Bird Study

ISSN: 0006-3657 (Print) 1944-6705 (Online) Journal homepage: http://www.tandfonline.com/loi/tbis20

Effects of a sea barrier on large-scale migration patterns studied by a network of weather radars

Nadja Weisshaupt, Adriaan M. Dokter, Juan Arizaga & Mercedes Maruri

To cite this article: Nadja Weisshaupt, Adriaan M. Dokter, Juan Arizaga & Mercedes Maruri (2018): Effects of a sea barrier on large-scale migration patterns studied by a network of weather radars, Bird Study, DOI: 10.1080/00063657.2018.1476457

To link to this article: https://doi.org/10.1080/00063657.2018.1476457

Published online: 21 Jun 2018.

BIRD STUDY
https://doi.org/10.1080/00063657.2018.1476457

Effects of a sea barrier on large-scale migration patterns studied by a network of weather radars

Nadja Weisshaupt[a], Adriaan M. Dokter[b], Juan Arizaga[a] and Mercedes Maruri[c,d,e]

[a]Department of Ornithology, Society of Sciences Aranzadi, Donostia-S. Sebastian, Spain; [b]Computational Geo-Ecology, Institute of Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, Netherlands; [c]Institute for Applied Mathematics, University of the Basque Country, Bilbao, Spain; [d]Basque Meteorology Agency (Euskalmet), Alava, Spain; [e]TECNALIA-Energy and Environment Division-Meteo Area, Miñano, Spain

ABSTRACT

Capsule: Nocturnal passerine migration patterns were studied by a network of weather radars within the East-Atlantic flyway providing large-scale information on the effect of a geographical barrier.
Aims: The aim of this study was to obtain a large-scale spatial overview of the effects of a sea barrier on migratory flyways in northern Spain/western France.
Methods: Weather radar data were used from five sites at the Bay of Biscay during nights in spring 2015 to calculate flight directions and migration traffic rates (MTRs).
Results: The highest MTRs were registered by the radars at the southeastern edge of the bay, with a gradual decrease northwards. Spring migration direction was generally NNE/NE. Continuous nocturnal migration pattern indicated migration over land in the south. The radar half way up the French coast exhibited bimodal migration intensities at night, indicating sea crossing, and the northernmost corner of the bay showed little migration.
Conclusions: Radar patterns indicated migration over land and sea during spring migration. Sea crossing occurred with flight distances of up to about 500 km. Most migration activity was observed in the radars along the southeastern section of the bay, indicating that the general migration flyway from Spain funnels through the eastern side of the north Iberian Peninsula.

ARTICLE HISTORY
Received 29 May 2017
Accepted 8 May 2018

Throughout the annual cycle, migratory birds transit various ecological barriers, such as deserts, mountain ranges or seas, which have few or no available stopover sites (Biebach 1990). Birds have developed a variety of strategies to optimize energy expenditure and ultimately survival, by avoiding these barriers and travelling on safe routes (Alerstam 2001, Newton 2008). Against the background of current population declines of many migratory bird species (Sanderson *et al.* 2006), it is important to disentangle both small- and large-scale migration dynamics, in order to improve conservation measures at potential stopover sites, in particular near ecological barriers.

Behavioural responses to water barriers include changes of flight altitudes and directions to undertake or avoid the flight over water (Bruderer & Liechti 1998, Fortin *et al.* 1999, Sjöberg & Nilsson 2015). Diehl *et al.* (2003) found both crossing and avoidance of a water barrier during migration events. While birds could theoretically shortcut their routes by crossing, some take safer routes over land instead. A similar divide of the migration flow at a water barrier was found by Gagnon *et al.* (2011), who observed birds both crossing the St. Lawrence estuary and following the coast. Also, time constraints might play a role when undertaking a particular route, for example, early arrival via a more direct route in spring would favour the occupancy of a good territory (Kokko 1999).

Additionally, meteorological conditions, such as precipitation or winds, have been identified as factors influencing the decision to cross barriers (Alerstam 1990, Liechti 2006). The decision on whether to make a safer, though longer journey, or to take risks in return for saving time is a trade-off between the overall benefits and risks anticipated by a bird in a particular area (Bruderer & Liechti 1998).

A variety of radar types has been used locally, mainly marine or tracking radars, to measure flight altitudes, speed, directions and densities of migratory birds near barriers (Bruderer 1997). However, barriers have hardly been studied on an appropriate scale to depict birds' behaviour from a large-scale perspective. Appropriate

CONTACT Nadja Weisshaupt nw@nweisshaupt.net Department of Ornithology, Society of Sciences Aranzadi, Alto de Zorroaga 11, Donostia-S. Sebastian 20014, Spain

monitoring tools are required to resolve the large-scale movements across such surfaces. One option would be operational weather radars, typically organized in networks such as the Next Generation Weather Radar (NEXRAD) in the USA and the Operational Program for Exchange of Weather Radar Information (OPERA) in Europe. The large spatial coverage of these networks enables the study of animals' responses at spatial scales that match the extent of barriers, which has not been possible with small-scale marine or tracking radars. Large-scale ornithological studies using the weather radar data stem mainly from the USA (Gauthreaux *et al.* 2003, Kelly *et al.* 2016). In contrast, in Europe, migration has been studied at various local sites by short-range radars (Bruderer 1999). These studies have provided data on migration intensities, directions and heights from individual sampling sites. Even though highly valuable, such studies would gain even more importance if they were set into a broader context, taking into account the spatial extent of bird migration movements across hundreds and thousands of kilometres. To this end, efforts are being made to render the OPERA data accessible to biologists by implementing bird migration quantification software at meteorological data centres in the European Network for the Radar Surveillance of Animal Movement, COST Action ES1305 (COST Action ENRAM, http://www.enram.eu; Shamoun-Baranes *et al.* 2014).

The aim of this study was to extract ornithological information from weather radars and to study large-scale passerine migration dynamics at a barrier. The Bay of Biscay was selected as a sample region because it is part of the East-Atlantic flyway, the major migration route across Western Europe, and represents a potential ecological barrier between Central Europe and the Iberian Peninsula. One of its particularities is its highly variable and harsh meteorological conditions (e.g. wind, precipitation; Gangoiti *et al.* 2002, Maruri *et al.* 2014), which could have an impact on migratory birds' decision to cross this sea.

The scarce literature available on bird migration at the Bay of Biscay focuses mainly on ringing data or land-based daytime observations of active migration in the southeastern edge of the bay in autumn (Lack & Lack 1953, Grandio & Belzunce 1987, Bruderer & Liechti 1999, Mendiburu *et al.* 2009, Arizaga *et al.* 2014). As to actual nocturnal migration, there are only a few local studies from the southeastern coast indicating seasonal and geographical variations in the migration flow (Weisshaupt *et al.* 2016a, 2016b, 2017). Based on these local findings (Weisshaupt *et al.* 2016a), we would expect to find sea crossing in spring which would show as variations in nocturnal migration intensities, for example, continuous migration intensities over land vs. bimodal migration intensity pattern throughout the night for crossing on the French coast. Such a bimodal pattern, as observed also on islands (Speich 1999), would be caused by migrants taking off at the departure coast around sunset, with low numbers venturing out to sea during the night, and with a morning peak indicating landing at the target shore. The general northeasterly migration direction anticipated for spring migrants on the East-Atlantic flyway (Zink 1970) could furthermore lead to E–W and S–N gradients in migration traffic rates (MTRs) along the coast. In order to clarify the spatial dynamics of nocturnal mass migration actual large-scale information is required, which can also deal with darkness, and weather radar networks are currently the only tools available to provide the necessary data.

Methods

Data input

Reflectivity and radial velocity data were obtained from four C-band weather radars in France: Momuy (43°37′28.1″N 0°36′33.8″W), Bordeaux (44°49′52.9″N 0°41′31.4″W), Tréillères (47°20′14.6″N 1°39′22.7″W) and Plabennec (48°27′39.2″N 4°25′47.3″W); and one of the Basque Meteorology Agency (Euskalmet): Kapildui (42°45′57.5″N 2°32′15.9″W) (Figure 1). These radars were selected because of their proximity to the coast. Originally, data from two coastal radars of the Spanish State Meteorological Agency (AEMET) were included to cover also the southern coast of the bay: Oviedo (43°27′49.0″N 6°18′01.8″W) and Jata (43°24′14.4″N 2°50′27.6″W). However, special meteorological filters had been applied upon collection of the radar data for these two stations, which made them unsuitable for biological analysis.

The study period was restricted to 1 March to 6 April 2015 to coincide with the peak migration period on the Basque coast in spring (Weisshaupt *et al.* 2016a). This early spring period coincides with migration of short-distance migrants, such as thrushes or finches, across the Iberian Peninsula (Finlayson 1992). Local findings from Weisshaupt *et al.* (2016a, 2017) involving all-season multi-year data indicated a nightly, seasonally and geographically variable migration flow at the southeastern edge of the bay. The present study provides the unprecedented large-scale view on the nocturnal migration dynamics along this part of the East-Atlantic Flyway.

Bird algorithm

When dealing with large data sets of multiple radars, it quickly becomes impossible to screen all data

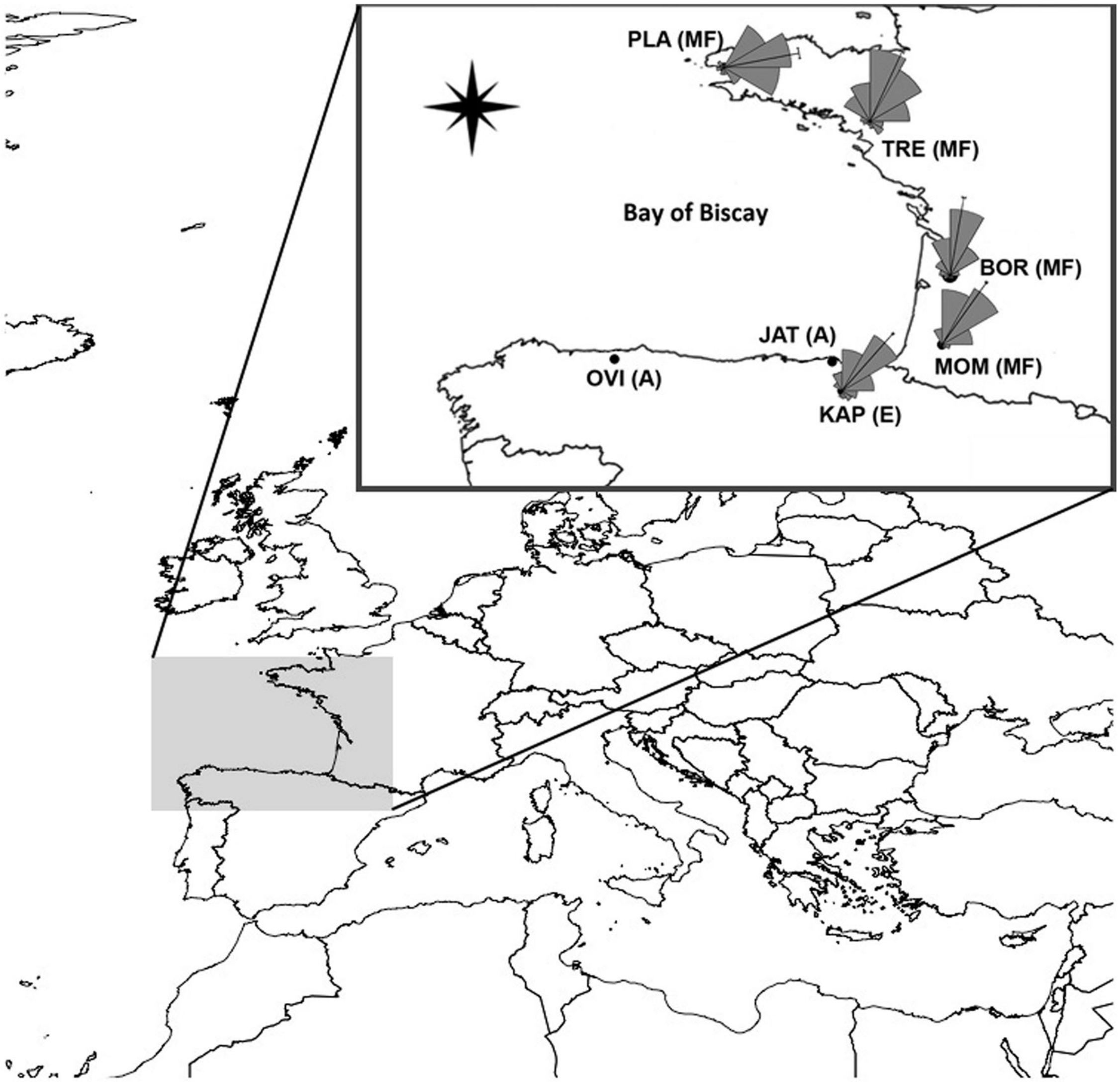

Figure 1. Radar sites along the Bay of Biscay included in this study and the nocturnal migration directions and mean resultant direction (± se) per site. Two radars are from the Spanish State Meteorological Agency (AEMET, A): Oviedo [OVI], Jata [JAT]; one radar from the Basque Meteorology Agency EUSKALMET (E): Kapildui [KAP]; and four radars from the French national meteorological service (Météo-France, MF): Momuy [MOM], Bordeaux [BOR], Tréillères [TRE] and Plabennec [PLA].

manually. Dokter *et al.* (2010) developed a specific bird algorithm to automatically separate birds from non-bird targets registered by weather radars in large volumes of data. Vertical profiles of bird densities can then be generated based on the bird algorithm output. Bird density was calculated by dividing measured reflectivity in cm^2/km^3 by a radar cross-section per bird of 11 cm^2 (Dokter *et al.* 2010). Flight speed and directions were estimated from radial velocity data (for details see Dokter *et al.* 2010) in a range of 5–25 km around the radars. In this limited radius, the beam is sufficiently narrow to sample distinct altitudes without having to compensate for any range-dependent biases (Buler & Diehl 2009).

The bird algorithm was used for all available elevations at an altitudinal resolution of 200 m (20 levels from 0 to 4000 m) of the radar data. Birds were identified and separated from other echoes based on a velocity volume processing retrieved radial velocity standard deviation of >2 ms^{-1} (see Dokter *et al.* 2010 for details). In the present study, the predetermined radius of 5–25 km covered movements over land until about 15–45 km from the coast in all selected radars, except for the Plabennec radar, where the radius covered the coastal sea (distance from coast: 18 km). As the radar systems – even if operating in the same country – are not homogenous with regard to their specifications (e.g. elevation angles) and data quality, it may be necessary to adapt the parameters in the algorithm on a trial basis to eventually achieve the best data quality. Therefore, for the Tréillères radar, sample volumes were included up to 40 km because the scan elevations were very low and only permitted height coverage up to about 1.3 km at a distance of 25 km. The extended range slightly improved the height coverage to about 2 km, which was just enough to depict the entire altitudinal extension of migration on most days (Figure 4).

As a result of the specific French radar-processing scheme (triple pulse repetition time Doppler scheme), the radial velocity data were relatively noisy in comparison with earlier studies (Dokter *et al.* 2013, Kemp *et al.* 2013). Consequently, some precipitation contamination occurred, which was manually removed after careful visual inspection. The final numbers of precipitation-free nights was then included in the analysis (Table 1; mean = 23 nights). The hours considered for the analysis were restricted to the period between sunset and sunrise because this time period represents the largest biological event observed in weather radars (Koistinen 2000).

Data analysis

Bird migration patterns were described in terms of MTRs and flight directions (Bruderer 1997).

MTRs were calculated as a mean of the four measurements per hour (six for Kapildui as per system specifications) per radar for each night and site using the following equation:

$$\mathrm{MTR} = \sum (\rho \times \Delta h \times v),$$

where ρ is bird density in birds/km^3, Δh is altitude bin width (0.2 km) and v is ground speed in km/h (for calculation of ground speed see Dokter *et al.* 2009), with the sum running over all altitude bins. Rho = eta/RCS where RCS is the radar cross-section in cm^2 (= 11 cm^2) and eta is the reflectivity in cm^2/km^3. MTRs (in birds/km/h) provide a measure of the number of birds passing a line of 1 km perpendicular to flight direction in one hour (Lowery 1951). The night duration was divided into deciles. Mean migration patterns were visualized using these deciles as the time axis to line up each night with respect to sunset and sunrise.

Table 1. Number of nights per radar included in the analysis out the 37 night total.

Radar	Number of nights included	Rain days	Unavailable days
Kapildui	21	10	6
Momuy	20	11	6
Bordeaux	14	8	15
Tréillères	27	10	0
Plabennec	33	4	0

Data were managed and analysed in the program R (R Development Core Team 2008). Nightly mean MTR values were log-transformed to attain a normal distribution and then normalized by dividing each site-specific nightly mean MTR by the sum of all site-specific nightly mean MTRs to even out night-to-night variations in overall migration intensity in between-radar comparisons. Then pairwise comparisons of MTRs between neighbouring radars were tested for significance by *t*-tests with Bonferroni correction. A *t*-test was also used to check for a significant difference between the increase of MTR at sunset and sunrise and the low activity in between in the Tréillères data. Analysis of variance and a Tukey test were used to compare the MTRs between sites.

Homogeneity between the mean directions at each radar site was tested by a Watson-Williams test after confirming von Mises distribution by a Watson-U^2 test. A Rayleigh test was applied to test for the variance associated with the site-specific circular distributions (uniform vs. concentrated). Only directions with bird densities of over 5 birds/km^3 were included, to avoid very low-density measurements for which the directional information is less reliable (following Dokter *et al.* 2010).

Backtracking was used to analyse the data regarding sea crossing. Therefore, the flight distance of the birds was estimated based on the time between one hour after sunset (departure) and the first visually discernible increase of bird densities in the morning hours of the respective dates on a 24-hour vertical bird profile plot (first appearance of grey areas with wind barbs in analysed plots similar to Figure 4). This time period (hours) was then multiplied by the respective mean ground speed (speed [m/s] relative to the ground defined as the sum of air speed and wind speed) registered in each morning considered, yielding flight distances (km). Only the flight directions of the birds forming the morning peaks were used for this backtracking estimation because these would be new birds that arrive directly from the sea. In contrast, flight directions from the onset of the night would stem from nocturnal migrants taking off at surrounding land sites after having arrived already on the previous morning. Plabennec was, therefore, excluded from the backtracking as it did not exhibit any morning activity. The flight directions were then plotted on a map with a corresponding scale.

Results

Migration traffic rates

Migration occurred in three main bursts during the sampled period, that is, approximately 6–10 March, 16–

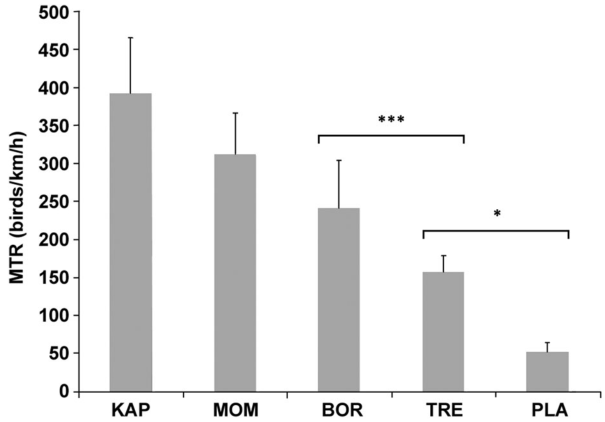

Figure 2. Comparison of nightly mean MTRs (mean MTR ± se) at each radar site (Kapildui: KAP; Momuy: MOM; Bordeaux: BOR; Tréillères: TRE; Plabennec: PLA) with significant differences between Bordeaux–Tréillères and Tréillères–Plabennec.

17 March and 1–5 April, with little or no activity in between. Mean nocturnal MTRs were highest in the Kapildui data and gradually decreased northwards, with the lowest MTRs at Plabennec (Figure 2). There were significant variations in MTRs between the sites Bordeaux–Tréillères ($t = 16.09$, df = 15, $P < 0.001$) and Tréillères–Plabennec ($t = 3.67$, df = 26, $P < 0.05$), as well as between Plabennec and all the other sites (all $P < 0.001$).

The typical general pattern of bird echoes was a sudden increase in MTRs at sunset and a rapid decrease at sunrise (Figures 3 and 4). Overall, there were three different nocturnal activity patterns: the two southernmost radars (Kapildui and Momuy) showed rather uniform nocturnal activity (MTRs) within nights. Bordeaux showed a similar tendency of uniform activity, though also a bimodal pattern on one night (3 April), indicating an increase in MTR in the evening (take-off) and morning (arrival). Tréillères showed a pronounced bimodal pattern with a peak each at the beginning and towards the end of the night (Figures 3 and 4). This pattern occurred in the three migration bursts in early and mid-March, and early April. There was a significant difference between the low MTRs of the middle decile and the peaks of both the first evening ($t = 2.40$, df = 16, $P < 0.05$) and last morning decile ($t = 2.16$, df = 16, $P < 0.05$). Plabennec showed very low MTRs overall, with minor peaks at sunset, if any (Figures 3 and 4). This pattern was consistent throughout the entire sampling period, without any difference during the migration peaks.

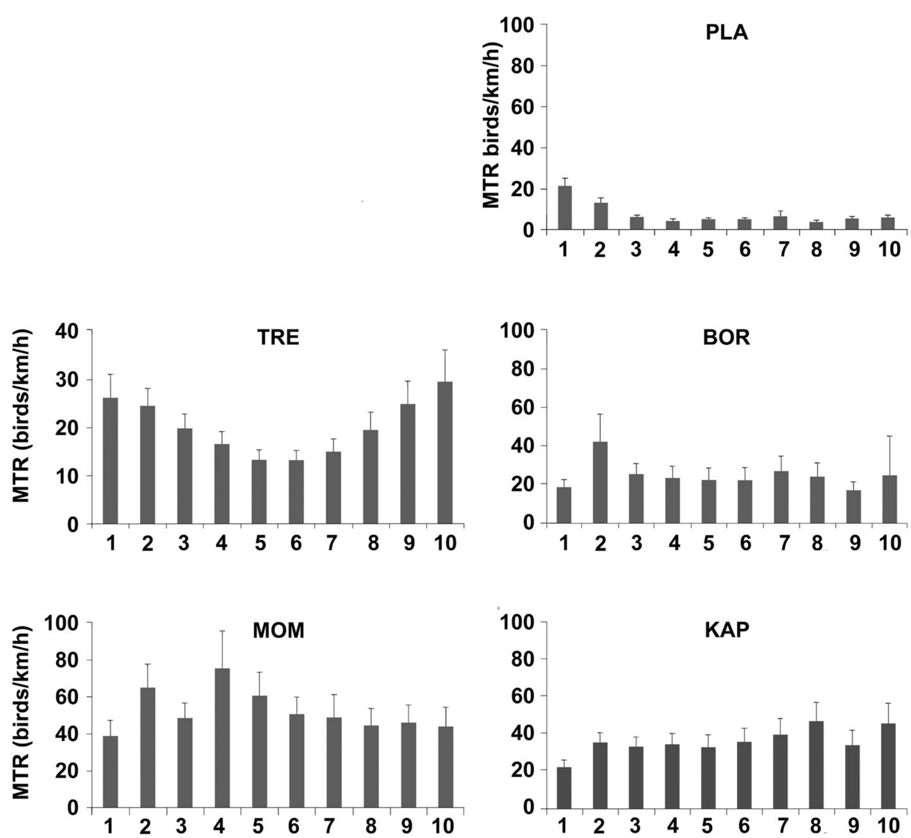

Figure 3. Comparison of hourly mean MTRs (mean MTR ± se) at the available radar sites on nights without precipitation, divided into deciles.

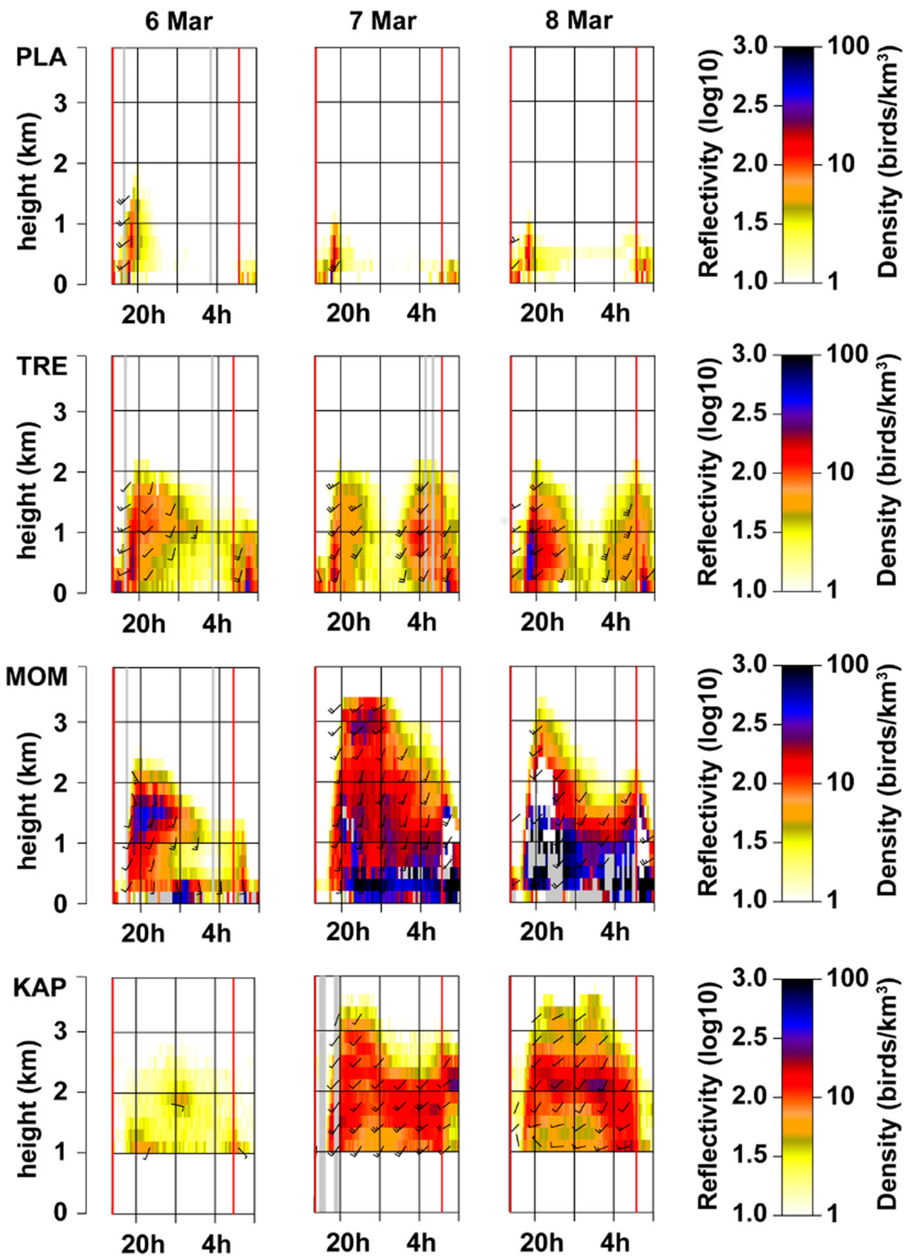

Figure 4. Examples of weather radar data from 6 to 8 March 2015: strong continuous patterns at Kapildui (KAP) and Momuy (MOM); bimodal pattern at Tréillères at 40 km (TRE); and evening peaks (20:00 hours) at Plabennec (PLA). Bordeaux was out of service. The red lines represent sunset and sunrise.

Table 2. Mean directions (± sd) of migrant birds and Rayleigh test results (*P* value) per site.

	Kapildui	Momuy	Bordeaux	Tréillères	Plabennec
Mean direction	42° ± 31.26°	36° ± 21.60°	10° ± 25.00°	25° ± 37.40°	80° ± 28.26°
Rayleigh test *P*	<0.001	<0.001	<0.001	<0.001	<0.001

Flight directions

Flight directions indicated a general northeast direction (range: 11.56–79.47°, Table 2) with a significantly different mean migratory direction at each site (Table 2, all $P < 0.001$). The southern radars Kapildui and Momuy had a more pronounced northeasterly direction than Bordeaux, which pointed almost north. Tréillères directions were again directed more towards the northeast, while Plabennec pointed eastward (Figure 1).

The mean direction of the birds that generate the morning peaks at Treilleres was 14.56° (Figure 5) and the mean flight speed was 12 m/s (43 km/h). Backtracking the birds with this direction identifies the region of Santander/Bilbao, Spain, as a possible departure site for the migrants, which would mean a flight distance of about 450 km over the open sea.

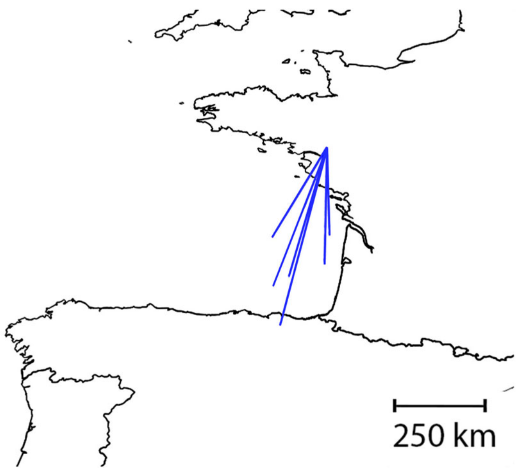

Figure 5. Backtracking of morning arrivals shown by the Tréillères radar, indicating the inner Spanish coast as a potential departure site.

Discussion

Flight directions, together with the MTRs decreasing northwards, show that the broad-front northeasterly migration generally assumed for spring (Zink 1970, Hilgerloh 1989, Trösch *et al.* 2005) is subject to certain constraints related to the sea barrier, specifically, the distance over the open water, together with general spring migration destination. The northeastern directions in the Kapildui radar and the bimodal MTR patterns at the Tréillères and Bordeaux radars indicate that the main migration proceeds at the southeastern edge of the bay with some birds crossing the sea, while some birds continue over land. In the event of uniform broad-front migration across the open sea, as suggested by Bruderer (1999), more similar MTRs would be expected between the sites, in particular also higher MTRs at the northern French coast combined with bimodal nocturnal patterns (see below) at the northernmost site. Such a divide of the migration flow was also proposed by Diehl *et al.* (2003) and Gagnon *et al.* (2011). In both these studies, only the lowest beam elevation was used to match the detection range of simultaneous counts either by short-range tracking radar (Diehl *et al.* 2003) or human observers (Gagnon *et al.* 2011). In front of barriers it is important, though, to sample the entire height profile to understand directional movements, as birds tend to ascend before venturing out on sea (Nilsson *et al.* 2014). The lowest heights might contain more migrants erring around indecisively (Weisshaupt *et al.* 2016a). So the present study certainly provides a representative account on directional movements by including all height levels.

The bimodal pattern observed in several clear nights of the Tréillères radar (and in one night in Bordeaux) is similar to patterns known from Mediterranean islands (Speich 1999) and has been interpreted as birds taking off on land in the evening and arriving from the sea in the morning, with few or no arrivals in between. These patterns occurred in the early morning hours between approximately 03:00 and 08:00 hours, during the same peak nights identified by local coastal radar and thermal imaging at the southeastern coast of the bay, that is, in the clear periods of 6–10 March, 16–17 March and 1–5 April (Weisshaupt *et al.* 2016a, 2017). Flight directions recorded in the same period on the Spanish coast pointed approximately to the Tréillères/Bordeaux region (Weisshaupt *et al.* 2016a). Considering the distance over water derived from the directions of the morning arrivals, it can be assumed that some of the Treilleres birds travel up to about 500 km over the open sea, which is up to 14 hours of flight. The stronger northeast direction at Tréillères compared to Bordeaux also supports the hypothesis of sea crossing. There is no obvious landmark which could have caused this sudden shift in direction at this latitude, which would be expected if birds had simply followed the coast from Bordeaux up to Tréillères. Sea crossing from the Basque coast would potentially allow the saving of flight time compared to flying over land. Assuming a departure from Kapildui to Tréillères over sea at a flight speed of 10 m/s (average flight speed of passerines *sensu* Bruderer & Boldt 2001) would yield a time saving of about 2–3 hours in still conditions, which could be an attractive energetic shortcut for a small passerine.

Considering the temporal occurrence of the arriving birds in the morning hours and the take-off time about 30–60 minutes after sunset from the Spanish coast (Weisshaupt *et al.* 2016a), the birds would have had to benefit from considerable tailwind (not addressed in this study), which would have increased their average travel speed of 12 m/s (40 km/h) measured at the radar site to 17 m/s (60 km/h) over sea in order to tackle the 500 km in 8 hours. The use of tailwind has been documented in previous studies (Liechti & Bruderer 1998, Dokter *et al.* 2013) and so such an increase in flight speed would be feasible for the birds.

The Bordeaux radar was out of order during the migration peak in early March and the remaining data set was too reduced to confirm or reject regular sea crossing at this site (only 1 night). The weak peaks at Plabennec at the beginning of the night, but no movements in the rest of the night, suggests that there is negligible nocturnal influx from the sea. In case of nocturnal sea crossing, a peak in the morning rather than in the evening would be anticipated for this northernmost site. The evening patterns could stem from birds that accumulated during the day over land and potentially head towards northwestern Europe. The eastward flight directions rather indicate that birds follow the coastline. Coming in from the sea on a west–east axis would not make sense for migrating songbirds in Europe. The overall low numbers at Plabennec could be linked to the long flight distance of about 550 km over water as well as generally increasing distance to land for more western departures at the northern Spanish coast, even though such a flight distance should be feasible for a passerine in one night (Bruderer & Boldt 2001). Similar avoidance of long flight distances over sea is known from the Mediterranean (Bruderer & Liechti 1999), which in the end leads to the high concentrations at the strait of Gibraltar and the Bosporus. Alternatively and probably more likely, it is possible that only few migrants, if any, take-off at the northwestern Spanish coast towards this northern corner of the bay. Such a trajectory could be too far west for most migrants heading northeastwards and might only be bypassed by birds travelling to northwestern Europe. Birds from Africa would be expected to travel more northeastwards across the Iberian Peninsula as their final destination lies somewhere in Central/Northern Europe (Alerstam 1990). Thus, they would not reach Portugal or northwestern Spain. In contrast, short-distance migrants, wintering on the Iberian Peninsula could readily depart from any site on the peninsula. The southeastern corner, in contrast, receives confluent migration from central and northern Iberia and possibly from Africa, with birds gathering in much higher quantities. Thus the observed pattern of partial sea-crossing results most likely from this large-scale flux of migrants in different quantities based on their different origins and destinations.

It remains to be studied how migration proceeds on the east–west axis and any potential impact on the observed north–south gradient in MTRs. For that purpose, it would be necessary to access unfiltered radar data in a compatible format from the northwestern Spanish coast.

The study underpins the importance of large-scale studies in migration research to understand migration dynamics and potential barrier effects from a broader bird's eye view. In particular for mass migration events such as nocturnal passerine migration, weather radar data represents a valuable source of information for research questions where the state of the art for individual tracking is not applicable. In the present study, the weather radar network successfully provided large-scale data confirming the previous hypothesis on nocturnal sea crossing in spring at the Bay of Biscay.

Acknowledgements

We acknowledge the valuable support provided by COST – European Cooperation in Science and Technology through the Action ES1305 'European Network for the Radar Surveillance of Animal Movement' (ENRAM) which facilitated the analysis in a short-term scientific mission. We further thank the Basque meteorology agency Euskalmet and AEMET for the Spanish data, the French meteorology agency Meteo France and in particular Dr Günther Haase from SMHI for providing the French radar data. Anonymous reviewers helped improve previous versions of this manuscript.

References

Alerstam, T. 1990. *Bird Migration*. Cambridge University Press, Cambridge.

Alerstam, T. 2001. Detours in bird migration. *J. Theor. Biol.* **209:** 319–331.

Arizaga, J., Fontanilles, P., Laso, M., Andueza, M., Unamuno, E., Azkona, A., Koenig, P. & Chauby, X. 2014. Stopover by reed-associated warblers *Acrocephalus* spp. in wetlands in the southeast of the Bay of Biscay during the autumn and spring passage. *Revista Catalana d'Ornitología* **30:** 13–23.

Biebach, H. 1990. Strategies of trans-Sahara migrants. In Gwinner, E. (ed) *Bird Migration: physiology and ecophysiology*, 399–412. Springer-Verlag, Berlin.

Bruderer B. 1997. The study of bird migration by radar. Part 1: the technical basis. *Naturwissenschaften* **84:** 1–8.

Bruderer, B. 1999. Three decades of tracking radar studies on bird migration in Europe and the Middle East. In Leshem, Y., Mandelik, Y. & Shamoun-Baranes, J. (eds.) *Proc. Int. Seminar on Birds and Flight Safety in the Middle East*, 107–141. Tel Aviv University, Tel-Aviv.

Bruderer, B. & Boldt, A. 2001. Flight characteristics of birds: 1. Radar measurements of speeds. *Ibis* **143:** 178–204.

Bruderer, B. & Liechti, F. 1998. Flight behaviour of nocturnally migrating birds in coastal areas: crossing or coasting. *J. Avian Biol.* **29:** 499–507. Optimal Migration.

Bruderer, B. & Liechti, F. 1999. Bird migration across the Mediterranean. In Adams, N.J. & Slotow, R.H. (eds.) *Proc. 22 Int. Ornithol. Congress, Durban*, 1983–1999. BirdLife South Africa, Johannesburg.

Buler, J.J. & Diehl, R.H. 2009. Quantifying bird density during migratory stopover using weather surveillance radar. *IEEE Trans on Geosci Remote Sens*. **47**: 2741–2751.

Diehl, R.H., Larkin, R.P. & Black, J.E. 2003. Radar observations of bird migration over the Great Lakes. *Auk* **120**(2): 278–290.

Dokter, A.M., Liechti, F. & Holleman, I. 2009. *Bird detection by operational weather radar*. KNMI Scientific report. WR 2009–06. De Bilt, Netherlands.

Dokter, A.M., Liechti, F., Stark, H., Delobbe, L., Tabary, P. & Holleman, I. 2010. Bird migration flight altitudes studied by a network of operational weather radars. *J. R. Soc Interface*. DOI:10.1098/rsif.2010.0116.

Dokter, A. M., Shamoun-Baranes, J., Kemp, M.U., Tijm, S., Holleman, I. & Saino, N. 2013. High altitude bird migration at temperate latitudes: a synoptic perspective on wind assistance. *PLoS One*. **8:** e523. DOI:10.1371/journal.pone.0052300.

Finlayson, C. 1992. *Birds of the Strait of Gibraltar*. T. & A. D. Poyser, London.

Fortin, D., Liechti, F. & Bruderer, B. 1999. Variation in the nocturnal flight behaviour of migratory birds along the northwest coast of the Mediterranean Sea. *Ibis* **141:** 480–488.

Gagnon, F., Ibarzabal, I., Savard, J-P.L., Bélisle, M. & Vaillancourt, P. 2011. Autumnal patterns of nocturnal passerine migration in the St. Lawrence estuary region, Quebec, Canada: a weather radar study. *Can. J. Zool.* **89:** 31–46.

Gangoiti, G., Alonso, L., Maruri, M., Navazo, M. & Pérez-Landa, G. 2002. UHF radar detection and numerical simulation of an episode of Foehn and Lee Waves over the Northern Coast of Iberia. *J. Appl. Meteorol.* **41:** 230–240.

Gauthreaux, S.A., Belser, C.G. & Blaricom, D.V. 2003. Using a network of WSR-88D weather surveillance radars to define patterns of bird migration at large spatial scales. In: Berthold, P., Gwinner, E. & Sonnenschein, E. (eds) *Avian Migration*, 335–346, Springer-Verlag, Berlin Heidelberg.

Grandio, J.M. & Belzunce, J.A. 1987. Migración posnupcial de carriceros (género Acrocephalus) y otros passeriformes típicos de carrizal en el Valle de Jaizubia (Guipúzcoa). *Munibe* **39:** 81–94.

Hilgerloh, G. 1989. Orientation of trans-Saharan passerine migrants in southwestern Spain. *Auk* **106:** 501–502.

Kelly, J. F., Horton, K.G., Stepanian, P.M., de Beurs, K.M., Fagin, T., Bridge, E.S. & Chilson, P.B. 2016. Novel measures of continental-scale avian migration phenology related to proximate environmental cues. *Ecosphere.* **7:** e01434. DOI:10.1002/ecs2.1434.

Kemp, M.U., Shamoun-Baranes, J., Dokter, A.M., van Loon, E., Bouten, W. & Norris, R. 2013. The influence of weather on the flight altitude of nocturnal migrants in mid-latitudes. *Ibis* **155:** 734–749. DOI:10.1111/ibi.12064.

Koistinen, J. 2000. Bird migration patterns on weather radars. *Phys. Chem. Earth (B)* **25**(10–12): 1185–1193.

Kokko, H. 1999. Competition for early arrival in migratory birds. *J. Anim. Ecol.* **68:** 940–950.

Lack, D. & Lack, E. 1953. Visible migration through the Pyrenees: an autumn reconnaissance. *Ibis* **95:** 271–309.

Liechti, F. 2006. Birds: blowin' by the wind? *J. Ornithol.* **147:** 202–211.

Liechti, F. & Bruderer, B. 1998. The relevance of wind for optimal migration theory. *J. Avian Biol.* **29:** 561–568.

Lowery, G.H. 1951. *A quantitative study of the nocturnal migration of birds*. Univ. Kansas Publ. *Mus. Nat. Hist.* **3:** 361–472.

Maruri, M., Romo, J.A. & Gomez, L. 2014. Aspects of quality control of wind profiler measurements in complex topography. *Atmos. Meas. Tech.* **7:** 135–148.

Mendiburu, A., Aranguren, I., Elosegi, Z., Jauregi, J.I., Sánchez, J.M., Cuadrado, J.F., Alonso, D. & Arizaga, J. 2009. Resultados de la primera campaña de anillamiento en el paso migratorio posnupcial en la vega de la regata de Jaizubia (marismas de Txingudi). *Revista de Anillamiento* **23:** 26–34.

Newton, I. 2008. *The Migration Ecology of Birds*. Academic Press, Elsevier Ltd, London.

Nilsson, C., Bäckman, J. & Alerstam, T. 2014. Are flight paths of nocturnal songbird migrants influenced by local coastlines at a peninsula? *Curr. Zool.* **60:** 660–669.

R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for statistical computing, Vienna. http://www.R-project.org.

Sanderson, F.J., Donald, P.F., Pain, D. J., Burfield, I.J. & van Bommel, F.P.J. 2006. Long-term population declines in Afro-Palearctic migrant birds. *Biol. Conserv.* **131:** 93–105.

Shamoun-Baranes, J., Alves, J.A., Bauer, S., Dokter, A.M., Hüppop, O., Koistinen, J., Leijnse, H., Liechti, F., van Gasteren, H. & Chapman, J.W. 2014. Continental-scale radar monitoring of the aerial movements of animals. *Mov. Ecol.* **2**(9): 1–6. DOI:10.1186/2051-3933-2-9.

Sjöberg, S. & Nilsson, C. 2015. Nocturnal migratory songbirds adjust their travelling direction aloft: evidence from a radiotelemetry and radar study. *Biol. Lett.* **11**. DOI:10.1098/rsbl.2015.0337.

Speich, S. 1999. Temporal and spatial pattern of nocturnal bird migration across the western Mediterranean Sea studied by radar. Diploma Thesis, University of Basel and Swiss Ornithological Institute. https://www.speich.net/about/diplomarbeit.pdf.

Trösch, B., Lardelli, R., Liechti, F., Peter, D. & Bruderer, B. 2005. Spatial and seasonal variation in nocturnal autumn and spring migration patterns in the western Mediterranean area: a moon-watching survey. *Avocetta* **29:** 63–73.

Weisshaupt, N., Maruri, M. & Arizaga, J. 2016a. Nocturnal bird migration at the southeastern Bay of Biscay as observed by thermal-imaging camera. *Bird Study* **63:** 533–542.

Weisshaupt, N., Maruri, M. & Arizaga, J. 2016b. Preliminary assessment of nocturnal bird migration at the Bay of Biscay as observed by moon-watching. *Munibe* **64:** 155–159. doi:10.21630/mcn.2016.64.03.

Weisshaupt, N., Lehmann, V., Arizaga J. & Maruri, M. 2017. Radar wind profilers and avian migration – a qualitative and quantitative assessment verified by thermal imaging and moon watching. *Methods Ecol. Evol.* DOI:10.1111/2041-210X.12763.

Zink, G. 1970. *Der Zug europäischer Singvögel. Ein Atlas der Wiederfunde beringter Vögel.* Vogelwarte Radolfzell, Radolfzell.