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Revealing patterns of nocturnal migration using the European weather radar network

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Nocturnal avian migration flyways remain an elusive concept, as we have largely lacked methods to map their full extent. We used the network of European weather radars to investigate nocturnal bird movements at the scale of the European flyway. We mapped the main migration directions and showed the intensity of movement across part of Europe by extracting biological information from 70 weather radar stations from northern Scandinavia to Portugal, during the autumn migration season of 2016. On average, over the 20 nights and all sites, 389 birds passed per 1 km transect per hour. The night with highest migration intensity showed an average of 1621 birds km^{-1} h^{-1} passing the radar stations, but there was considerable geographical and temporal variation in migration intensity. The highest intensity of migration was seen in central France. The overall migration directions showed strong southwest components. Migration dynamics were strongly related to synoptic wind conditions. A wind-related mass migration event occurred immediately after a change in wind conditions, but quickly diminished even when supporting winds continued to prevail. This first continental-scale study using the European network of weather radars demonstrates the wealth of information available and its potential for investigating large-scale bird movements, with consequences for ecosystem function, nutrient transfer, human and livestock health, and civil and military aviation.

Keywords: avian migration, weather radar, migration flyways

Introduction

Billions of mammals, birds, insects and other animals make seasonal round trips between their breeding and non-breeding sites each year, with multitudinous effects on populations, communities and ecosystems (Bauer and Hoye 2014, Hu et al. 2016). Seasonal flows of extremely abundant migrants represent an enormous transfer of biomass, nutrients, propagules, pathogens and parasites, with effects on essential ecosystem services, processes, and, ultimately, ecosystem function (Bauer and Hoye 2014). Many bird species exhibit long-distance seasonal movement across entire continents (Newton 2008) and at least 2.1 billion birds are estimated to migrate between Europe and sub-Saharan Africa alone (Hahn et al. 2009). However, reliable quantification of bird migration is inherently difficult as many migrants go undetected, particularly at night or when flying at high altitude.

Mapping the large-scale spatial variation (locations, directions, routes) and variable timing (phenology in relation to weather and location) of migration has several important applications. From a conservation perspective, it is important to identify major flyways, migratory strategies and crucial stopover areas (for example before the birds cross wide ecological barriers), to be able to pinpoint areas in extra need of protection (BirdLife International 2010). From a perspective of human safety, large-scale migration information can improve military and civil aviation safety (Shamoun-Baranes et al. 2017) and provide a basis for mapping and predicting the spread of pests and disease vectors (Bauer et al. 2017). However, the sheer magnitude of migratory movements, both in terms of numbers of animals involved and the spatial and temporal scales over which this process takes place, creates logistic, technical and technological challenges to map migration and to reliably quantify its main properties.

Networks of weather radar stations offer unique possibilities to analyse animal movement at large spatial scales and at a flyway-wide level, enhancing our ability to understand general movement patterns and make predictions (Shamoun-Baranes et al. 2014, Kelly and Horton 2016, Bauer et al. 2017), especially in light of global environmental changes that are affecting migrating birds (Cox 2010, Møller et al. 2010, Tomotani et al. 2018). Despite these possibilities, the use of biological information gathered by continental networks of weather radar stations remains limited in Europe due to technical challenges in accessing and processing the large volume of data produced by radars, restrictions on data usage by national weather services, and a lack of international scientific cooperation and standardization of available data across Europe. Recent advances in algorithms to process the data (Dokter et al. 2011, Sheldon et al. 2013), as well as computational power, has, for the first time, made it feasible to explore the biological information that is registered by weather radars on continental scales. Through several initiatives the data has also become more accessible. In the US the long-term national archive of NEXRAD weather data is available as open data (Ansari et al. 2018) and in Europe the recent COST Action 'ENRAM' (European Network for the Radar surveillance of Animal Movement) is working with the European Meteorological Services Network (EUMETNET) which runs OPERA (Operational Program for the Exchange of Weather Radar Information; Huuskonen et al. 2014) to make the data from the European weather radar network available to biologists. The European effort involves the standardization of data collection; data formats and storage. Now that several of these issues have been dealt with and accomplished, we are able to for the first time integrate biological data from the European weather radar network on a continental scale.

As a case study, we have chosen a part of the autumn migration season of 2016 to describe the nocturnal flow of avian migrants over the continent and to test the influence of wind as an important environmental variable on these large-scale migration flows.

Methods

Radar data processing

We have extracted information on bird migration from 84 weather radars operated by the (hydro-) meteorological agencies of Sweden, Germany, Finland, France, the Netherlands, Czech Republic, Slovenia, Poland, Belgium, Portugal, Catalonia and Bulgaria between 19 September and 9 October 2016. This time period was chosen as it is characterized by strong passerine migration throughout Europe (Busse 2000, Hüppop and Hüppop 2004). We retrieved polar volume data of reflectivity and radial velocity either through OPERA or directly from the meteorological agencies (in the cases of Germany, Poland, Belgium, Portugal, Catalonia) and Air Traffic Services Authority (in Bulgaria). In these countries a data sharing policy between OPERA and ENRAM permitted data exchange for scientific research, and data formats were directly compatible with our bird migration quantification algorithm (vol2bird; Dokter et al. 2011). The radar volume data was processed into vertical profiles of birds following procedures described by Dokter et al. (2011), using the vol2bird algorithm (ver. 0.3.13–0.3.16) in the R-package bioRad (see Dokter et al. 2019 for a detailed analysis roadmap). Radial velocity data was dealiased when necessary using an implementation of a torus mapping method (Haase and Landelius 2004), dealiasing all resolution samples within each altitude layer at once. Bird profiles were calculated based on samples in a range of 5–25 km from the radar position. The range was extended to 40 km in the case of four radars that scanned only at relatively low elevations, to warrant sufficient altitudinal coverage (Fig. 1A). To convert reflectivity measures into bird densities we assumed a radar cross section (RCS) per individual of 11 cm^2, following Dokter et al. (2011).

Only data between sunset and sunrise (at each individual site and for each date) were included. For each site the

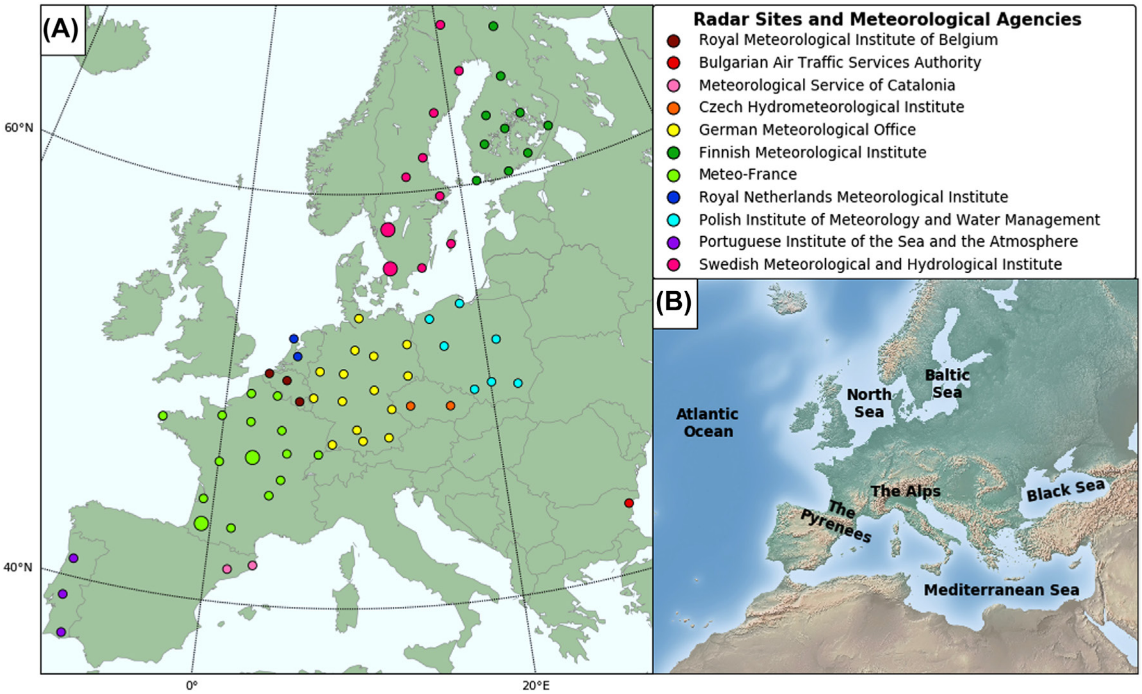

Figure 1. (A) Map of Europe showing the weather radar sites: the spatial coverage at each site is indicated by the size of the circle (small circles indicate a radius of 25 km centred on the radar, large circles indicate a radius of 40 km), and the meteorological agency which runs each site is indicated by colour. (B) Topographical map of Europe with the major topographical features discussed labelled.

lowest altitude bin (up to 200 m above ground level (a.g.l.)) was excluded to avoid potential ground clutter contaminations. Consequently, our migration intensity calculations are likely a conservative estimate of the actual numbers of traveling birds, since low elevation migration intensity is known to be substantial at some sites (Bruderer et al. 2018). Radar data were obtained in 15-min intervals, except for Poland and Portugal (10 min), Belgium and Bulgaria (5 min) and Catalonia (2 min). Bird profiles were calculated at these different time resolutions and then aggregated to nightly means.

Quality control and data selection

For consistency we decided to only proceed with radars operating at C-band wavelengths, excluding five S-band radar stations (for a description of radar types, see Fabry 2015). Five stations with more than two nights of completely missing data within the sampling period and one radar with poor altitude coverage were excluded from the analysis as well. As the analysis focuses on nightly means, sites with small amounts of scattered missing data were retained. For some scans in Finland the dealiasing algorithm produced incorrect velocities, but these did not seem to affect overall mean speeds and directions, which fell within expected ranges, so these sites were retained.

After processing, vertical profiles of migration were plotted and manually inspected to assess gaps and additional rain contamination that was not filtered out by vol2bird (Dokter et al. 2019). Periods of residual rain contamination were manually excluded from the analysis. Three French sites were excluded due to low-quality radial velocity data of biological echoes, potentially related to the unique French triple-PRT Doppler scheme. See 'vp_processing_settings.yaml' for details regarding all data selection (Nilsson et al. 2018b). In total, 70 stations were retained for analysis (Fig. 1 and Supplementary material Appendix 1 Table A1 for all radar locations included in this study).

Data analysis

Intensity of migration was expressed as migration traffic rate (MTR), defined as the number of birds that pass a theoretical 1-km transect perpendicular to the direction of movement during one hour. MTR was calculated as the product of density (birds km^{-3}), ground speed (km h^{-1}) and altitude bin height (0.2 km), and was then summed over all altitude bins (Desmet and Nilsson 2018, Dokter et al. 2019). Nightly average MTR was calculated as the mean MTR from sunset to sunrise. Mean directions per night and station were calculated by taking the migration ground speed vectors and computing the direction and length of the mean resultant vector (length of the resultant vector, r, corresponds to the amount of variation in the directions, where 0 is uniform distribution and 1 a perfectly directed distribution), using the R-package circular (Agostinelli and Lund 2017). Only altitude bins containing a bird density higher than 5 birds km^{-3} per scan where used for the calculation of mean directions.

Zonal and meridional wind speed, temperature and geopotential height at the 1000 hPa, 925 hPa, and 850 hPa levels were extracted from the NCEP reanalysis (Kalnay et al. 1996). Zonal and meridional winds (u and v, respectively) were transformed into wind speed (V_{wind}) and wind direction (α_{met}) via

$$V_{wind} = \sqrt{u^2 + v^2}$$

and

$$\alpha_{met} = (180/\pi) \times atan2(-u, -v),$$

where α_{met} represents the meteorological wind direction, i.e. the direction the wind is blowing from, and atan2 is the four-quadrant arctangent function. The geopotential height was used to interpolate the data to a standard level of 500 m above each radar station, and the wind speed and direction at 00 UTC was used to represent the wind conditions of the night.

For each night a tailwind component was calculated using the equation:

$$TC = V_{wind} \times cos(\alpha_{wind} - \alpha_{migration})$$

Where TC = tailwind component per night and site, V_{wind} = wind speed, α_{wind} = wind direction (towards which wind is blowing, i.e. $\alpha_{wind} = \alpha_{met} \pm 180$ degrees) at the site that night, and $\alpha_{migration}$ = the overall mean migration direction for the whole sampling period at the site (Fig. 2). We use it as an overall measure of how supportive, on average, the winds per night were, without going into details of the birds' flight behaviour and drift strategies. This equation implicitly assumes that wind blowing in the direction of the mean track direction is beneficial (Kemp et al. 2012).

We tested the effect of tailwind component on the mean nightly MTR with a restricted maximum likelihood linear mixed model (Bates et al. 2015). Radar id was included as a random effect to take site-specific differences into account, and country was included as a random effect to take into account country-specific differences in hardware, signal processing, etc.

Rain (yes/no) was included as an explanatory variable to account for lower detection of biological targets during rainy nights and the manual exclusion of data when it was raining. In the model 'rain nights' were defined as nights when more than 40% of the timestamps in our data contained rain, defined as profiles having over 5 altitude layers with a reflectivity factor > 7 dBZ (cf. quantity DBZH in bioRad, the reflectivity factor average including samples classified as precipitation). Therefore, our model takes into

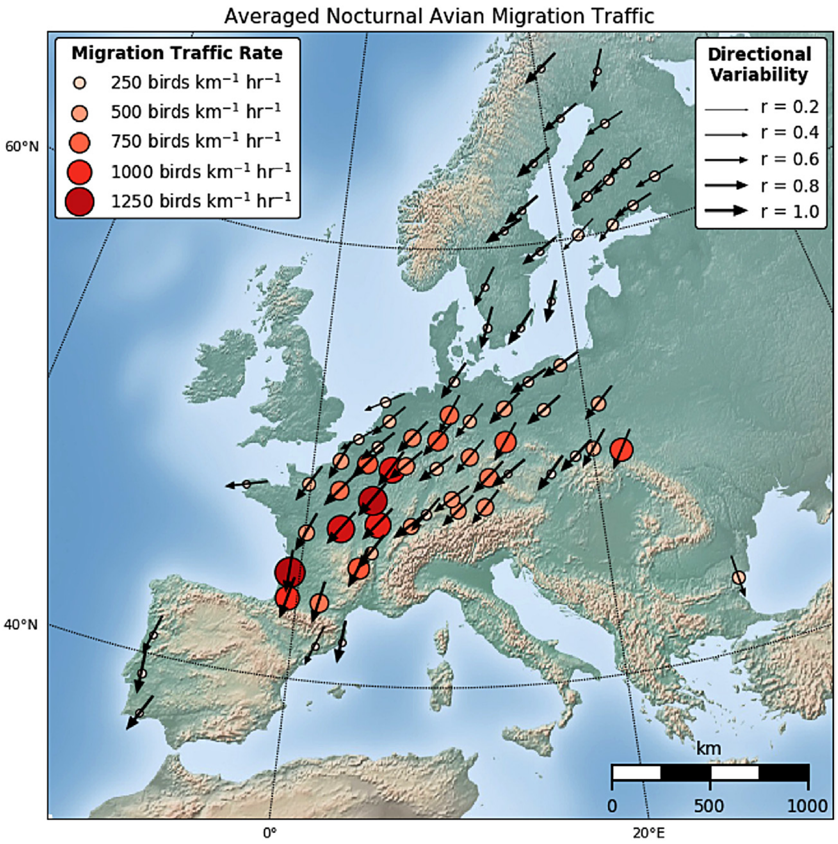

Figure 2. Topographical map of Europe with the mean direction of migration at each site indicated by the direction of the black arrows (see Supplementary material Appendix 1 Table A1 for site directions), and the mean MTR at each site shown by the size and colour of circles, averaged for the entire sampling period (19 September to 8 October 2016, only night time data included). The width of each arrow represents the circular r-value, with wider arrows indicating more concentrated migration directions and thinner arrows indicating greater directional scatter.

account the expected lower MTR during nights classified as containing rain.

Tailwind component, change in tailwind component relative to the preceding night (tail wind change $=\mathrm{TC}_{\mathrm{night}} - \mathrm{TC}_{\mathrm{night\text{-}1}}$), the change in temperature relative to the preceding night (temp change $=\mathrm{temp}_{\mathrm{night}} - \mathrm{temp}_{\mathrm{night\text{-}1}}$) and the interactions between the tailwind component and both tail wind change and temp change were also included as explanatory variables. Analyses were performed in R (ver. 3.4.1, R Core Team) with function 'lmer' in package lme4 (Bates et al. 2015) and evaluated with p-values from package lmerTest (Kuznetsova et al. 2016). Non significant variables were excluded by backwards stepwise selection.

Visualizations

For visualization purposes data within the altitude band of 200–2000 m were aggregated per hour (for details, see 'vp_to_flowviz.Rmd' in Desmet and Nilsson 2018) and only altitude bins with a density above or equal to 10 birds (birds km^{-3}) were included. As a result not all radars are included and not all included radars always contribute data (due to density threshold and gaps in data coverage).

To visualize the flow of migration over the continent, we used the bird migration flow visualization v2 (Desmet et al. 2016, Shamoun-Baranes et al. 2016), which extrapolates the migration over the entire sampling date range, not taking topography or water bodies into account, and shows the ground speed (length of arrows) and direction of migration over time. See 'flowviz.mov' in the reposited data for a screencast of the visualization. Note that density is not shown: low density movements can therefore appear as strong as high density movements when ground speeds are similar.

The same data were loaded into CARTO to create an interactive map, visualizing migration density (size of circles) and mean direction (colour) over time. The interactive map is available at <https://inbo.carto.com/u/lifewatch/builder/8685140f-8d8c-4d06-9e1e-25d051d43748/embed> or see 'cartoviz.mov' in the reposited data for a screencast of the visualization.

Data repository

Data, filters and visualizations are available from Zenodo: <https://doi.org/10.5281/zenodo.1172801> (Nilsson et al. 2018b).

Results

The flyway

Migration intensity

By quantifying the mean MTR (birds h^{-1} km^{-1}) for each site we estimate the amount of nocturnal birds migrating past that site during the study period. Together with the calculation of the mean directions of the movement, the western and central parts of the nocturnal migration flyway over Europe are mapped, and additional information is provided from a single site in SE Europe (Varna, Bulgaria).

There is a clear spatial pattern of high numbers of birds passing sites in central France and Germany, while MTR at sites further towards the coast or towards the Alps is lower (Fig. 2). Large numbers of birds also concentrate in the passage between France and Iberia, with the highest numbers along the Atlantic coast towards the western Pyrenees (Fig. 2).

The total number of birds migrating above each site increased from north to south (see for example Fig. 2, Fig. 5A and Supplementary material Appendix 1 Table A1). This pattern however does not hold for the five most southern sites, in Portugal and Catalonia, where MTR values are comparatively low. Unfortunately, we only have data from coastal sites in this region, which are potentially not representative for the main flyway. The overall mean of the Swedish and Finnish sites show 41 and 189 birds h^{-1}, respectively, passing a 1 km transect, while the overall mean for France is 744 birds passing h^{-1} km^{-1}. The intensity of migration in Sweden (41 birds h^{-1} km^{-1}) seems lower than expected in relation to other sites that are located in similarly high latitudes such as Finland (189 birds h^{-1} km^{-1}), even though this is during peak migration time in this area (Karlsson and Ehnbom 2017). However, we note that the southwestern most site in Sweden actually shows similar amounts (mean MTR 136 birds h^{-1} km^{-1}) of migratory movements as that of the most northerly German site (198 birds h^{-1} km^{-1}, Supplementary material Appendix 1 Table A1, Fig. 2). The site with the highest mean MTR during this period was in Bordeaux, along the southwestern coast of France, where, on average, 1292 birds h^{-1} passed. The highest nightly mean MTR was recorded in Eisberg, south eastern Germany. There, on the night between 4 and 5 October, an average of 7282 birds h^{-1} km^{-1} passed. The overall average MTR for all sites and all nights was 389 birds h^{-1} km^{-1}, and the highest overall migration activity was on the night of 4 October, when 1621 birds h^{-1} km^{-1} passed.

Migration directions

The main outline of the flyway is also seen by the mean directions across sites (Fig. 2). Overall, most sites have a clear south-west migration direction (overall mean 212 degrees, see also Supplementary material Appendix 1 Table A1), indicating that the main part of the flyway down through Europe passes through Iberia, rather than over the Alps, which would have been implied by more straight southerly mean bird flight directions (Fig. 2, flow visualization). The overall mean directions show limited impact of the easterly route around the Mediterranean. The most easterly sites in Poland however do show more southerly directions than other sites, and the most south-easterly site, in Bulgaria, has a clearly south-easterly mean direction (161 degrees). There is also variation in directions both within nights (see flow visualisation) and between nights (see interactive map) that are not reflected by the overall mean directions. On some nights significant numbers of birds in central Europe take a more easterly route than suggested by the overall mean (flow visualization, interactive map).

While most sites showed little variation in mean migratory direction (74% of sites had an r-value of 0.7 or higher, Supplementary material Appendix 1 Table A1), some sites did show variation in directions, as exemplified by the two sites in Fig. 4. These two sites, along the North Sea coast, show movements both in the expected south western direction, but also out over sea towards the UK as well as along the coast in the opposite direction.

Weather effects

Migratory movements along the flyway largely depend, as expected, on weather conditions. Our analysis illustrates how a synoptic weather system affects different parts of the European flyway simultaneously. The intensity of migration along the flyway varies such that heavy migration occurs in parts of the continent where tailwinds prevail, while there is much less migration activity under headwinds, as described in further detail below.

To visualize how a wave of migration moves through Europe during a period of fair weather, we calculated the peak migration date for each site after a large-scale shift in wind conditions over the continent. From 28 September and a few days forward most sites experienced headwind conditions, which then shifted to beneficial winds on 3 October (Fig. 3A, B, Fig. 5B). During the first few days after 3 October heavy migration is evident from north to central Europe (Fig. 3C, B). Then migration intensity at sites in the north decreases, likely because these sites start emptying out. Concomitantly, sites to the very south exhibit marked increase in migration

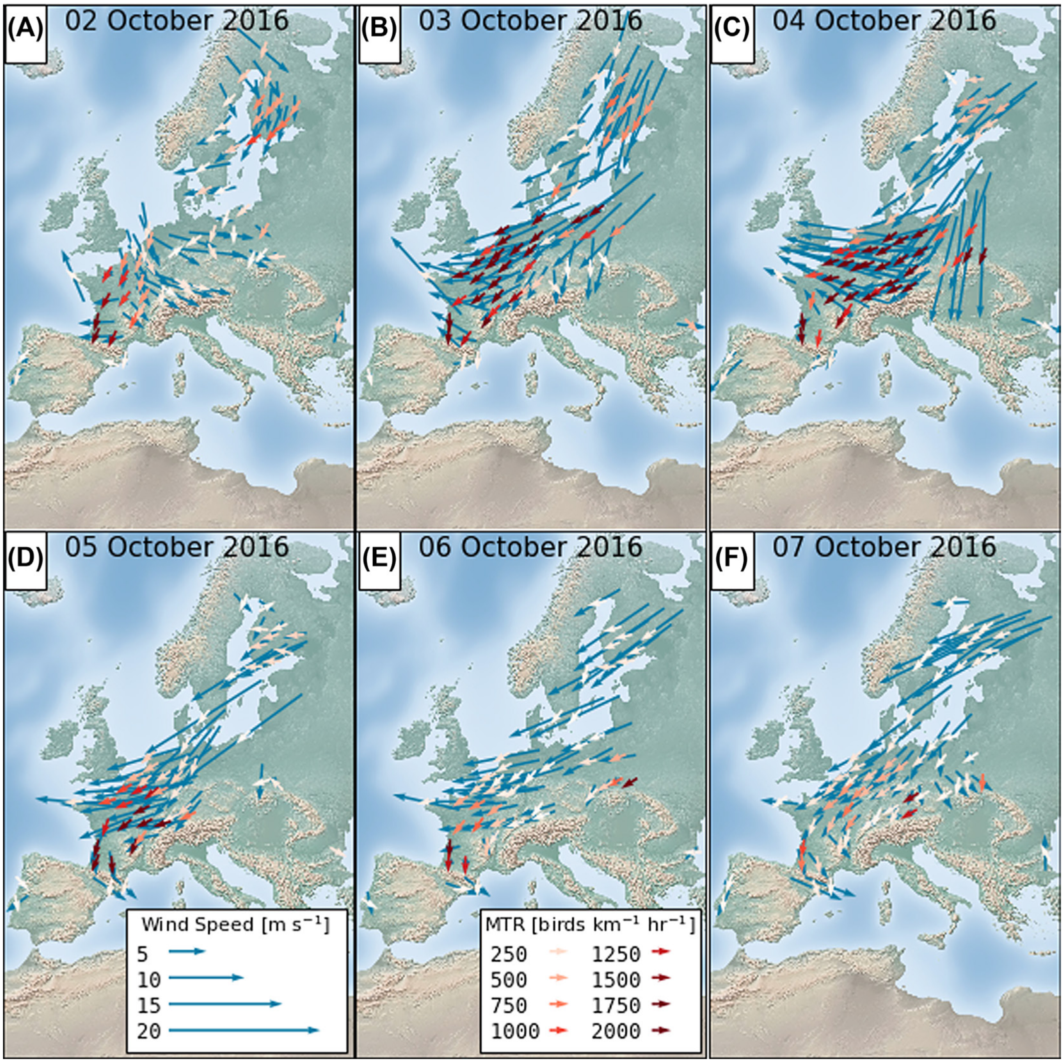

Figure 3. Figure showing the amount and direction of migration and wind speed and direction (from NCEP reanalysis model at midnight each night) at each site on six nights. On 2 October winds are not very supportive and there is low activity. As soon as winds improve, activity increases all along the flyway, but quickly empties out and in the end there is little activity despite beneficial winds. The mean flight direction at each site shown in red arrows, coloured by the nightly mean MTR. Not all sites have activity each night. Blue arrows show wind direction, sized by wind speed.

intensity (Fig. 3D, E). Despite the continuation of beneficial wind conditions on the nights of 6 and 7 October (Fig. 3E, F), there is not much activity in the northern parts of the flyway. Notably, there is very little activity overall on 7 October. The low MTRs on the last nights of this beneficial weather period is not due to rain suppressing migration, as there were no large areas of precipitation in this region during these nights (Supplementary material Appendix 1 Fig. A1). Over this 11-night period (28 September to 8 October) the night of maximum MTR at a site tended to be earlier in the sites at higher latitudes and later at lower latitudes (Fig. 5A), indicating the passage of a large-scale migration wave from north to south. To further explore this migration peak, we compared these peak migration dates to the pattern of tailwind component at each site during the same time period (Fig. 5B). We found that the maximum MTRs occurred in the beginning of a period of positive tailwind components for most sites, suggesting that migration peaked as soon as winds turned supportive (Fig. 5B). This indicates that the temporal pattern of nocturnal bird migration within the migration seasons is largely governed by wind and that most migration will be initiated as soon as wind conditions improve.

In the model explaining the mean MTR per night at a site, we found a significant effect of tailwind component, tail wind change from the previous night as well as the interaction between tailwind component and the tail wind change, Table 1. Temperature change and the interaction between temperature change and tailwind component showed no significant effect and were therefore excluded from the final model. Including the effect of the random intercepts (radar id and country) significantly improved the model in a likelihood ratio test. The direct effect of tailwind speed on MTR confirms that tailwind is an important determinant of migration intensity over continental Europe. The interaction shows that the effect of a high tailwind component on MTR is greater when the tailwind component had improved from the previous night, indicating that birds have been waiting for nights with favourable wind support.

Discussion

The flyway

Migration intensity

The pattern of migration intensity we observed demonstrate the large-scale effects of continental topography on the flyways of nocturnal migrants. During our study period the highest number of birds passed through central France, and judging by the highest migration intensities and mean flight directions they seem to funnel between the Alps and the Atlantic Ocean, demonstrating the spatial extent of this part of the European flyway (Fig. 2). Large amounts of birds likely pass over the Pyrenees into Spain, where they seem to aggregate mainly in the western part of the crossing between France and Spain, close to the Atlantic coast, as seen by the larger MTRs at the two most westerly sites in southern France, compared to the more easterly site in France and the two Catalonian sites (Fig. 2, see also Weisshaupt et al. 2016, 2018). This indicates that this area is very important for nocturnal migration in Europe, as has previously been shown also for diurnal migration (Lack and Lack 1953, Vansteelant et al. 2017) and insects (Lack and Lack 1951), however, more data from the Iberian peninsula is needed to confirm this pattern.

As expected, MTR generally increased from north to south, with the exception of the most southern sites. The test of the mean MTR per night showed that there were differences between countries in migration intensity. This could be a geographical/latitudinal effect, but it is also possible that it is due to differences in data collection and processing between countries. The low migration in northern Sweden could be explained by fewer birds passing as the hinterland to the north is limited, while the comparably low MTRs in southern Sweden are supported by a recent validation campaign (Nilsson et al. 2018a). Similarities with the closest German sites also suggest that this variation in bird migration is a genuine geographical/spatial pattern rather than a radar- or country-specific artefact. Sites outside the main flyway (such as along the coasts) also show similar low numbers irrespective of country. However, further, country specific, validation is required to fully exclude country specific artefacts.

Migration directions

Our finding of a mainly south-western direction of migration confirms theoretical predictions that birds should use optimal detours to avoid long barrier crossings, in this case the Mediterranean Sea and the Sahara Desert (Alerstam 2001). Ringing recoveries have shown a complicated pattern of autumn migration directions in this area, with migratory divides between the western and eastern routes both within species and between closely related species (Bønløkke et al. 2006, Fransson and Hall-Karlsson 2008, Bairlein et al. 2014). Ringing recoveries are in general more abundant along the western route, but this could be

Table 1. Results of restricted maximum likelihood linear mixed model on mean MTR per night. Radar id and country were included as random effects. p-values based on Satterthwaite's approximations anova.

Fixed effects	Estimate	Std error	df	t value	p value	
Rain (yes)	–316	74.4	1298	–4.2	2.34e-05	***
Tailwind component	33	3.3	1284	10.6	< 2e-16	***
Tail wind change	10	4.2	1266	2.4	0.016	*
Tailwind component × tail wind change	3	0.5	1271	6.4	2.00e-10	***

influenced by re-encounter probabilities (Procházka et al. 2017). Local radar observations (Casement 1966, Bruderer and Liechti 1999) have also shown a non-uniform distribution of nocturnal migrants over the Mediterranean, with larger concentrations in both the western and eastern parts of the region. The Alps also play a role in shaping such a pattern of spatial distribution (Bruderer and Jenni 1990, Liechti et al. 1996). Our data shows a dominance of the westerly detour, with overall mean track directions mainly towards south west. The magnitude of the eastern detour around the Mediterranean is much more limited in our data, with only some sites in eastern Poland showing mean track directions slightly more to the south than other sites. While this pattern may reflect actual main migration directions in these areas, it is possible that it holds true only for limited time period during which data was available for our analyses, and the pattern could be somewhat different when considering the entire autumn migration. When looking at specific nights and times it is also clear that during some periods south-easterly directions do dominate (see flow visualisation and interactive map). It is also possible that track directions change farther south, outside of the coverage of our data. Our most southeastern site, in Bulgaria, shows the expected south-south/eastern direction (Zehtindjiev and Liechti 2003). We hope that future analyses will integrate data from the entire autumn and include additional radars from central and eastern Europe to decipher the migratory divide of bird migration directions over Europe, which still remains to be fully resolved.

Although our analysis has focused on the continental scale topography effects on nocturnal migration, it is also possible to see the influence of local topography at specific sites. As an example, two sites on the North Sea coast show low r-values (Supplementary material Appendix 1 Table A1, Fig. 4), indicating a high spread in directions. When plotting these two sites in detail it is clear that there is an effect of coastlines at these sites. Although the main movements are to the southwest, as most other sites, there are also movements following the coast to the northeast, which might be reverse migration or local movements. There is also evidence of some movements out over sea towards the UK, which could be migrants en route to wintering grounds in the UK, a known migratory route (Lack 1963) for example for starlings *Sturnus vulgaris* (Perdeck 1982).

Weather effects

As expected, wind conditions had a significant impact on the intensity of migration occurring at any given site, with the largest volume of birds moving on nights with good conditions immediately following nights with less wind support. This supports the 'sit-and-wait' hypothesis of optimal migration, suggesting that in many circumstances the gain in flight distance obtained by flying in beneficial winds would outweigh the costs of waiting out less beneficial winds (Liechti and Bruderer 1998, Åkesson and Hedenström 2000, Gauthreaux et al. 2005). This is also in agreement the concept of 'Zugstau' (Schüz 1952). Our results indicate that, on average, for every 1 m s^{-1} increase in tailwind component, approximately 33 more birds will pass a 1 km transect per hour. A further 10 birds h^{-1} will pass for every increase in tailwind component from the previous night, and an additional 3 will be added in the interaction between the two. That wind conditions have a large impact on migratory activity is well in agreement with previous studies (Richardson 1978, Liechti and Bruderer 1998, Erni et al. 2002, Liechti 2006, Van Belle et al. 2007). After the period of favorable winds, sites seemed to empty out as indicated by the substantial decrease of migration activity even despite the prevalence of beneficial conditions (Fig. 3, Fig. 5). This effect is more noticeable in the northern parts of the flyway, such as in Finland, probably due to less hinterland to the north, limiting the influx of migrants.

During the time period we investigated, most migration generally passed through a site during only a few of the nights, and the pattern was heavily affected by wind conditions. This implies that migration should be forecastable (Van Belle et al. 2007), and that directed conservation efforts over relatively few days could have large impacts (Hüppop et al. 2019). Such directed efforts could involve shutting down wind turbines in certain areas (Hüppop et al. 2006), decreasing artificial lights during specific times (McLaren et al. 2018, Van Doren et al. 2018) or altering flight plans for aviation (Shamoun-Baranes et al. 2017).

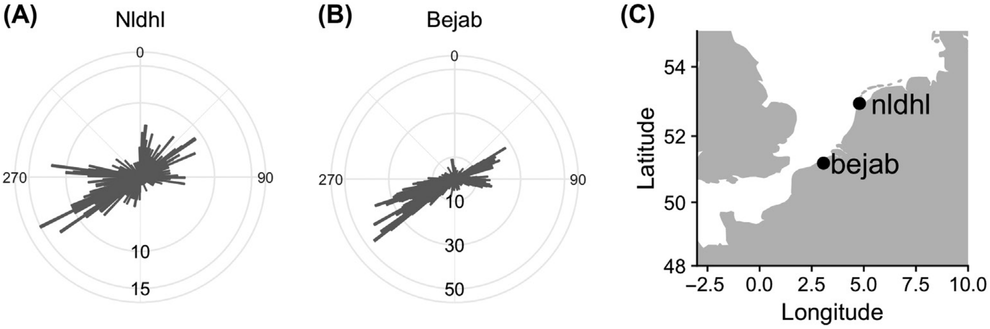

Figure 4. (A–B) Histograms with count of the mean migration directions (per timestamp) for two sites along the North Sea coast. Only scans with a bird density of 5 birds km^{-3} or over and only sunset to sunrise data included. (C) Map of the locations of the two sites.

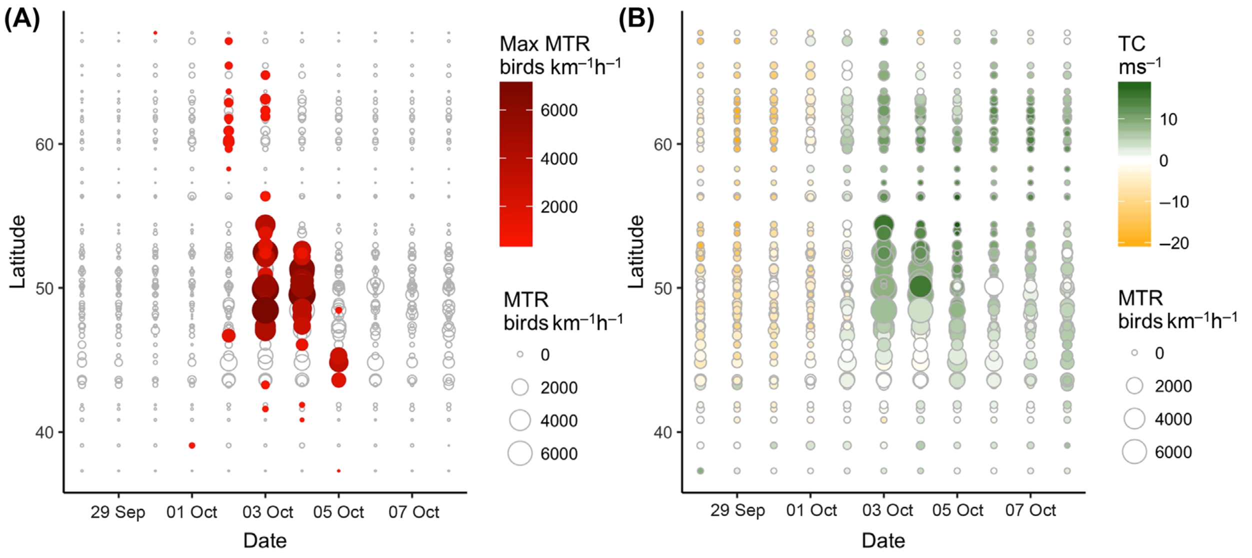

Figure 5. Latitudinal variation on (A) mean MTR per night (size of grey circles) per site and date with the maximum MTR (size and colour of red circles) at each site. (B) Mean MTR per night (size of grey circles) and tailwind components (TC, colour of circles) for each night at each site. Positive tailwind components indicate supporting winds. Nights between 28 September and 8 October 2016 shown.

Conclusions

Previous methods for mapping large-scale spatial patterns of nocturnal bird migration over Europe have been limited because of data scarcity, for example when deducing spatial patterns from ring recoveries of a few individuals (Hedenström and Pettersson 1987) or due to limited and often poor spatial coverage as in studies integrating radar and infrared measurements or moon watching at individual sites (Bolshakov and Dolnik 1985). Making inferences of large scale migration patterns from single sites is difficult, as the amount of overall migratory activity under certain conditions cannot be easily separated from the selection of different migration routes under those conditions. Even larger scale studies involving moon-watching (Zehtindjiev and Liechti 2003, Trösch et al. 2005) were mostly limited to certain regions, and suitable observation conditions such as clear air and a full moon.

Our large-scale coverage has allowed us to map the spatial structure of avian nocturnal migration pathways through Europe, the migration intensity and migratory directions that define a part of the European flyway, and show how the migration intensity at individual sites is affected by winds. In extension, these large-scale findings will have many important practical applications, related to the flow of biomass (Hu et al. 2016) at a continental scale, including the transport of nutrients, energy and pathogens (Bauer and Hoye 2014), the risk imposed by migrating birds to aircraft (van Gasteren et al. 2019), potential implications for conservation of birds during cross-country flight as they pass through tall anthropogenic structures (wind-turbines, communication towers, etc.) (Hüppop et al. 2006, 2019, Shamoun-Baranes et al. 2017) and on the ground while stopping to rest and refuel (Buler et al. 2007, Hüppop et al. 2019). Importantly, our findings can serve as a benchmark and useful reference point for the large amounts of individual migration tracks that are being collected for some species (Tøttrup et al. 2012, Arlt et al. 2015, Åkesson et al. 2016), and also to put other data, such as local bird counts or ringing recoveries, into a larger context. Expanding this data to include all of Europe should be a top priority, as it represents an accessible wealth of new information on bird migration from an already existing sensor network. Of special importance is to work towards including data from countries such as Spain, Italy and countries from Balkan Peninsula, to be able to map southern parts of the flyway and the important passage over the Mediterranean. In addition, data from countries in east and south-east of Europe would allow quantifying the migration flow over the eastern part of Europe and provide a comparative framework between flyways in terms of volume and phenology. Being able to access detailed, continent wide, information on bird migration over Europe is certainly within reach, conditional on the continued collaboration between meteorologists and biologist throughout Europe.

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Supplementary material (Appendix ECOG-04003 at <www.ecography.org/appendix/ecog-04003>). Appendix 1.