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Geographic barriers and season shape the nightly timing of avian migration

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Abstract

Aim: Millions of birds take to the air for nocturnal migrations. Although it is widely recognized that migrants generally depart after sunset, nightly migration timing and their dependence on geographic features are hardly known at a continental scale, yet highly important for the mitigation of human-wildlife conflicts. Using weather radars, we investigate barrier and seasonal effects on the timing of nocturnal bird migration.

Location: North western Europe: United Kingdom, Germany, Belgium, the Netherlands, France, Sweden and Finland.

Time Period: 2014–2020.

Major Taxa Studied: Aves, nocturnal migrants, predominantly passerines.

Methods: We use nocturnal bird migration distributions extracted from 55 weather radars. The variation between these temporal distributions is captured using a principal component analysis, barrier effects and seasonal differences are investigated with a general linear model.

Results: Most variation in nightly migration timing can be explained by a univariate axis that distinguished a more evenly spread migration from a skewed migration. We found migration to be more evenly spread in spring and to have a clear peak early in the night in fall. Furthermore, migration is more peaked early in the night on locations close to or just upstream of major geographic barriers.

Conclusions: Our study shows that migration fluxes tend to be more skewed during the night along coastlines and more uniform inland, far from water barriers. Regional and seasonal differences in nocturnal timing can provide vital information for adjusting the timing of wind park curtailment, lights-out initiatives or other conflicts between migratory birds and human activities.

KEYWORDS

aeroecology, diel timing, East Atlantic flyway, geographic barriers, macrosystems, migration phenology, nocturnal bird migration, weather radar

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1 | INTRODUCTION

Cumulatively, billions of birds migrate across continents during the night (Dokter et al., 2018; Nussbaumer et al., 2021). These migratory fluxes have a complex phenology that combines seasonal and diel trends. Seasonal trends are generally driven by the birds' annual cycle (Gwinner & Helm, 2003), modulated by environmental conditions such as weather (e.g. Erni et al., 2002; Haest et al., 2020; Kranstauber et al., 2022) and resource availability as well as the internal state of migrants (Deppe et al., 2015).

Diel trends are suggested to be driven by a bird's circadian rhythm, with migration readiness expressed shortly after sunset (Van Doren et al., 2017). Diel trends can further be modulated by environmental conditions (Van Belle et al., 2007; Van Doren & Horton, 2018). Field studies on individual birds have shown that nearly all migrants depart after sunset and before midnight (Deppe et al., 2015; Goymann et al., 2010; Müller et al., 2016; Packmor et al., 2020; Zúñiga et al., 2016). Yet, there is great variation in exact departure, and migration times (Briedis et al., 2020). Variation in diel timing of departure has been linked to fuel load, cloud cover and tail wind assistance (Packmor et al., 2020). Another driving factor is likely the presence and vicinity of ecological barriers. Tracking studies of individual songbirds have shown that they can fly for extended periods of time when crossing geographical barriers such as stretches of mountain or seas, from hours up to several days (DeLuca et al., 2015; Deppe et al., 2015; Gómez et al., 2017) and in several species, flights may continue into the daytime (Jiguet et al., 2019). The duration of migratory flights is less frequently studied when barriers are absent. Only a few measurements exist from radio telemetry and activity loggers, and those studies suggest a high variation in flight time up to the full length of the night but generally ceasing at sunrise (Bowlín et al., 2005; Liechti et al., 2018; Sjöberg et al., 2021). Following nocturnal flights sometimes short morning flights are observed (Tuck et al., 2018; Van Doren et al., 2016).

Due to the unknown influence of geography and absence of comparative studies, it is unclear how these individual behaviours contribute to resulting fluxes of migratory activity throughout the night at a continental scale. Barriers for migratory land birds, such as mountain ranges, deserts or large water bodies, either need to be crossed or circumvented (Alerstam, 2001; Gagnon et al., 2022). When confronted with a barrier that must be crossed, birds can choose to either cross in the remainder of the night or cease migration for the night. Birds arriving later in the night may choose a risk-averse strategy, i.e. ceasing migration earlier as they would not be able to cross within the remainder of the night (Bruderer & Liechti, 1998). Consequently, birds will accumulate near the barrier and resume migration in a synchronized departure wave at the beginning of the next suitable migration night. Similarly, if birds stop shortly after crossing a barrier to replenish energy stores, migrants will accumulate just after the barrier resulting in a synchronized departure after the following sunset. If birds have the ability to stop within a barrier (e.g. Schmaljohann et al., 2007), these predictions change. It is unclear what the dominant processes and resulting diel

timings are around barriers and whether spatial variation in the distribution of migrants throughout the night are observed at a continental scale.

Understanding when within a night and for how long per night birds migrate is not only crucial for understanding the ecology of migrants but is also fundamental for the setup of efficient management and mitigation measures in human-wildlife conflicts, e.g. flight safety (Van Gasteren et al., 2019), light pollution (Horton et al., 2019) and wind turbine collisions (Thaxter et al., 2017). The abundance of many bird populations, especially of those with a migratory lifestyle has significantly decreased over the last decades (Rosenberg et al., 2019). A multitude of direct and indirect factors, such as predation by pets, collisions with buildings and habitat degradation, contribute to this decline (Buchan et al., 2022). An increasing threat to migratory species is the use of wind power (Marques et al., 2014), resulting in mortality (Loss et al., 2013). Various measures are discussed to reduce collision risk for nocturnal migrants including wind energy curtailment during periods of intense migration. Yet, to maximize energy production and minimize economic loss but still safeguard the majority of aerial migrants, shutdowns should be as short as possible and adjusted to the nightly timing of migration. Thus mitigation measures would be most cost-effective when applied to the part of a night when most migrants are on the move. Similarly, campaigns promoting the reduction of light pollution for migrants and the associated consequences (Horton et al., 2019) could target periods when most migrants pass (Horton et al., 2021).

Here, we aim to investigate the nocturnal timing of avian migrants across Europe in relation to season and water barriers using data from 55 weather radars in Europe over the period 2014–2020. This macrosystem approach (Kelly & Horton, 2016) provides a basis for setting up regionally and seasonally optimized mitigation measures for reducing aerial conflicts.

2 | METHODS

To investigate which factors shape the nightly timing of migration, we first calculate an average distribution of the timing of migration within a night per radar location and season. We relate the variation between these distributions to season and the distance to and from barriers.

2.1 | Data

We used data from 55 weather radars across major parts of Europe from two data sources: data for the *United Kingdom*, *Germany*, *Belgium* and *the Netherlands* were derived from polar volume data obtained directly from the respective national meteorological services (Met Office, dwd, kmi and knmi), and for data from *France*, *Sweden* and *Finland* we relied on the enram data archive (<https://aloftdata.eu/>). Most data originated from C-band radars, with the exception of three French S-band radars. To ensure the different

radar types do not influence results, we repeated the analysis omitting S-band radars (Supporting information A). Data comprise the years 2014–2020 (tabulation across seasons and years Supporting information B), and we selected data for the months *February, March* and *April* for spring while in fall we use data from *September, October* and *November*. For all data, we calculated vertical profiles using *vol2bird* (Dokter et al., 2019). As the *vol2bird* algorithm sometimes filters intense migration when directional alignment among migrants is high (i.e. radial velocity standard deviation drops below the threshold of 2 m/s), we retained density estimates from small regions (10 or less adjacent bins in the vertical profile time series) where this filtering occurs. This criterion was decided on after visual inspection.

As intense migration events that are well characterized on weather radar only occur on few nights in the migratory seasons, we aimed for a representative selection of these migratory nights for each radar in each season and proceeded as follows: First, we selected the data between civil dusk and dawn for each night. The sampling interval of radars was either 5 or 15 min. To ensure we have a sample of representative measurements for each migration night, nights where more than 20% of the expected observations were missing were omitted from the analyses. Data were vertically integrated to migration traffic rate (count/h/km), temporal gaps were interpolated using a nearest neighbour approach (1.7% of the expected observations used in our final analysis were missing). The traffic rate is thus determined by both the number of birds aloft and the speed of their movements (a combination of wind and air speed). We included nights during which at least 5000 birds passed (migration traffic rate integrated over the night) and nights that were among the top 5 ranked by the number of passing birds per season, radar and year. This ensures all radars and season are represented and no nights with intense migration nights are omitted. While *vol2bird* distinguishes between birds and precipitation, on rare occasions, rain can still contaminate migration estimates. Therefore all night's meeting any of the initial criteria were visually inspected using plots of the vertically integrated density and migration rate over time. We also visualized the estimated ground speeds and altitudinal distribution of migrants over the night. This inspection was blind with respect to radar, date and season. Of the 4104 radar nights that met the initial criteria, 3051 nights were retained. As our primary aim was to

describe the distribution over the night rather than the overall number of migrants, the density of migrants was not a selection criterion at this screening stage. We omitted radar-season combinations that yielded less than five nights after inspection with at least two nights in two different years. This resulted in 55 different radars with on average 31.8 nights selected for each radar-season combination.

2.2 | Analysis

We standardized night length (between civil dusk and dawn) to remove the effect of variation in migration timing that is solely due to variation in sunrise and sunset times. For each combination of radar and season, we estimated a density distribution of nightly passage times. To ensure our analysis is stratified for nights (i.e. all night contributes equally) and no single night with high migrant abundance can drive the distribution patterns, we standardized the number of migrants between nights by repeatedly sampling (one thousand replicates) a time and migration direction (to later calculate the average direction of migration and distance to a barrier) from the observations for each night and pooled these per radar and season. Using these samples combined per radar season, Gaussian kernels were used to create a single distribution of passing migrants over the night (Figure 1). Metrics calculated from these distributions are compared between season using the non-parametric Wilcoxon signed-rank test.

We characterized these nightly distribution patterns by calculating four metrics that describe when in a night most birds migrate, and how spread or peaked over time they are migrating. First, we calculated the time at which migration peaks within the standardized night, i.e. when most migrants pass, as well as the density at that time. The density was log transformed to avoid patterns being driven by a few radars with very high migration peaks. Furthermore, we calculated the interquantile range of the migration distribution and its median, i.e. the time when 50% of the migrants had passed. As these four metrics are interdependent, we summarized them with a principal component analysis. The first component was selected as it captured the major variation in the distribution of nocturnal migration.

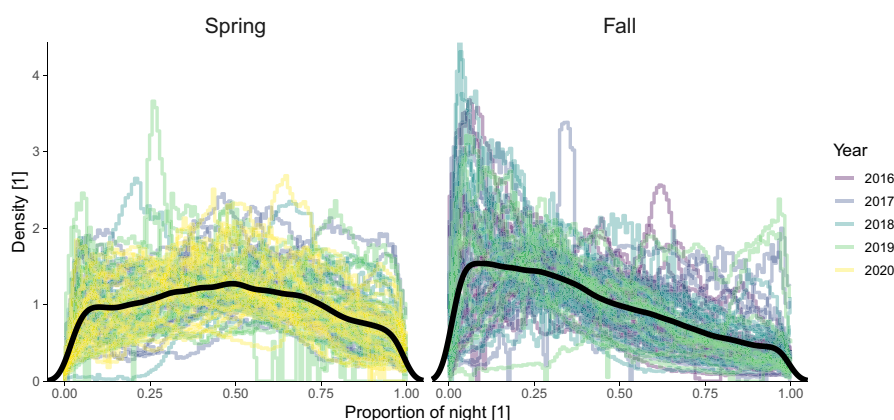


FIGURE 1 An example of the standardized distribution of migrants over the night for the weather radar located in Herwijnen, the Netherlands (nl/hrw). Each translucent line represents one night, coloured per year ($n_{\text{spring}} = 85$, $n_{\text{fdl}} = 69$). The black line is the standardized distribution as estimated through the Gaussian kernels.

We also characterized each radar location with respect to travel distance to the nearest water barrier, i.e. water bodies that could not be crossed with a speed of 10 m/s (Bruderer & Liechti, 1998) in 2 h of travel (72 km). Travel distance to nearest barrier is here defined in the direction of travel (and not simply as distance to barrier) and may thus vary between seasons. We derived the average migration direction per season and radar from the sampled distribution of directions and projected a great circle route departing from the radar location into this direction. We calculated the distance over land from the radar location both towards and from a barrier (d_{towards} and d_{from} , respectively, Supporting information C).

2.3 | Models

To identify the main determinant of nocturnal migration timing, we explored 17 models that included the first principal component as a response variable as explained by the distance to barriers and season. We fit models including all single and combined effects (first order interactions) of season, the log transformed distance to or from a barrier and the minimal distance to a barrier (Table 1). We added 72 km to all distances towards and from a water barrier, such that small differences in distance at the lower end of the scale were not exaggerated. Furthermore, each general linear model contained a spatial covariance structure (Gaussian) per season and used a Gaussian

error term. For model fitting we used the R package *glmmTMB* (Brooks et al., 2017).

3 | RESULTS

We derived average nocturnal timing distributions for 41 radars in spring and 55 in fall. A total of 1131 and 1920 nights had been selected in spring and fall, respectively, with a median of 24 ($Q_1 = 11$, $Q_3 = 36$) nights per radar in spring and 34 ($Q_1 = 18.5$, $Q_3 = 48.5$) in fall. Before standardizing, these nights had a median duration of 10.2 h ($Q_1 = 9.4$, $Q_3 = 11$) in spring and 11.5 h ($Q_1 = 10.9$, $Q_3 = 12.3$) in fall with variation in night length resulting from both differences in latitude and date. Through the standardized distributions (Figure 1), nocturnal timing patterns can be compared between radars, locations, and seasons (Figure 2).

There are clear differences in how migration is spread over the night: while migration is almost evenly distributed over the night in spring, migration clearly is more intense in the first hours of the night in fall. In spring, median peak of migration is at 42.8% ($Q_1 = 28.4$, $Q_3 = 48.6$) of the night's duration, while in fall 28.2% ($Q_1 = 17.7$, $Q_3 = 36.9$), i.e. almost in the middle of the night in spring but much earlier in fall. This migration peak is thus 14.6% of the standardized night duration later in spring ($W = 544.00$, $p < 0.001$). In spring, the interquartile range of migration covered 41.1% ($Q_1 = 38.6$, $Q_3 = 42$) of the night while in fall it is slightly shorter 38.3% ($Q_1 = 36.3$, $Q_3 = 40$). Migration is thus more evenly distributed throughout the night in

TABLE 1 Summary of all fitted models, ordered by increasing AIC.

	AIC	BIC	DF	σ	ϕ [100km]	Δ_{AIC}
Season + log (min (d_{towards} , d_{from}))	289.10	304.49	90	1.18	2.02	0.00
log (min (d_{towards} , d_{from}))	289.16	301.98	91	1.23	2.23	0.06
Season $\times$ log (min (d_{towards} , d_{from}))	289.69	307.64	89	1.14	2.05	0.59
log (d_{towards}) $\times$ log (d_{from})	292.31	310.26	89	1.24	2.39	3.22
Season + log (d_{towards}) $\times$ log (d_{from})	292.96	313.48	88	1.19	2.23	3.86
log (d_{towards})	294.43	307.25	91	1.39	2.59	5.33
Season $\times$ log (d_{towards}) + Season $\times$ log (d_{from}) + log (d_{towards}):log (d_{from})	294.50	320.14	86	1.18	2.21	5.40
Season $\times$ log (d_{towards}) + Season $\times$ log (d_{from})	295.50	318.58	87	1.28	2.34	6.40
Season + log (d_{towards})	295.63	311.02	90	1.36	2.51	6.53
log (d_{towards}) + log (d_{from})	296.12	311.50	90	1.36	2.51	7.02
Season + log (d_{towards}) + log (d_{from})	297.21	315.16	89	1.32	2.42	8.11
Season $\times$ log (d_{towards})	297.56	315.51	89	1.36	2.51	8.46
Season $\times$ log (d_{from})	301.54	319.49	89	1.43	2.47	12.44
	302.83	313.09	92	1.58	2.79	13.73
Season	303.33	316.15	91	1.52	2.65	14.23
log (d_{from})	304.07	316.89	91	1.52	2.64	14.97
Season + log (d_{from})	304.31	319.69	90	1.45	2.48	15.21

Note: All top fitting models include distance to the closest barrier in either direction (min (d_{towards} , d_{from})). Using the Bayesian information criterion (BIC), the same models are identified as the best-fitting models. With improving model fit standard deviation (σ) and distance (ϕ) of the spatial covariance decrease.

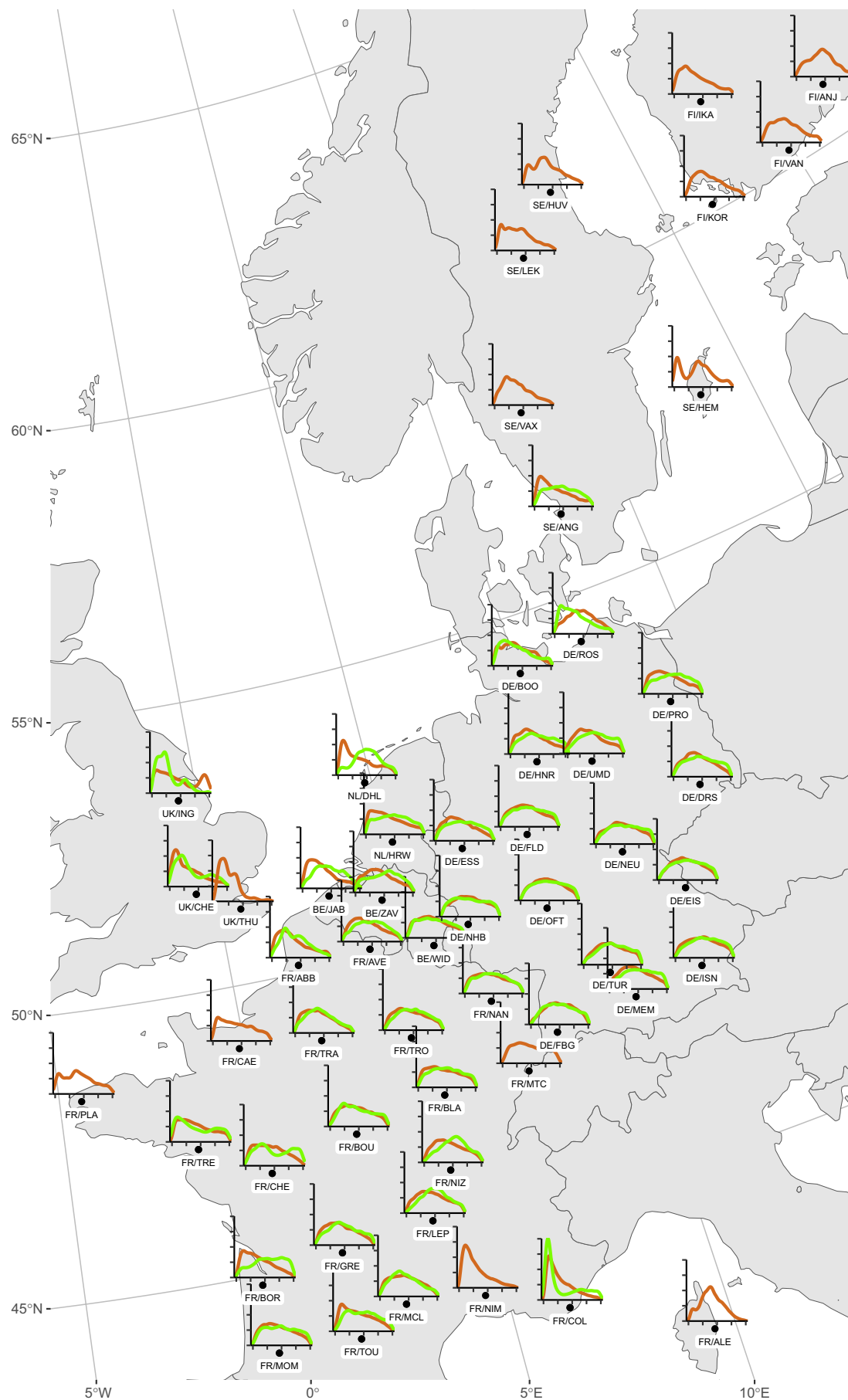


FIGURE 2 The distribution of radars and nightly migration patterns in spring and fall across Europe. Clear differences between spring and fall within coastal locations are visible, while more continental radars are more uniform between seasons and radars. For each radar (black dots with identification code), we derived an average distribution (inset diagrams with density of passing migrants on y-axis) for spring (green lines) and fall (brown lines) over standardized night time (x-axis).

spring, than in fall as the median interquartile range of the standardized migration distributions is 2.8% longer ($W=727.00$, $p=0.003$). However, the duration of nights, averaged per radar, in spring (10.3 h, $Q_1=10.1$, $Q_3=10.6$) is shorter than fall nights (11.5 h, $Q_1=11.3$, $Q_3=11.8$). Therefore, even though the interquartile range for a standardized night length (i.e. the proportion of the night used for migration) is slightly longer in spring, this results in a shorter duration ($W=1,524.00$, $p=0.003$) of the interquartile range in spring (4.1 h, $Q_1=4$, $Q_3=4.3$) compared to fall (4.4 h, $Q_1=4.2$, $Q_3=4.7$).

By summarizing nocturnal migration timing using the PCA, the majority of variance is explained by the first principal component (65.1%), which is substantially greater than for randomized data (95% interval of the variance explained by the first axis: 27.6%–35.2%). High values of the first PCA axis correspond to more continuous migration throughout the night while lower values correspond to early migration peaks. Thus, the first PCA captures the differences between early, highly peaked migration and more continuous, uniform migration throughout the night (Figure 3). The second PCA axis explains 26.4% of the variation; there is not direct interpretation of this axis, therefore, we did not analyse it further (Supporting information D).

There were substantial spatial differences between radars in nightly migration patterns (Figure 2, for the seasons separated, see Supporting information E). Generally, migration near barriers appeared to be more peaked than at inland locations. Models that use both a seasonal term and the distance towards or from a water barrier (whichever is closer) best describe the variation in nocturnal timing, as captured by the first principal component (Table 1, model estimates E.3). That means, migrations were more uniformly distributed throughout the night when farther away from the barriers

(Figures 2 and 4) and more peaked early in the night when close to barriers. Furthermore, the model confirmed the earlier result based on interquartile ranges, showing that migration is more evenly distributed in spring.

4 | DISCUSSION

Nightly migration timing varied spatially and seasonally. Timing patterns are predictable and depend on season and distance to major water barriers. In all areas, migration begins shortly after sunset, and we show that closer to barriers migration is much more concentrated at the start of the night. Since both distance from, or towards a barrier were retained in the best-performing models, our findings support the assumption that two complementary mechanisms influence the diel timing. First, at locations just before major barriers birds arrive throughout the night but stop and accumulate later in the night to avoid crossing the barrier during the day. Due to this accumulation, there tends to be a peak in migration intensity early in the subsequent suitable night of migration when birds that have arrived at the barrier the previous night start crossing simultaneously. Second, at locations directly behind a barrier, birds arrive asynchronously and may stop to recover after crossing or avoid flying longer into the daytime. On the following suitable night, all birds that have accumulated depart more or less at once, leading to a clear peak early in the night. As our analysis involves various sea crossings (i.e. Baltic Sea, North Sea and the Mediterranean) that show similar migration distributions, our findings can likely be generalized. Case studies around the Great Lakes in North America have shown similar peaks early

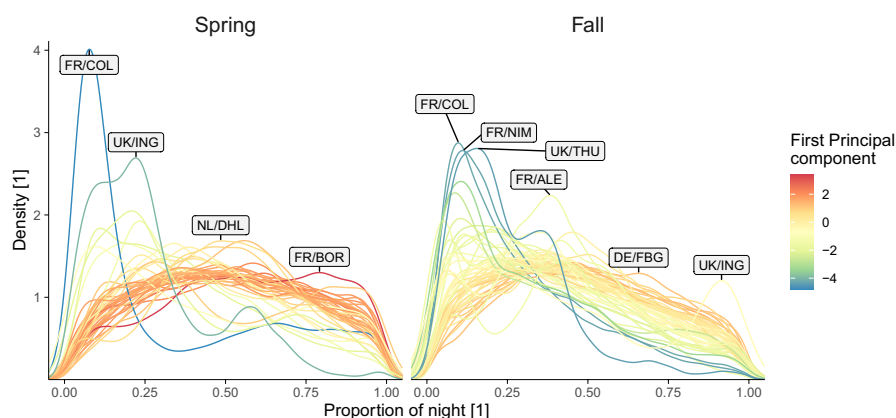


FIGURE 3 Visualizing the standardized distribution per radar per season. Lines are coloured according to the first principal component: Low values (blue and green shades) indicate peaks early in the night whereas higher values (yellow and red) indicate a more uniform distribution of migrants over the night. Differences between spring ($n=41$) and fall ($n=55$) are clearly visible with a more uniform distribution in spring. Radars with the pronounced distributions are labelled by their code, for reference to their location see Figure 2. In both seasons there are radars where most migrants pass early in the nights, these are coastal radars.

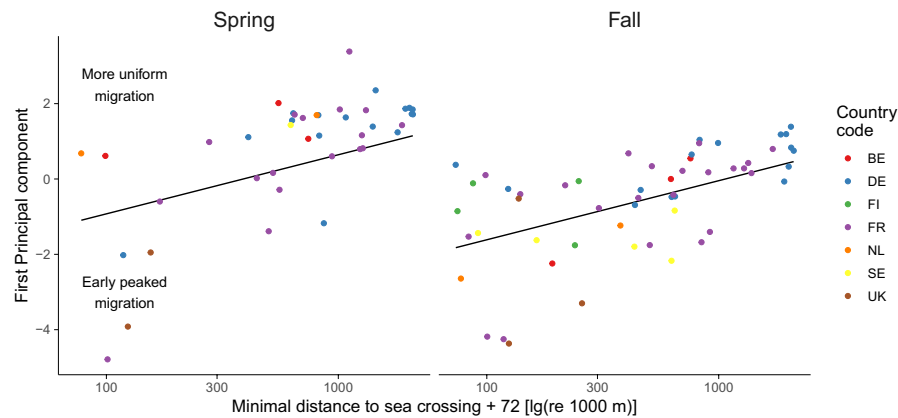


FIGURE 4 Visualization of the best fitting model, as the distance to a water barrier increases higher values for the first principal component are observed. This means that passing migrants are more uniformly distributed across the night when they are farther away from a barrier. The first principal component values in spring ($n=41$) are generally higher than fall ($n=55$), meaning that migrants use a larger proportion of the night. The solid black line visualized predictions from the model, while coloured points reflect the observations. Observations are coloured according to country of origin to confirm no country-specific biases occur.

in the night (Archibald et al., 2017), where also migratory flows change during the night (Gagnon et al., 2022). For specific radars, there might be deviations from these general patterns, e.g. the SE/HEM radar, located on Gotland island, has a midnight peak in fall as well (Figure 2). As this radar is relatively close to the mainland, the midnight peak can be a product of birds either arriving or passing from the mainland in a synchronized fashion.

Nightly migration timing differs between spring and fall. Migration is more evenly distributed throughout the night in spring while fall migration shows a stronger peak early in the night and migratory intensity declines in the second half of the night. These differences might be explained by the pressure for a timely arrival in spring. As competition for breeding opportunities favours early arrival in spring (Kokko, 1999), birds might use a longer part of the night to progress towards the breeding grounds, leading to more evenly distributed migration fluxes throughout the night. In fall, birds might have less incentive to migrate fast. Note, however, that the total duration of peak migration (interquartile range) resulted in a very similar number of hours in both seasons, suggesting that the duration of flights may be quite similar across seasons. Another difference between the seasons is that in fall, a cohort of experienced juveniles is migrating. Due to their inexperience, these birds might behave differently, for example, by having shorter flights and departing more readily at sunset. First-year birds also have less experience with barrier crossing and thus might caution more before departing on a crossing.

Weather patterns are distinctly different between seasons in the northwestern part of Europe. Conditions are generally more favourable in spring than in fall (Kemp et al., 2010; Nussbaumer et al., 2022), which results in higher flight speeds and/or less energy used per distance flown. In fall, many nights feature opposing wind patterns (Kemp et al., 2010), which might deplete energy reserves sooner and force the birds to stop more often after shorter flight bouts. In addition, surface wind speeds over land generally slow

down as the night progresses (Stull, 1988). Birds might cease migration as the tail winds die down during the night in fall. To investigate if weather plays a causal role in the seasonal difference, our approach can be applied on a nightly basis and relate the reduction of passing migrants to covariates such as changes in temperature or wind support within the night.

For the migration of landbirds, three types of major geographic barriers are frequently discussed – mountain ranges, deserts and large water bodies. Here we emphasized water barriers as the dominant barrier in the East Atlantic flyway. Similar effects, to the ones we describe, can be expected at other barriers, yet, the magnitude of their effects might be lower if species differ in their capacities for crossing mountainous and arid areas. That would result in less synchronous stopping behaviour over time and space compared to the comparatively discrete land water boundary (Schmaljohann et al., 2007).

The timing patterns we described clearly take a macroecological perspective. They represent regional averages derived from multiple species moving through an area and obviously, individual birds or species might deviate from these overarching patterns. However, for many ecological and societal questions, these macroecological patterns are key (Kelly & Horton, 2016), for example, in the setup of mitigation measures for aerial conflicts. Quantifying and understanding when biomass flows are generally expected to be most intense can assist in the development of curtailment regimes for wind turbine operations and the planning of flight schedules to avoid bird-aircraft collisions (Kranstauber et al., 2022; Van Gasteren et al., 2019) or lights out procedures to reduce the effects of light pollution. When local and near real-time information is lacking, long-term, seasonal and regional patterns could be a first step in focusing mitigation measures to relevant and sensitive periods. Our results show that over very large areas, mitigation measures could be made cost-effective yet highly efficient when generally confined to a smaller proportion of the night, and specifically, to the first half of the night in fall and near ecological barriers.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Polar volume data for the Netherlands is publicly available (CC0 1.0, <https://datapatform.knmi.nl/dataset/radar-volume-denhelder-2-0> & <https://datapatform.knmi.nl/dataset/radar-volume-full-herwi-jnen-1-0>). Vertical profile data from aloft is public (CC0 1.0, <https://aloftdata.eu/>). The calculated migration profiles and modelling dataset are available at <https://figshare.com/s/3777a0a93ee4cb8ec484>.

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BIOSKETCHES

Bart Kranstauber wants to understand how animal movement, migration, and space use and its consequences is influenced by variation between individuals and environmental conditions, to do so he uses novel computational approaches.

Silke Bauer is interested in the migration of animals, in particular the timing of migration, the cues animals use before and during migration and how the level of environmental information affects migration strategies and their consequences.

Judy Shamoun-Baranes aims to understand how intrinsic and external factors influence animal movement at different scales in space and time and what the consequences of movement strategies are for individuals, populations and species.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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