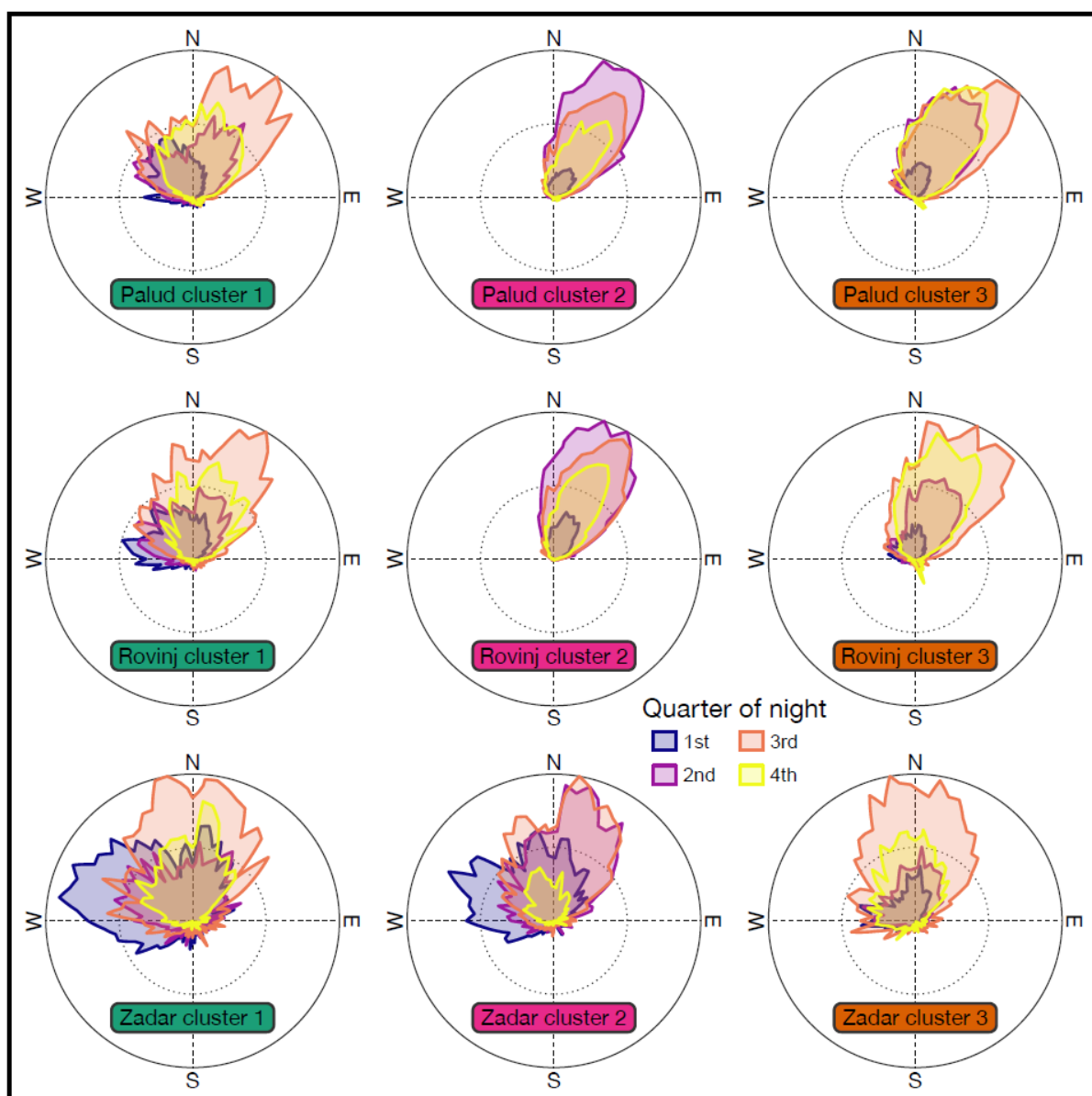


Figure-corrected 5. Distribution of recorded flight directions per site and cluster. Bird echoes have been quantified per 5-degree segment of the circle and standardised for comparability. Colours represent quarters of the night with blue just after sunset, purple before midnight, orange just after midnight, and yellow before sunrise.

II. Underlying technical problem

The data were collected with BirdScan MR1 radars (manufactured by Swiss Birdradar Solution, www.swiss-birdradar.com). Radar calibration is conducted at two stages. First, with each newly installed receiver, the conversion of received voltage to decibels is calibrated using a signal generator (Radar Test Set 75 manufactured by Giga Instrumentation for BS223, BS225, BS226; Anritsu 68367C for BS227). The calibration values (zero voltage, steepness of the linear relation between received voltage and measured decibels, saturation points) are registered in the database with the acquisition of the echoes and used as key parameters to convert the voltage into decibel by the embedded software. Second, the radars undergo a yearly service and replacement of the magnetron. This service is associated with measurements of the key radar parameters: power sent, and duration of pulse length. These measurements are registered in the database associated with the acquisition of the echoes.

Measurement quality and reproducibility aim for a precision of 2-3 dB, resulting in a difference in detection range of 12 to 19 %.

Description of Error

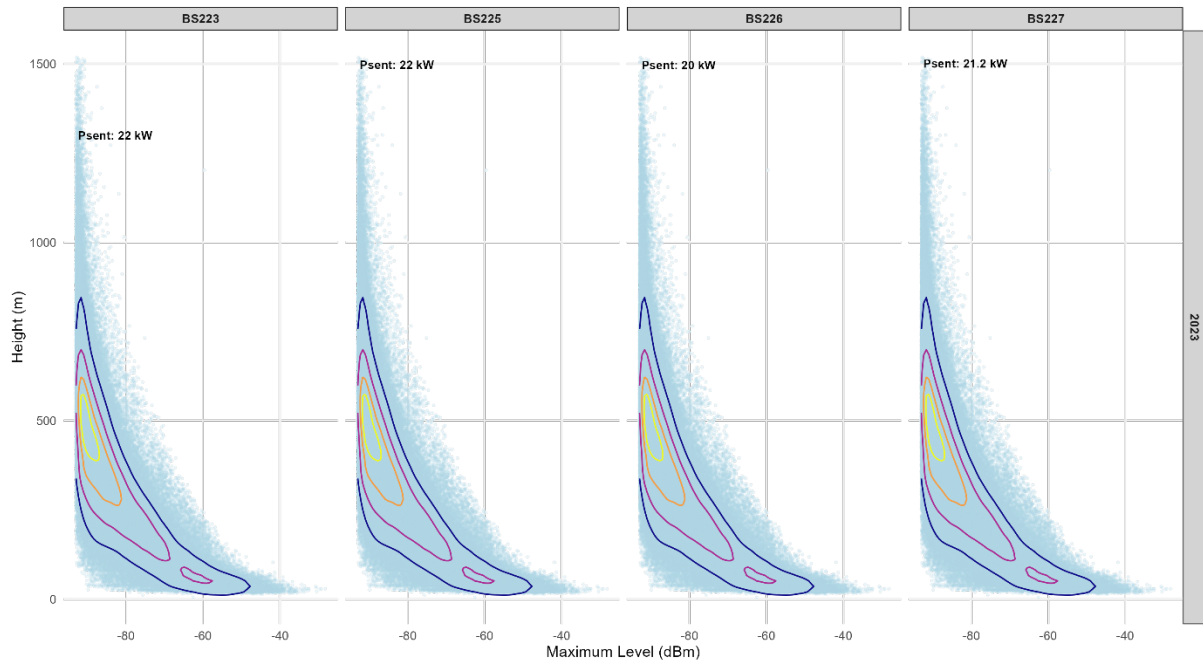
The sensitivity of radar BS223 was abnormally low, resulting in shorter detection range, fewer detections, and misclassification of the detected echoes.

During our data analyses, we were puzzled by the unexpectedly low number of birds detected at Vransko Lake. We initially found no evidence of malfunction. After the annual replacement of the magnetron, values were all within range. Likewise, additional radar parameters registered during data acquisition (e.g. disruption of received voltage as indices for a malfunction of the radar receiver) showed no sign of malfunction. In the absence of clear sign of malfunction, we considered the data as surprising but plausible in the original publication.

Unsatisfied by the puzzling results from BS223, we pursued our investigation in spring 2025. To investigate sensitivity loss, we produced new figures to compare the height distribution of the maximum level of the echo intensity (after a lowpass filter applied by the custom BirdScan-software, feature14, Schmid et al. (2019); Supp. Fig. A1). The radar BS223 showed significantly lower detection range, but also lower levels of echo intensity at e.g. 500 m agl (Supp. Tab. A1).

Supp. Tab. A1. Quantiles (1, 0.99, 0.95, 0.90, 0.75) of the distribution of echo intensity (dBm, class: passerine- and wader-type) registered within 500 ± 25 m for all four radars in Croatia in March-May 2023, and in Sempach in May 2025.

Radar-ID	Site	Year	Number of echos	Quantile				
				1.00	0.99	0.95	0.90	0.75
BS223	Vransko Lake	2023	3644	-81.1	-83.6	-86.3	-87.4	-90.1
BS225	Rovinj	2023	14172	-70.8	-78.6	-83.4	-84.6	-86.9
BS226	Palud	2023	14342	-70.3	-77.5	-82.1	-83.6	-86.2
BS227	Zadar	2023	6231	-74.8	-79.6	-84.7	-86.7	-89.2
BS223	Sempach	2025	223	-92.2	-92.2	-92.3	-92.3	-92.4
BS225	Sempach	2025	996	-76.6	-76.9	-81.4	-83.4	-86.0
BS226	Sempach	2025	1092	-75.9	-76.5	-80.4	-83.4	-85.9
BS227	Sempach	2025	485	-82.7	-83.4	-84.4	-86.4	-88.7



Supp. Fig. A1. Detection range (m above ground level) and intensity (dBm) of detected echoes (class: passerine- and wader-type) in Croatia in spring 2023. Isolines represent the 0.25 (dark blue line), 0.50 (violet line), 0.75 (orange line), and 0.90 (yellow line) density quantiles.

A decreased sensitivity also reduced the cross-section of the radar beam, resulting in shorter echo duration. Furthermore, the echo classification algorithm uses the distance-corrected measure of the echo intensity, known as the radar cross section (RCS). Together, shorter duration and smaller RCS of the echo ultimately influence the classification outcome. The lower sensitivity directly impacts the detection range of bird echoes. Following the radar equation (Schmid *et al.*, 2019), a difference of 7 dBm (as possibly observed with radar BS223 in 2023) induces a reduction of the detection range of 66.7% (about 500 meters).

Because the nearest reference point to Vransko Lake was in Zadar (30.4 km away; 189.9 km for Palud, 196.5 for Rovinj), the data collected across multiple sites did not allow us to determine whether the observed differences were due to a technical malfunction or a biological phenomenon. For instance, differences in species composition with smaller or lower flying birds at Vransko Lake as compared to Zadar, would induce lower levels of echo intensity and lower detection range. To resolve this uncertainty, we tested the four radars in parallel at the same site to rule out potential technical issues.

The four radars ran in parallel on the roof terrasse of the Swiss Ornithological Institute (Sempach, Switzerland, Supp. Fig. A2) in May 2025. These pulse radars can run in proximity because the pulse length is 8000 times shorter than the pulse repetition (pulse repetition frequency: 1800 Hz, pulse length: 70 ns), and the timing of the pulse repetition for a radar is slightly modulated at random. It is therefore unlikely that a radar registers the energy of pulses emitted by a neighbouring radar.

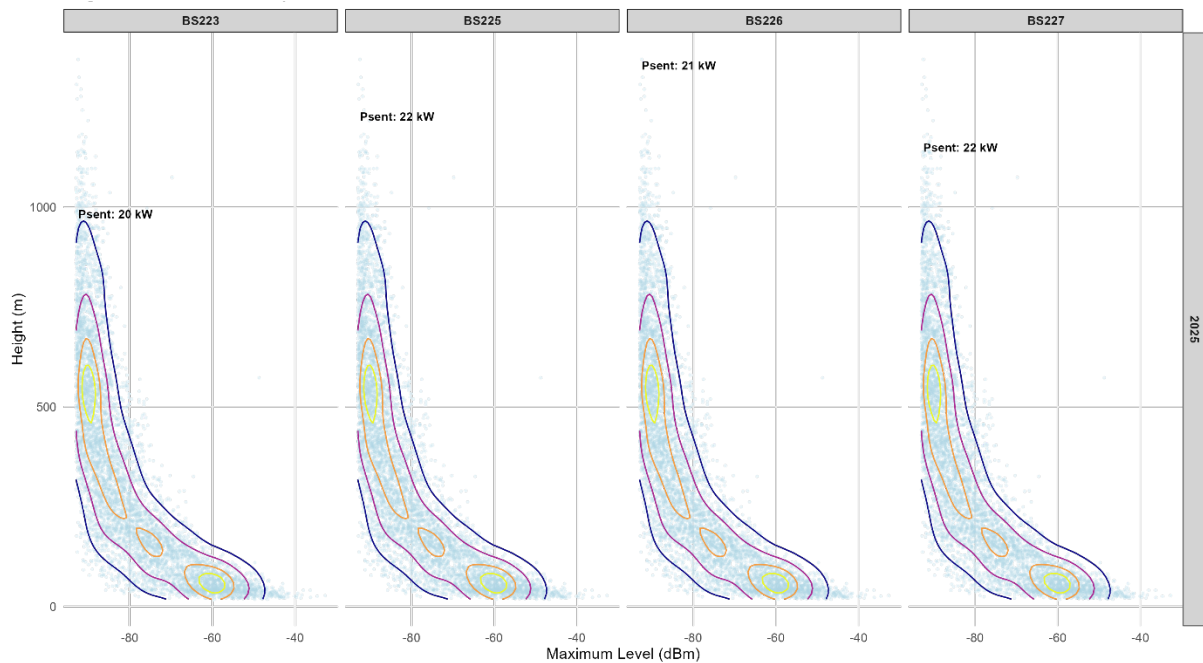


Supp. Fig. A2. Subsequent calibration with parallel measurements of the four BirdScan MR1 radars used in the study, in Sempach, Switzerland, May 2025.

Inspection of the collected data revealed important malfunction of the radar deployed at Vransko Lake (radar-ID: BS223). During this calibration campaign, BS223 had a defect receiver and hardly detected any echo. We do not discuss any further these data from BS223 in May 2025.

BS227 (deployed in Zadar in 2023) showed reduced detection range and maximum echo intensity (Supp. Fig. A3): i) 500 m lower detection range of BS227 compared to BS225 and BS226, ii) and lower echo intensity detected at a given height (e.g. 0.95 quantiles at 500 m agl: -84.4 dBm for BS227, -81.4 dBm for BS225, -80.4 for BS226, Supp. Tab. A1). We are still in the process to elucidate the technical cause of the lower sensitivity of BS227 as compared to BS225 and BS226 observed in May 2025. In spring 2023, the radar BS227 showed similar levels of echo intensity and detection range as BS225 and BS226 (Supp. Fig. A1, Supp. Tab. A1). We therefore consider that the data collected at Zadar with radar BS227 as reported in the publication is reliable.

We unfortunately cannot compare the performance of BS223 in May 2025 with that of spring 2023. Nevertheless, investigating the relationship between the maximum echo level (in dBm) and the detection height allowed to detect performance loss. While the 3-4 dBm sensitivity loss of BS227 in May 2025 still need to be fully elucidated, the even stronger (ca. 7 dBm) sensitivity loss of BS223 in spring 2023 are strong indication of the so far undetected malfunction. We conclude that the data collected at Vransko Lake (BS223) were erroneous, requiring their retraction from the publication.



Supp. Fig. A3. Detection range (m above ground level) and intensity (dBm) of detected echoes (class: passerine- and wader-type) in Sempach in May 2025. Isolines represent the 0.25 (dark blue line), 0.50 (violet line), 0.75 (orange line), 0.90 (yellow line) density quantiles.

Acknowledgements

We thank Thomas Steuri (formerly at the Swiss Ornithological Institute), Fabian Hertner, and Dominik Kleger (Swiss Birdradar Solution AG) for their support in the evaluation of the calibration campaign.

Authors' contributions

List of the authors' contribution, following the CRediT framework (<https://credit.niso.org>): SH: formal analysis, validation, visualisation, writing - review and editing. BS: conceptualisation, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, supervision, validation, visualisation, writing - original draft, writing - review and editing. BH: funding acquisition, project administration, resources, supervision, validation, writing - review and editing. RW, PR, DC, SB, VT, LT, MBL: writing - review and editing.

Funding

The research underlying the project was financed by internal funding sources.

Competing Interests

The authors declare no competing interests.

Appendix B: Supporting Information for the article “Avian spring migration at the East Adriatic coast: coastal and sea-crossing dynamics of intensity, timing, and flight directions.”

Note: the supporting information for Chapter 2 has been updated in line with the erratum, for example Vransko Lake has been removed and the clustering has been updated.

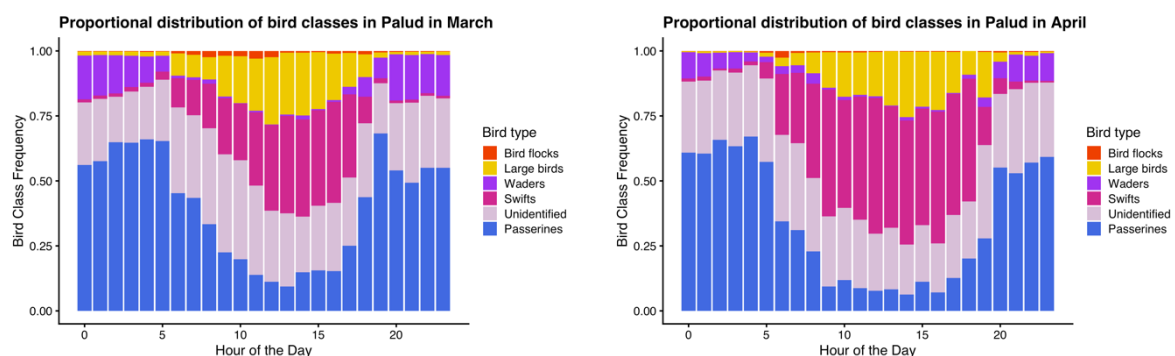
Overview

Here the reader will find additional information on, firstly, the occurrence of bird radar echo types across sites, months and times of day; secondly, the phenology of migration across the season by bird radar echo type; thirdly, additional information on the distribution of migration intensity profile types across the season.

Methods

Bird types over the day

The radar software roughly classifies bird echoes based on wing flapping pattern and radar cross section. Classes roughly translate into taxonomic groups, e.g., passerine-type, wader-type, swift-type, large birds, bird flocks, and unidentified birds that do not match the criteria for any other group or where the uncertainty of classification is too large. The proportion of birds of any of these classes varies greatly over the course of the day and night (Supp. Fig. B1). While the proportion of unidentified birds remains relatively constant over the course of the day, large birds and swifts predominantly occurred during daylight. During the night, passerine- and wader-type birds prevail. In this study, we focused on small- to medium-sized, constant- (wader-type) and intermittent-flapping (passerine-type) birds.

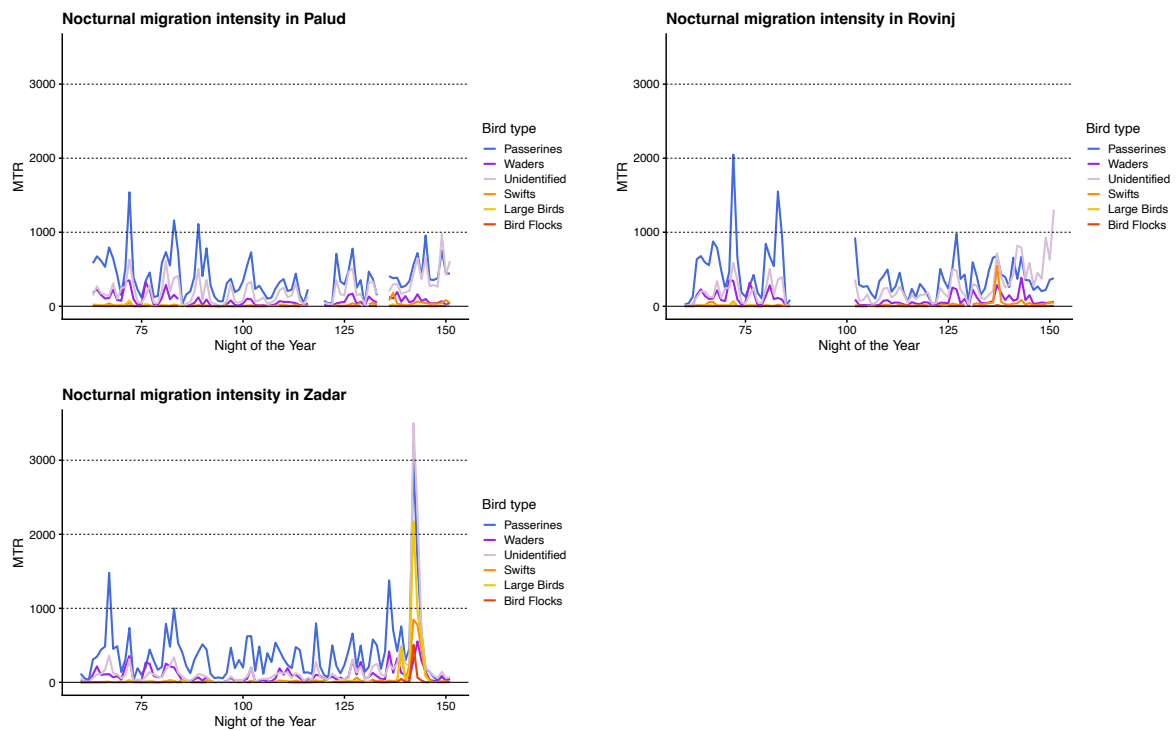




Supp. Fig. B1. Proportion of bird echo classes over the course of the day and night by site and month.

Bird types during the night across the season

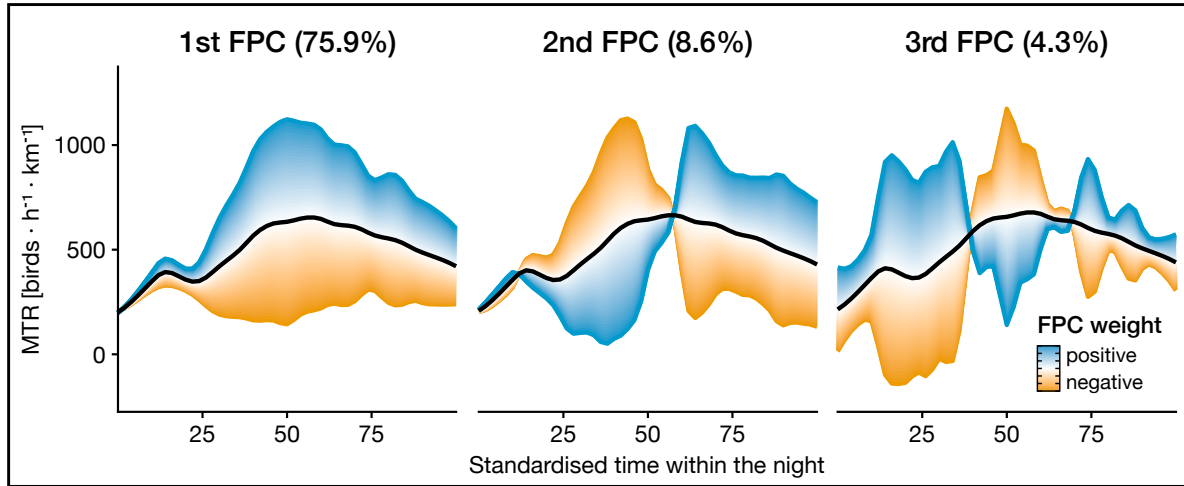
Here, we show the activity of different bird types across the whole season. In the main article, we focus on passerine- and wader-type birds only, but do not further differentiate between the two types when analysing migration intensity and flight directions. Despite the likely different migration strategies, peak migration nights of all recorded bird types largely overlap (Supp. Fig. B2).



Supp. Fig. B2. Nocturnal migration intensity of the full spring season 2023 across the three radar sites. Individual curves display the estimated number of birds for different classes, as classified by the radar software.

FPCA and clustering: the third FPC

Here we show migration intensity profiles as a linear function of the estimated mean function $\mu(t)$ and one of either first, second, or third FPC with varying eigenvalues, from negative to positive (Supp. Fig. B3).



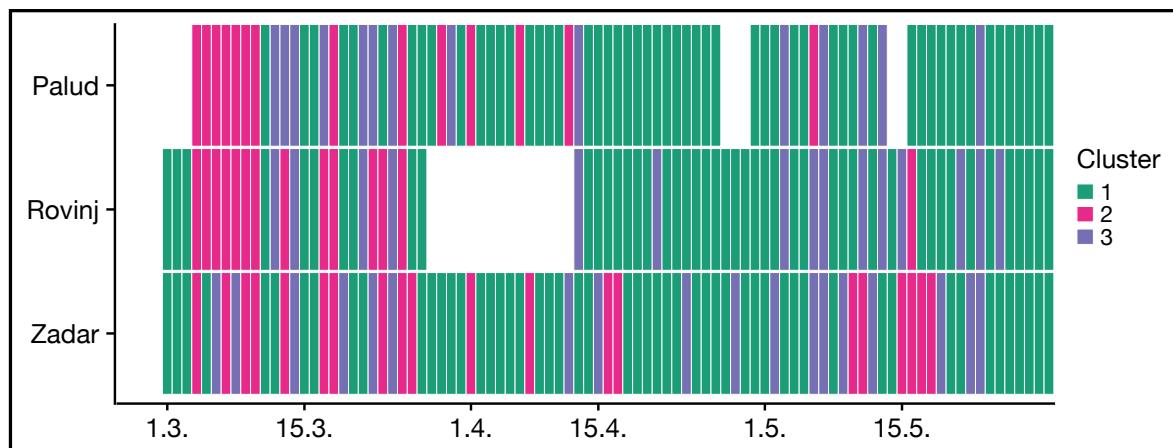
Supp. Fig. B3. Simulated migration intensity profiles as linear combination of mean function $\mu(t)$ plus first (left), second (middle), and third (right) FPC $\phi(t)$ with varying (from negative, orange, to positive, blue) eigenvalues ξ . The duration of nights has been standardised.

We excluded explaining the third FPC in detail in the main manuscript because it only accounted for less than 5 % of the total variability in within-night timing of migration intensities. We have nevertheless used it in the classification algorithm because it takes into account in particular the occurrence of two peaks within single nights (Supp. Fig. B4), probably related to coastal migration at the beginning of the night and sea crossing later on, while both groups were similar in strength.

Results

Distribution of migration intensity profile types across the season

We observed radar nights assigned to each cluster in every month (Supp. Fig. B4). Most radar nights were assigned to the low intensity Cluster 1.

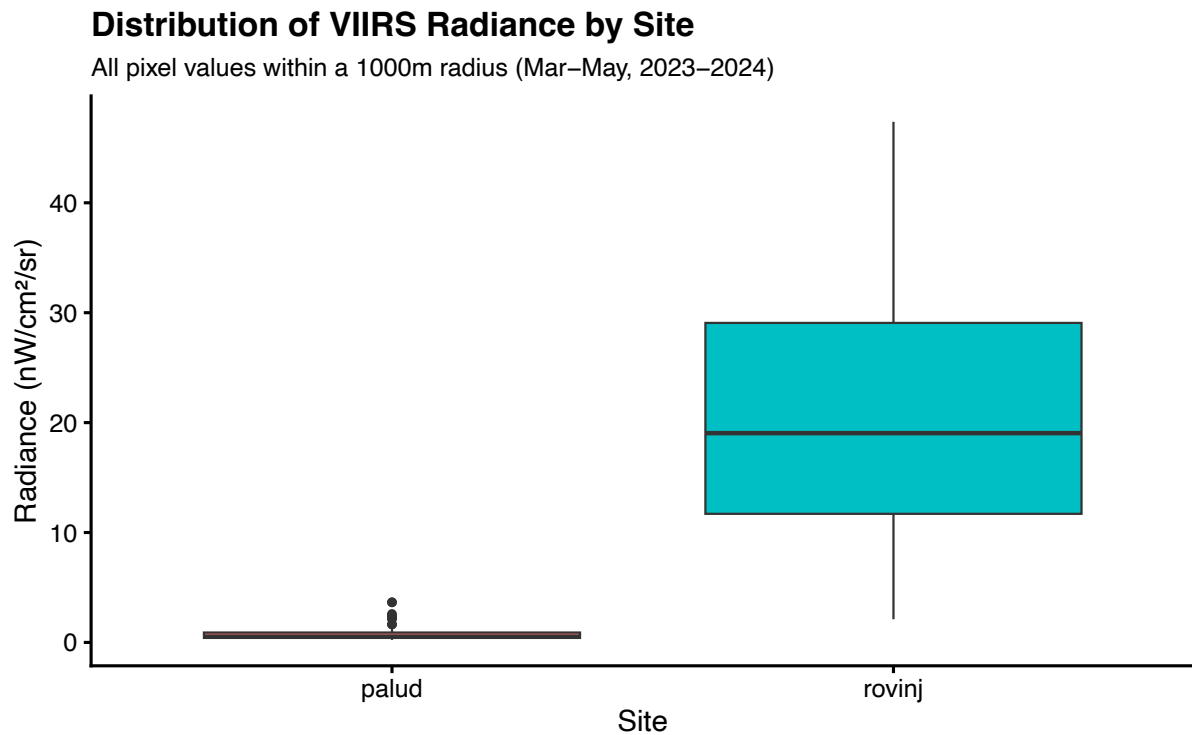


Supp. Fig. B4. Per site typification of nightly migration intensity profiles of the spring migration season 2023. Cluster 1: low intensity; Cluster 2: high intensity with early peak; Cluster 3: high intensity with late peak.

Appendix C: Supporting Information for the article “When nocturnally migrating birds encounter low-level patchy light pollution: a case study from the Croatian coast”

Methods

Here we show the upward radiance within a 1000 metre neighbourhood around the two radar sites.

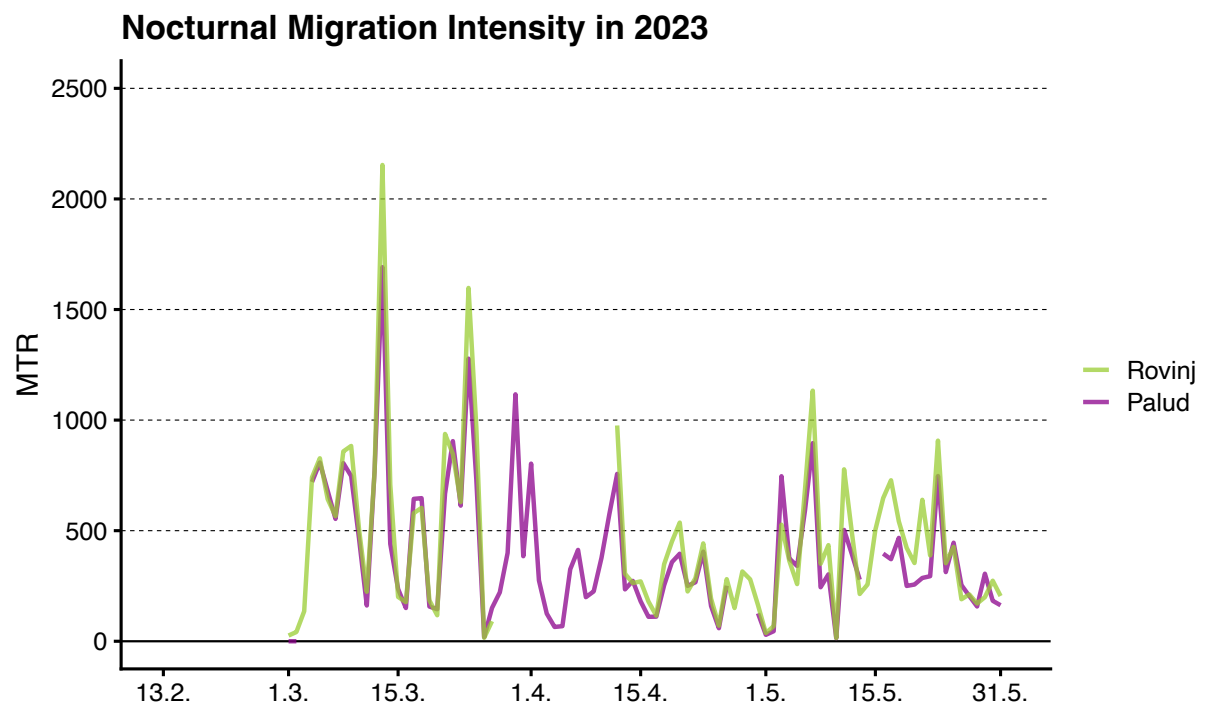


Supp. Fig. C1. Upward radiance, quantified within a 1000-metre neighbourhood around each of the two radar sites using the March to May 2023 and 2024 data sets from the VIIRS DNB.

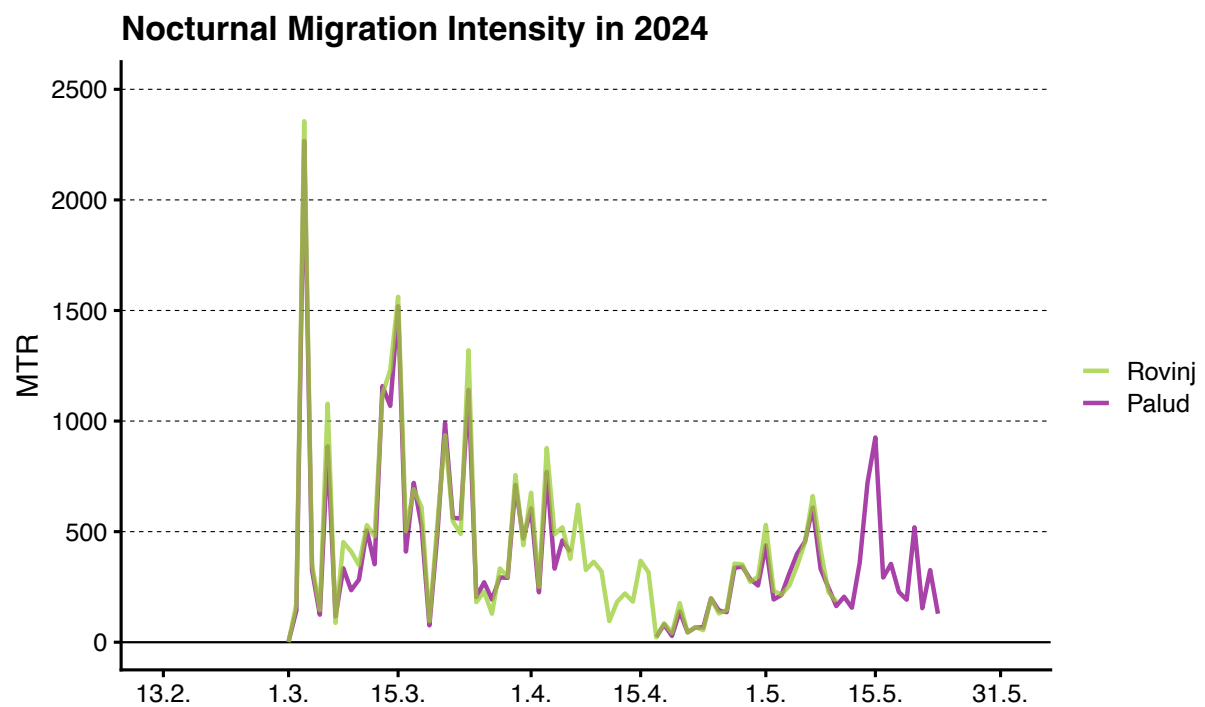
Results

Migration phenology

Here we show the measured migration intensity (MTR) in the spring of 2023 and 2024.



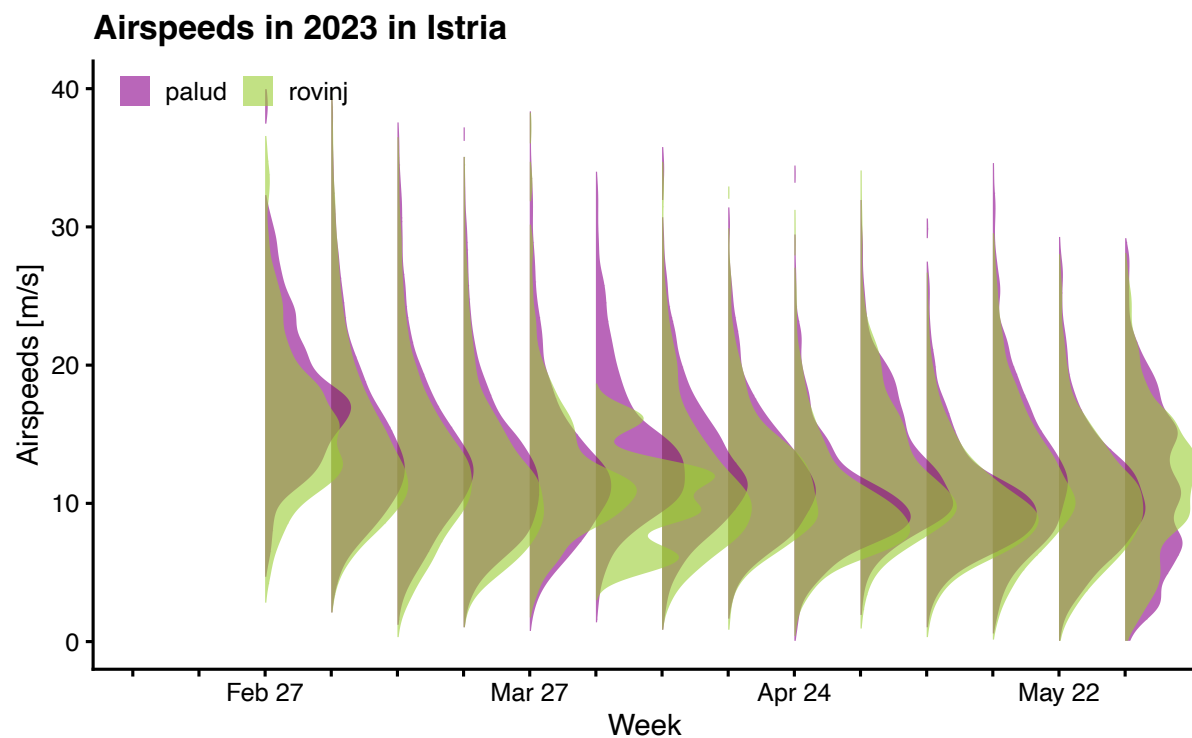
Supp. Fig. C2. Spring migration intensity in 2023.



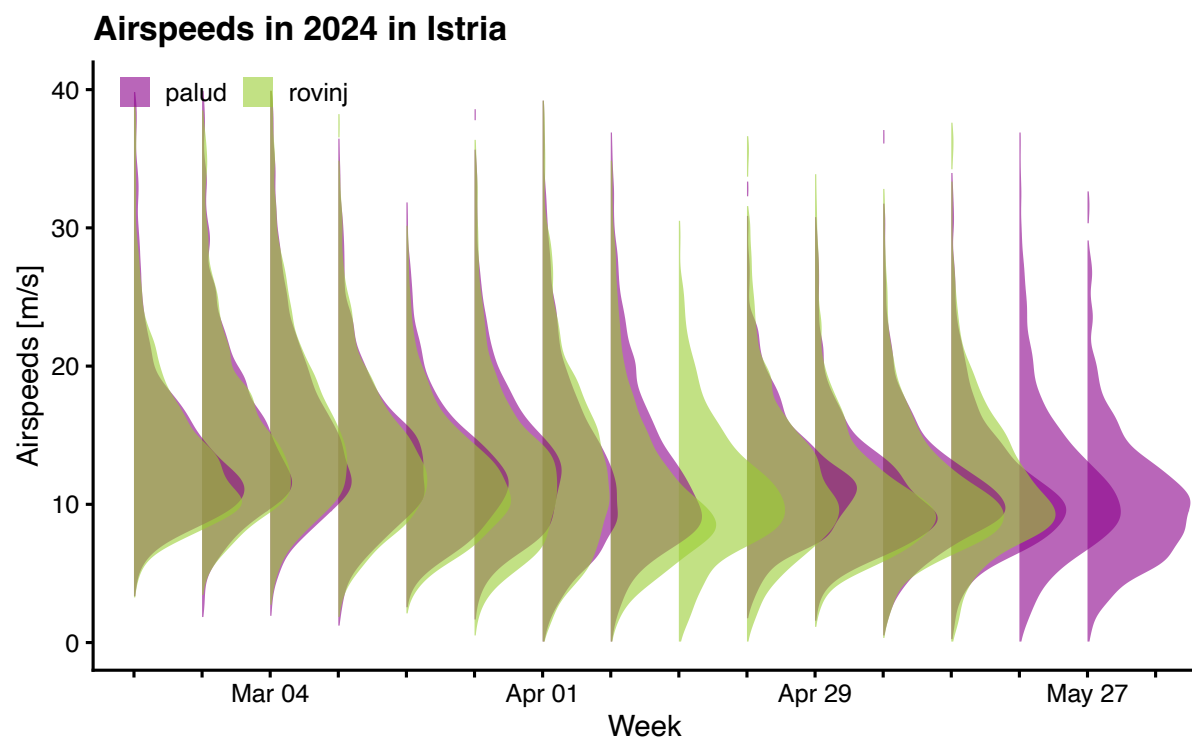
Supp. Fig. C3. Spring migration intensity in 2024.

Airspeeds

Following are the airspeeds that we have measured at the coast of Croatia.



Supp. Fig. C4. Airspeeds calculated from recorded ground u- and v-movement and u- and v-wind vectors in 2023.

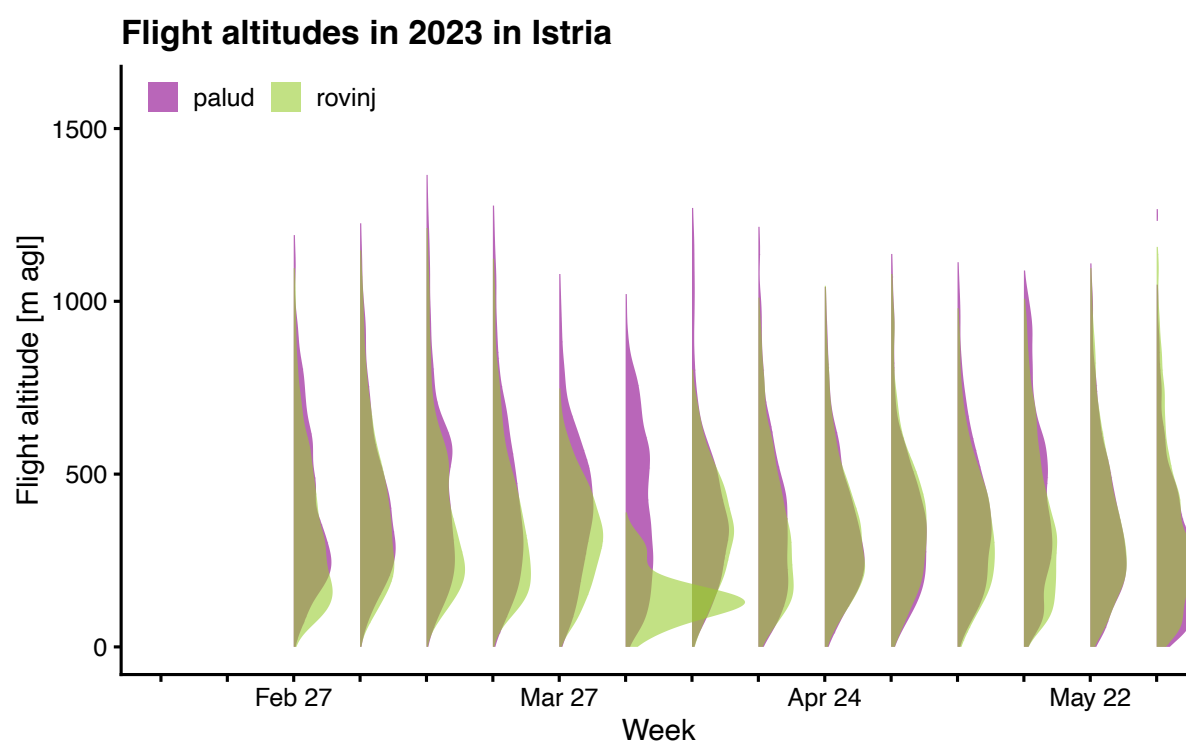


Supp. Fig. C5. Airspeeds calculated from recorded ground u- and v-movement and u- and v-wind vectors in 2024.

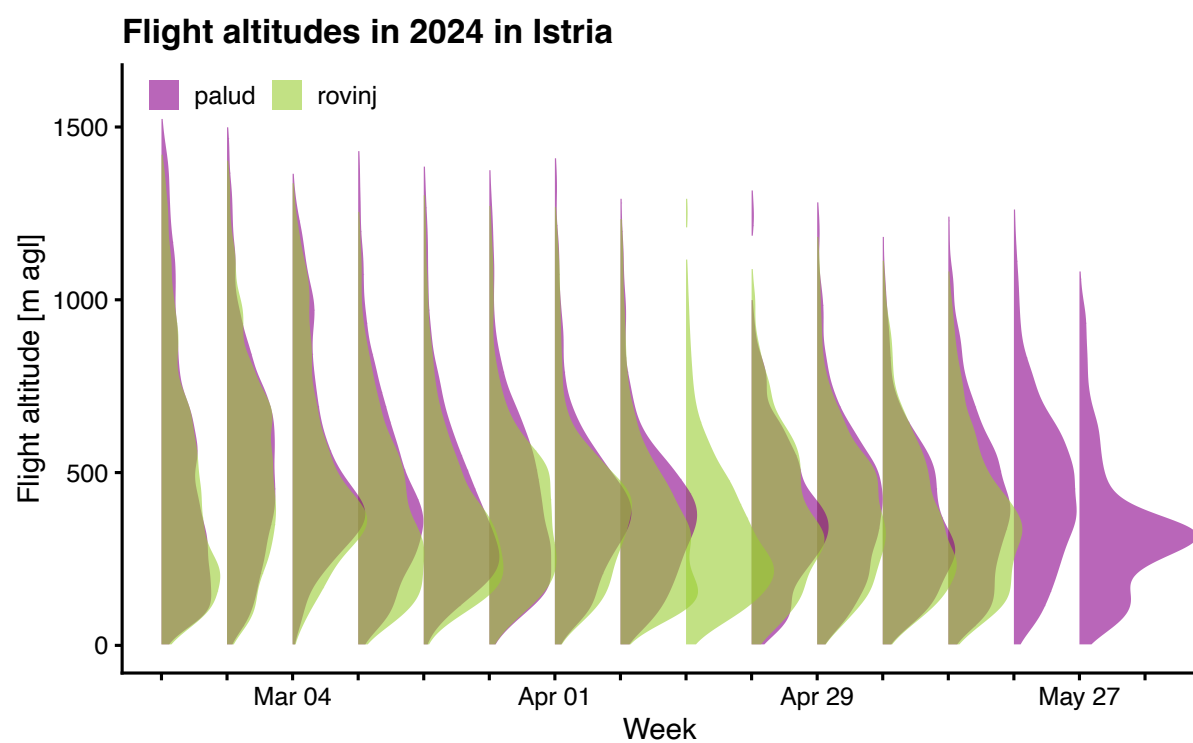
Flight altitudes

These are the recorded flight altitudes above ground level that we have measured at the coast of Croatia.

Note: The radar in Rovinj only operated for one night during the first week of April 2023, while Palud recorded data throughout the entire week (Supp. Fig. C6). This one night was likely a night when flight altitudes were very low, which affected the distribution shown here (see Supp. Fig. C2).



Supp. Fig. C6. Flight altitudes in metres above ground level recorded in 2023.



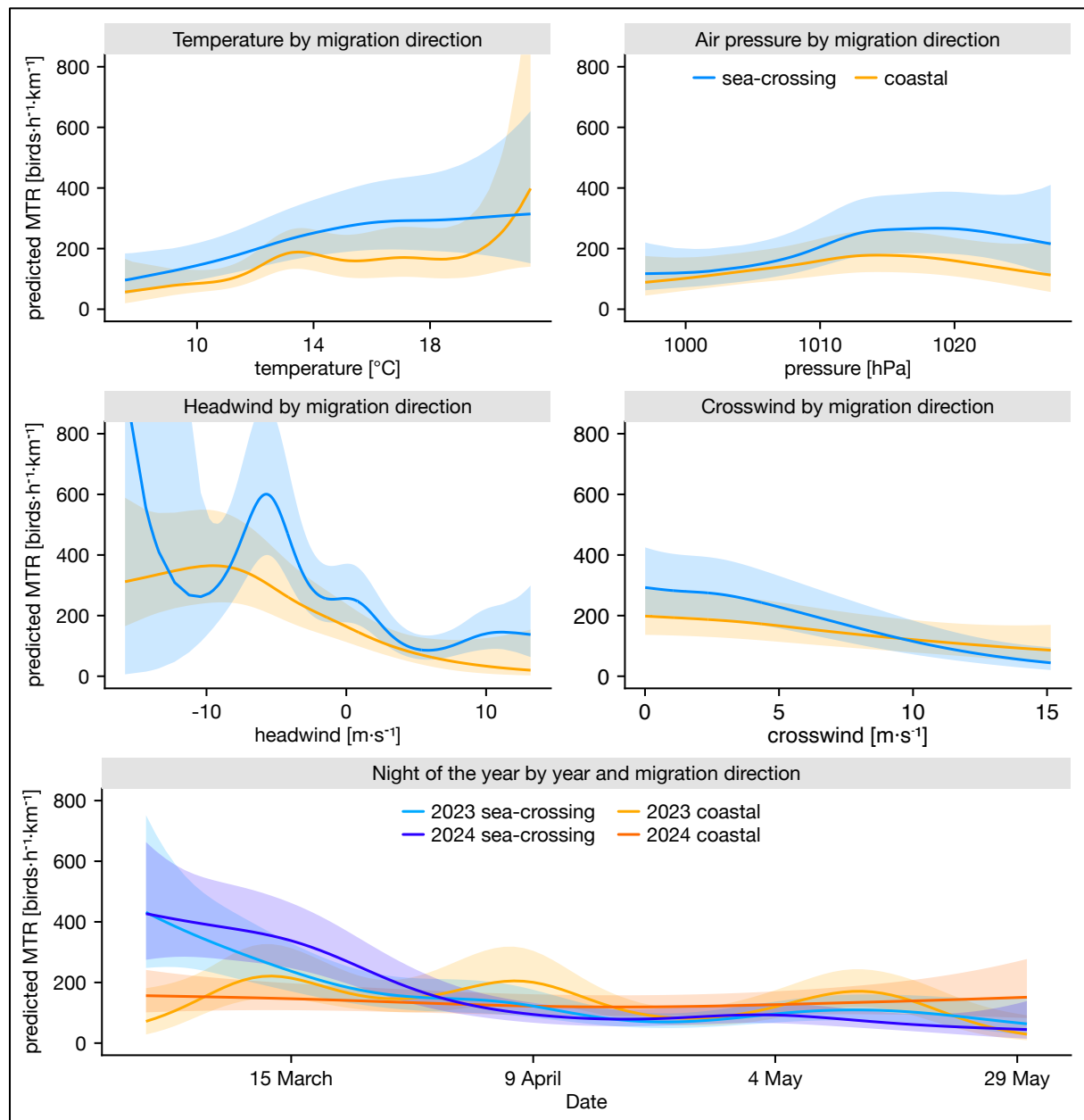
Supp. Fig. C7. Flight altitudes in metres above ground level recorded in 2024.

Atmospheric and seasonal effects on migration intensity

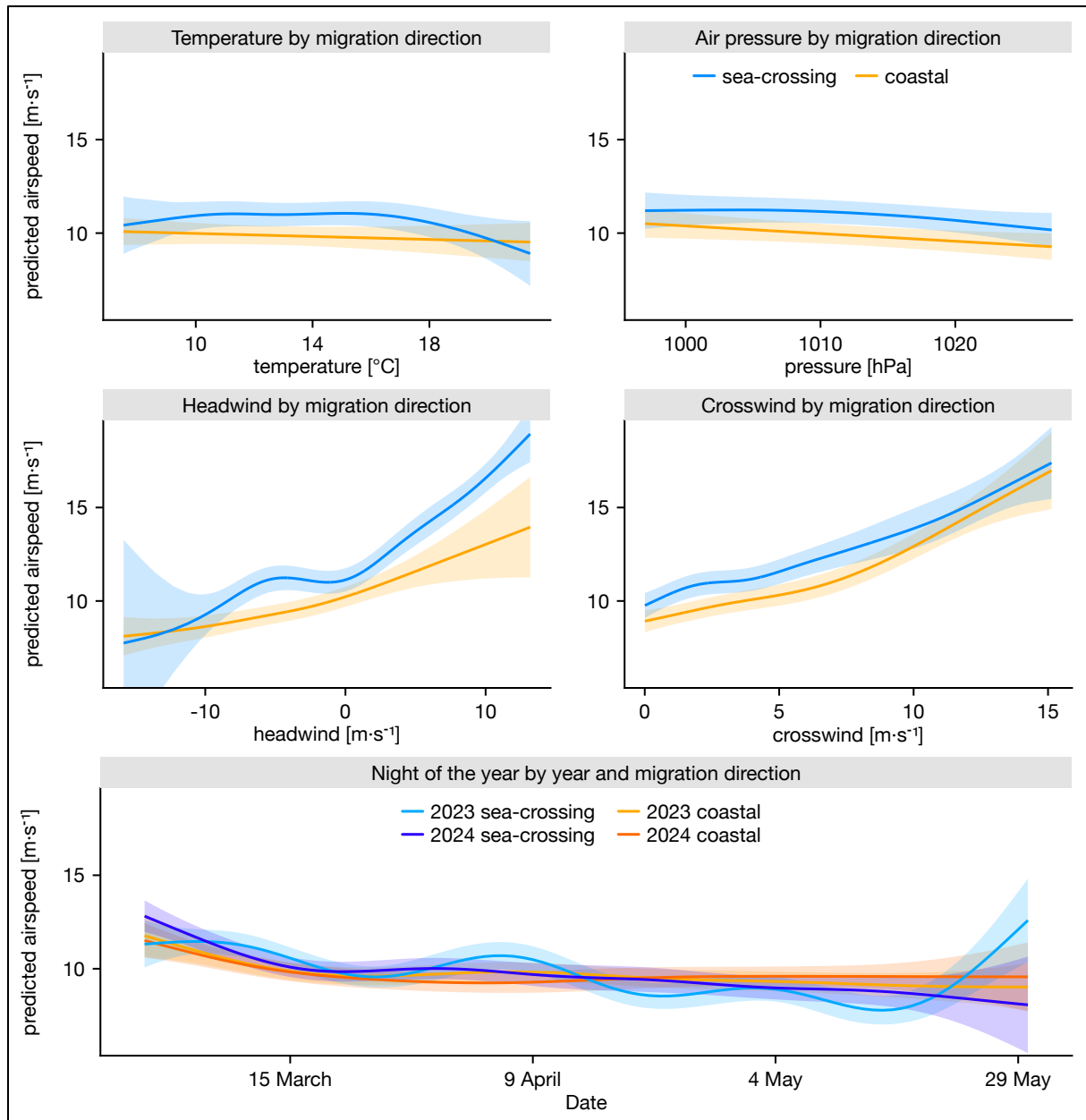
From downloaded u- and v-wind components, we calculated head- and crosswind for the mean nightly flight direction for sea-crossing and coastal migration.

To account for atmospheric and seasonal effects in the modelling of a light pollution induced reaction of migratory birds, we included two-metre above ground level temperature, air pressure at sea level, headwind, crosswind, and night of the year in the generalised additive models that aimed to explain variability in migration intensity, airspeed, and flight altitude.

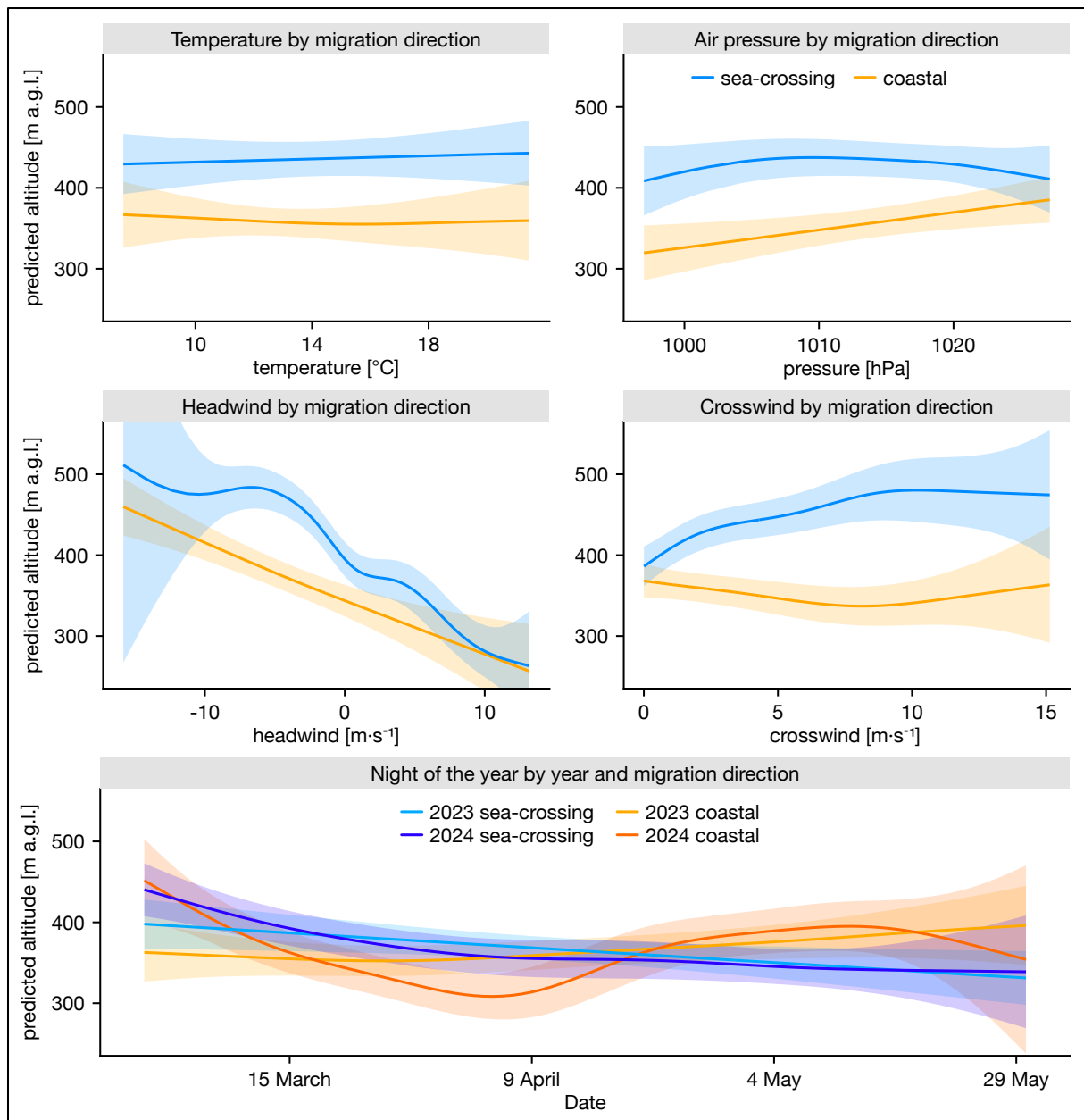
Here, we present the marginal effects of each of these atmospheric and seasonal predictors on migration intensity during the spring migration seasons in 2023 and 2024.



Supp. Fig. C8. Marginal effects of atmospheric and seasonal predictors on migration intensity.



Supp. Fig. C9. Marginal effects of atmospheric and seasonal predictors on mean airspeed.

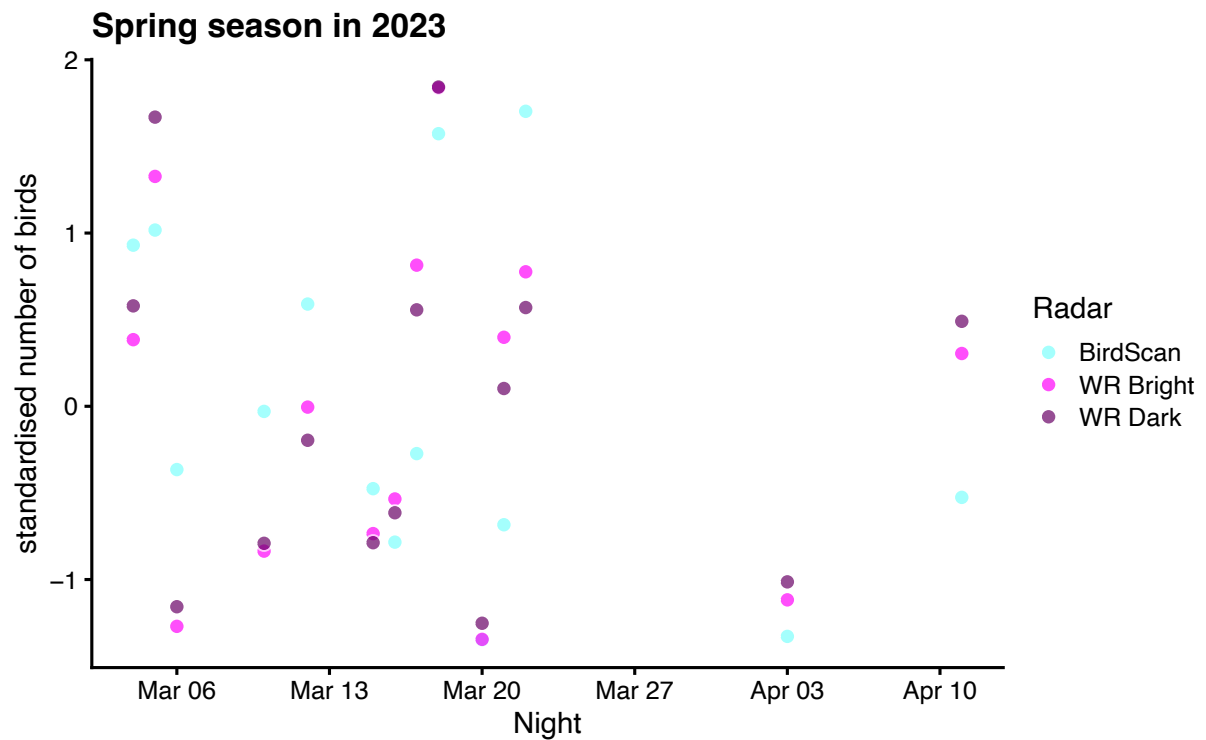


Supp. Fig. C10. Marginal effects of atmospheric and seasonal predictors on mean flight altitude.

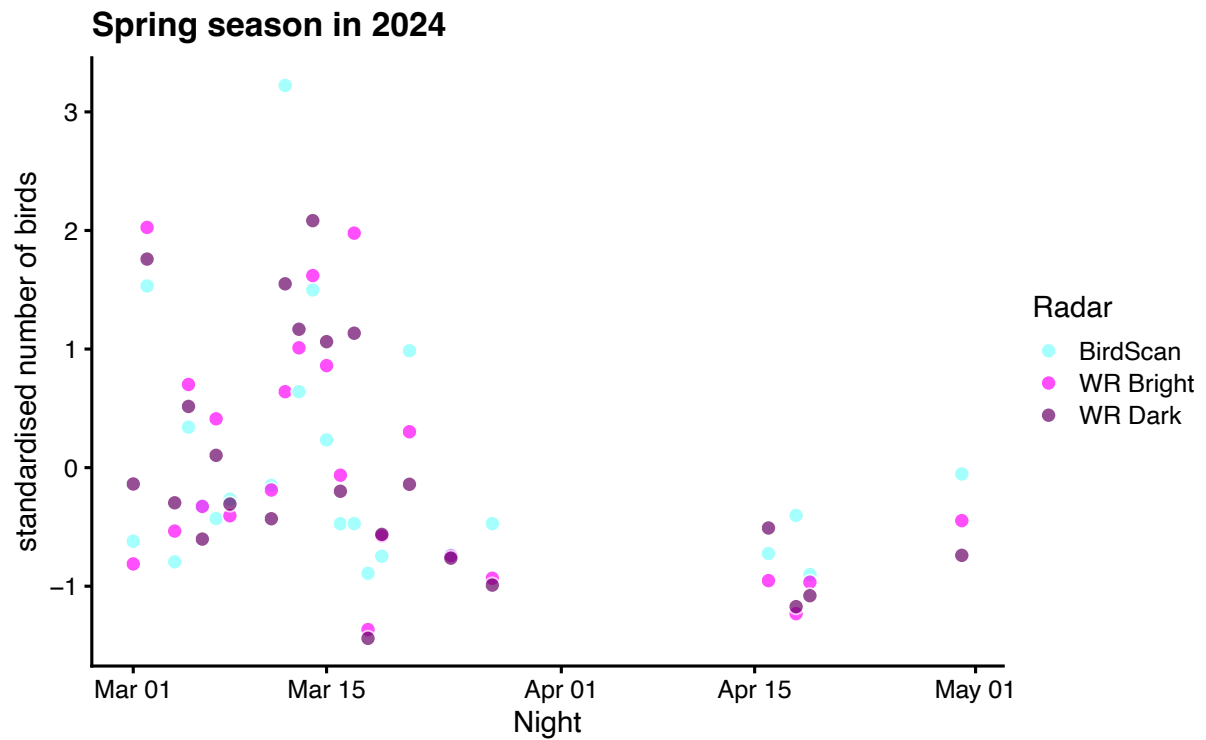
Appendix D: Supporting Information for the article “Redistribution of sea-crossing bird migration in response to coastal artificial illumination”

Methods

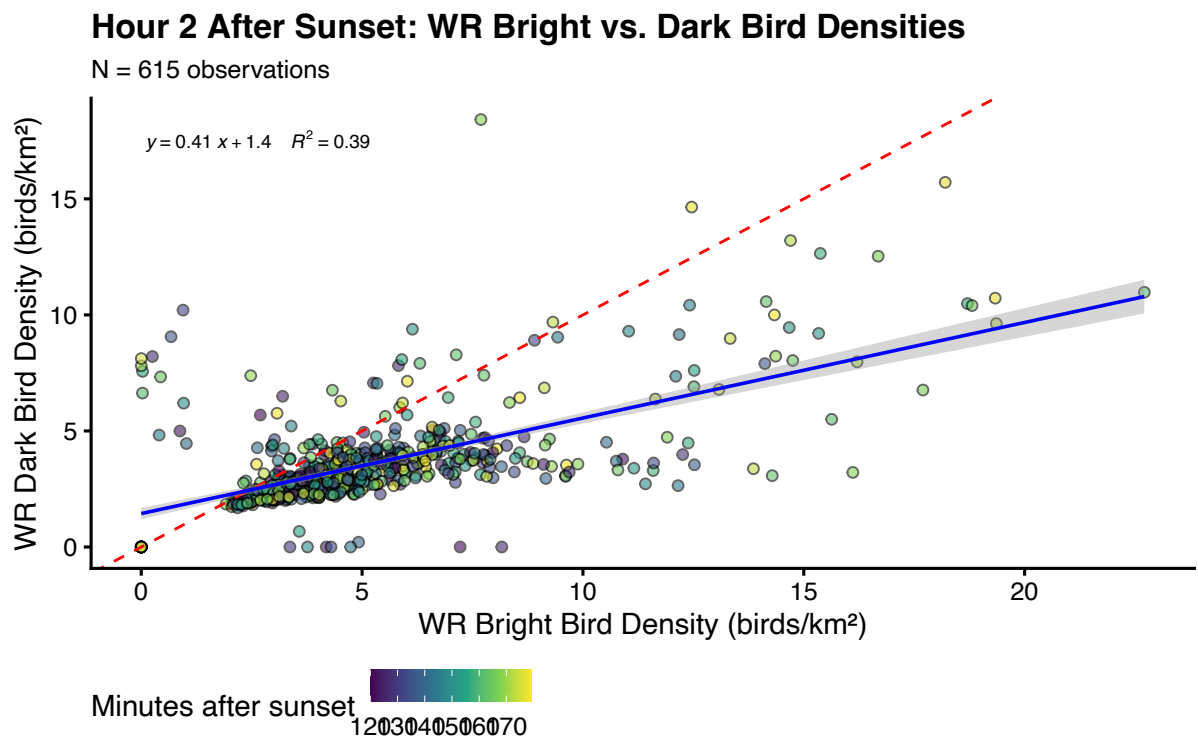
Here we show the standardised number of birds for each sampling night within the two spring migration seasons 2023 and 2024.



Supp. Fig. D1. Comparison of bird numbers between BirdScan and the two sampling areas of the Debeljak WR over the spring migration season 2023. Values have been standardized across the season to ensure comparability between radar systems.



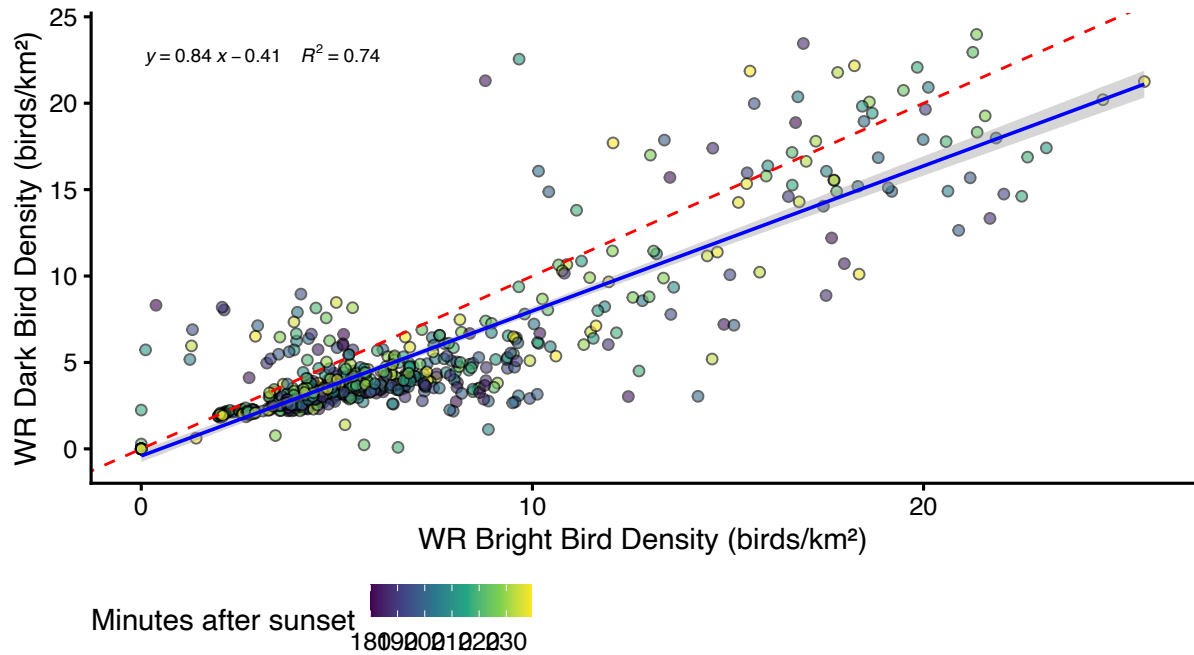
Supp. Fig. D2. Comparison of bird numbers between BirdScan and the two sampling areas of the Debeljak WR over the spring migration season 2024. Values have been standardized across the season to ensure comparability between radar systems.



Supp. Fig. D3. Correlation of measured bird densities between bright and dark sampling areas of the Debeljak WR for the second hour after sunset.

Hour 3 After Sunset: WR Bright vs. Dark Bird Densities

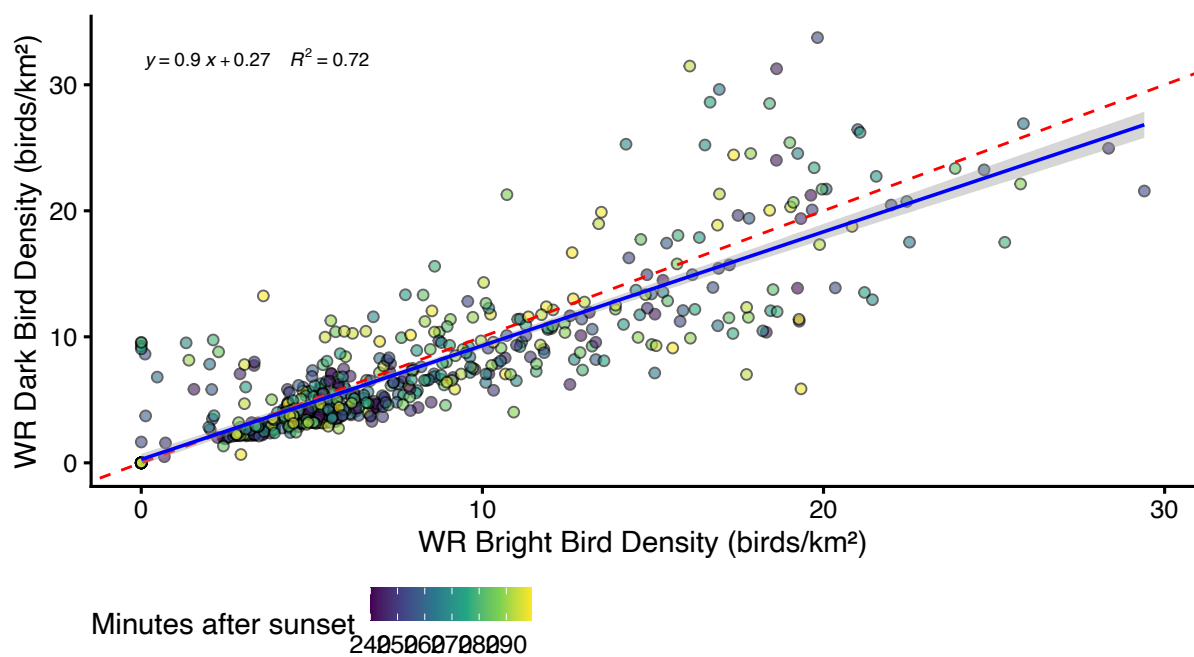
N = 589 observations



Supp. Fig. D4. Correlation of measured bird densities between bright and dark sampling areas of the Debeljak WR for the third hour after sunset.

Hour 4 After Sunset: WR Bright vs. Dark Bird Densities

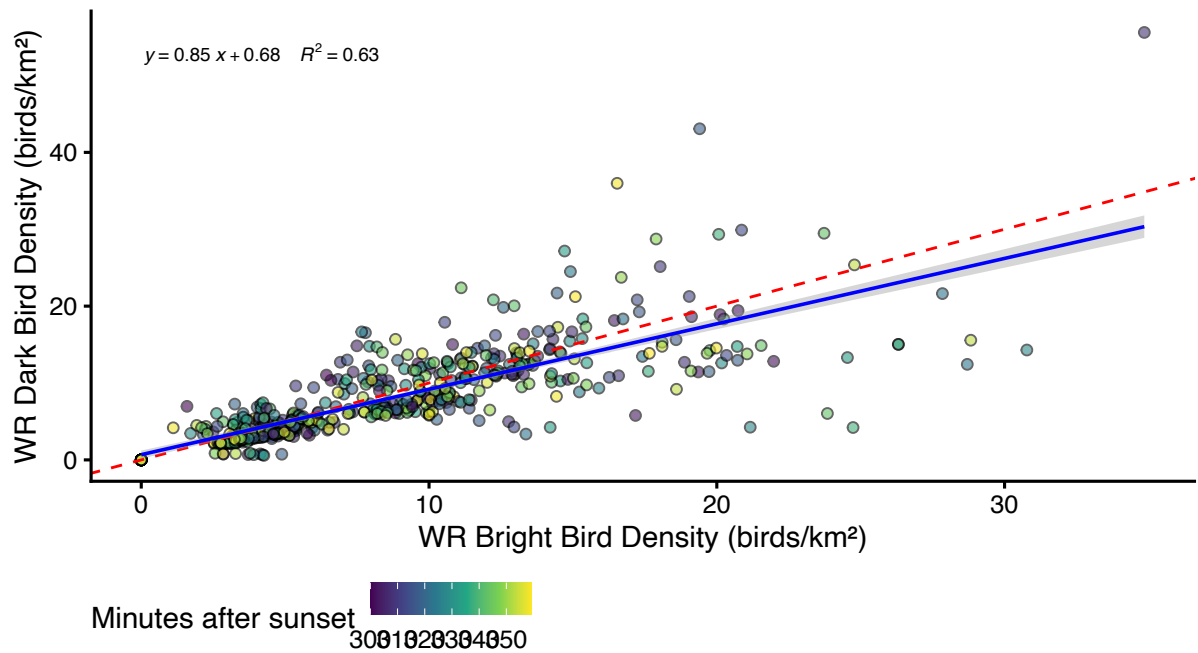
N = 571 observations



Supp. Fig. D5. Correlation of measured bird densities between bright and dark sampling areas of the Debeljak WR for the fourth hour after sunset.

Hour 5 After Sunset: WR Bright vs. Dark Bird Densities

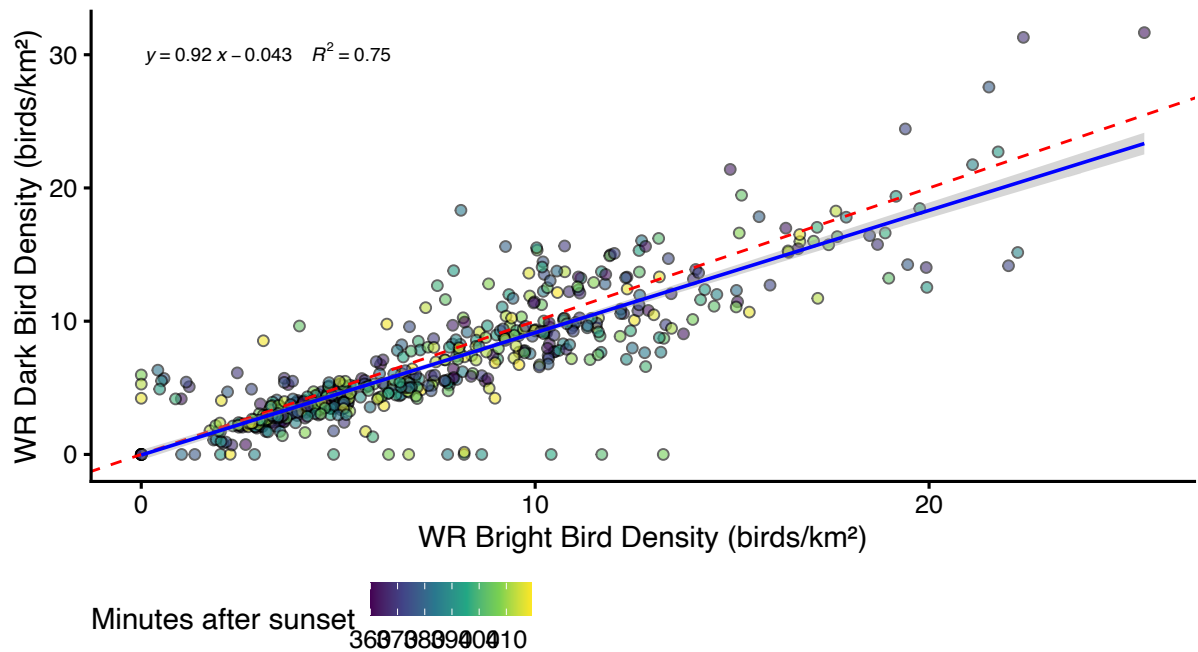
N = 581 observations



Supp. Fig. D6. Correlation of measured bird densities between bright and dark sampling areas of the Debeljak WR for the fifth hour after sunset.

Hour 6 After Sunset: WR Bright vs. Dark Bird Densities

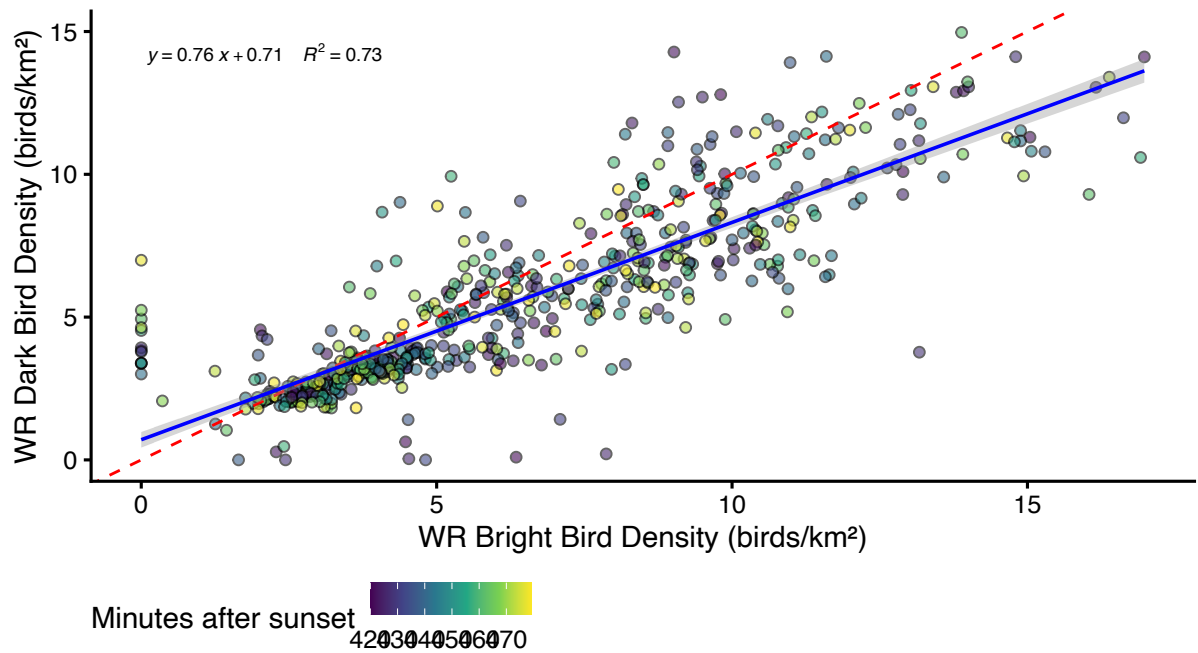
N = 568 observations



Supp. Fig. D7. Correlation of measured bird densities between bright and dark sampling areas of the Debeljak WR for the sixth hour after sunset.

Hour 7 After Sunset: WR Bright vs. Dark Bird Densities

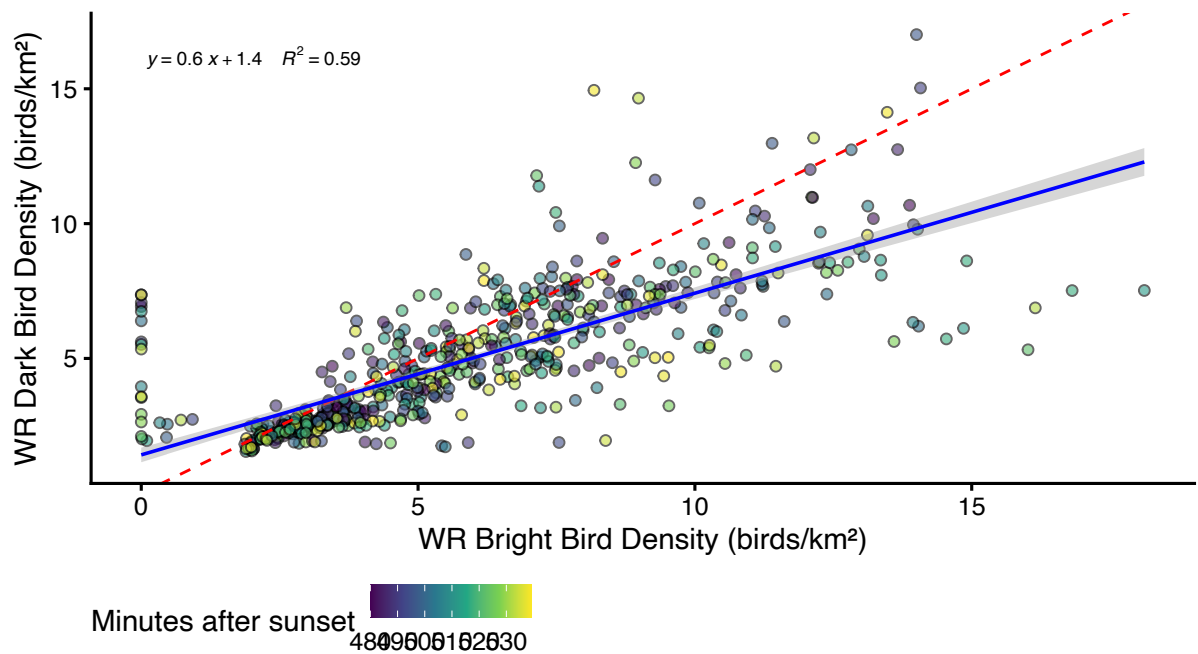
N = 597 observations



Supp. Fig. D8. Correlation of measured bird densities between bright and dark sampling areas of the Debeljak WR for the seventh hour after sunset.

Hour 8 After Sunset: WR Bright vs. Dark Bird Densities

N = 601 observations



Supp. Fig. D9. Correlation of measured bird densities between bright and dark sampling areas of the Debeljak WR for the eighth hour after sunset.

Declaration of the usage of AI

I hereby declare that the submitted thesis is the result of my own independent work. All external sources are explicitly acknowledged in the thesis.

I used AI tools, namely ChatGPT ⁵ and DeepL Write ⁶, for English proofreading and sentence refinement.

Zürich, 19. Dezember 2025



Simon Hirsachhofer

⁵ OpenAI (2025). ChatGPT (GPT-5.1) [large language model].

⁶ DeepL (2025). DeepL Write [writing assistant software]. <https://deepl.com>