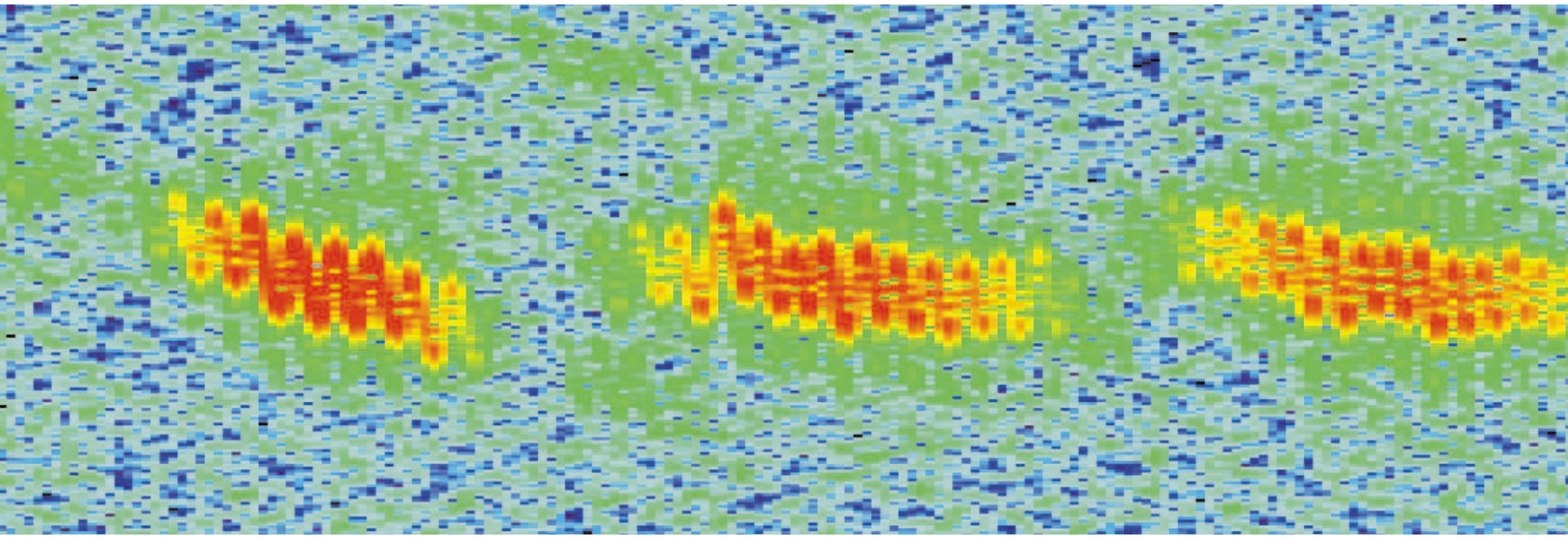
The role of seas as a geographical barrier for migratory landbirds. An approach to the Bay of Biscay.



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The role of seas as a geographical barrier for migratory landbirds. An approach to the Bay of Biscay.

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I. Weisshaupt, N., Arizaga, J. and Maruri, M. The use of radar wind profilers in ornithology: a review. Ibis: submitted.

II. Weisshaupt, N., Maruri, M. and Arizaga, J. Nocturnal bird migration at the southeastern Bay of Biscay as observed by thermal-imaging camera. Bird Study: accepted on 16 Sept 2016.

III. Weisshaupt, N., Maruri, M. and Arizaga, J. (2016) Preliminary assessment of nocturnal bird migration at the Bay of Biscay as observed by moon-watching. Munibe, 64.

IV. Weisshaupt, N., Lehmann, V., Arizaga, J. and Maruri, M. Radar wind profilers and avian migration - a qualitative and quantitative assessment verified by thermal imaging and moon watching. Methods in Ecology and Evolution: in revision.

V. Weisshaupt, N., Dokter, A., Arizaga, J. and Maruri, M. Effects of a sea barrier on large-scale migration patterns studied by a network of weather radars. Manuscript.

Sunset at Punta Galea meteorological station.

ABSTRACT

The East-Atlantic flyway represents one of the main bird migration routes worldwide, comprising the Bay of Biscay as an inherent geographical barrier. So far, the significance of the Bay of Biscay for migrants and its potential impact on migratory routes have not received much attention in research. The general aim of this thesis is to unravel the role of the Bay of Biscay as a geographic barrier both at a small and large scale shaping the nocturnal migration of landbirds moving along the East-Atlantic flyway. All observation tools available in the study region deemed suitable for nocturnal studies were employed: operational wind profiler and weather radars, thermal imaging and moonwatching. Previous knowledge from visual observations and bird ringing available in literature was also taken into account. Furthermore, in a pioneer approach, the study assessed the potential use of wind profiler data in an ornithological context. An objective qualitative and quantitative approach validated by thermal imaging was established to extract migration parameters.

Migration traffic rates, flight directions and altitudes obtained by the two types of radars and thermal imaging for various sites along the bay are provided and discussed in a meteorological and ecological context. Vertical historical wind profiler and current thermal imaging data indicated pronounced broad-front migration in early spring vs. more eastward (i.e. sea-avoidance) migration in autumn. Moonwatching provided additional information on bird composition and confirmed predominance of passerines. Finally, horizontal weather radar data revealed a north-south gradient along the French coast in spring, with higher intensity in the south-eastern study area close to the main migration axis of the East-Atlantic flyway.

Study region in La Rioja.

INTRODUCTION AND OBJECTIVES

Bird migration, the annual movement of millions of birds between their breeding and wintering grounds, has fascinated humankind for centuries and incited extensive research. Even though we nowadays know that swallows do not overwinter at the bottom of lakes, there are still many unsolved questions because of the manifold external and internal factors influencing migratory species on their journeys.

One key characteristic of migratory species is that they transit large geographical areas throughout the annual cycle (Newton 2008). As a consequence, the population dynamics and ultimately the conservation of the migratory species are affected not only by events in the breeding areas, but also by those during migration and in the wintering grounds up to several thousands of kilometres away (Zwarts et al. 2009). Therefore, it is essential both from a biological and ecological point of view to identify the migratory flyways connecting breeding and wintering areas as well as stopover sites en route (Webster and Marra 2005). In this context, the geographical barriers play a significant role as they shape migratory routes and strategies.

GEOGRAPHICAL BARRIERS

The migratory flyways of landbirds are strongly determined by geographical barriers such as deserts, extensive mountain ranges and large water bodies. These barriers often have a deterrent effect on birds because of scarce or inexistent refuelling opportunities, and adverse atmospheric conditions with an inherent high risk of drift and detours compromise survival (Alerstam 1990).

In regard to water bodies, it is well-known that landbirds have developed migratory strategies to avoid or reduce sea crossing (Kerlinger 1985, Alerstam 2001), or alternatively to accumulate large fat reserves before crossing (Schaub and Jenni 2000). The Bay of Biscay as part of the Atlantic Ocean is situated in western Europe and is one of the main geographical barriers along the East-Atlantic flyway between Scandinavia and Iberia. Galarza and Tellería (2003) presented data favouring the hypothesis that European landbirds tend to avoid crossing the Bay of Biscay during migration, even though this might entail a longer journey between breeding and wintering areas. In contrast, there are quite many observations of landbirds in active flight over the Bay of Biscay, reported from ships out on the sea (Arizaga pers. comm.) and from the coast (Lack and

Lack 1953). When, how and under which circumstances migratory landbirds decide to cross the Bay of Biscay is still largely unknown. Data obtained at coastal ringing sites seem insufficient to disentangle these dynamics, since this information is biased towards those birds that decide to land just before or after the barrier. However, ringing does not provide any answer as to whether and to what extent birds cross the open sea.

It would be important to gain a comprehensive overview over the migration dynamics along and across the bay to correctly assess the significance of its coastal ecosystems as stopover sites for migratory birds. If landbirds readily crossed the bay, the coastal ecosystems would be important as refuelling sites before and/or after crossing. If landbirds avoided crossing the bay, the coastal ecosystems of the region might play a secondary role, as migrants might pass further inland and/or migrate in short hops not requiring the accumulation of large energy quantities (Delingat et al. 2006).

EXTERNAL DRIVERS OF MIGRATION

Various external factors have been identified which potentially have an impact on a bird's decision whether or not to cross a barrier. Meteorological conditions, such as wind velocity and direction (head vs. tailwinds), visibility and precipitation play a major role as they could have an impact on orientation and/or general survival (Alerstam 1990). Then, the urge to reach the breeding grounds in a timely manner and to establish a territory leads to more direct routes in spring than in autumn (Koko 1999), even if this might entail taking greater risks and crossing larger geographical barriers (Zink 1973-1985, Agostini et al. 2005). From that it could be inferred that the proportion of birds crossing the Bay of Biscay is higher in spring than in autumn, potentially also under suboptimal meteorological conditions.

STUDYING LARGE-SCALE MOVEMENTS

In order to study such large-scale mass movements of free-flying birds appropriate observation tools are indispensable (Millikin 2005).

Studying diurnal mass migration offers the advantage of employing manifold observation aids such as binoculars or telescopes, paired with the fact that daytime migration predominantly involves large species and dense flocks (Alerstam 1990, Gschweng et al. 2008), which are more easily detected by mere human vision.

Nocturnal migration, in contrast, consists mostly of small passerine migrants traveling individually and requires a particular set of observation tools (Millikin 2005). Studying active nocturnal migration excludes certain sampling methods per se such as ringing and visual counts based on the inherent conditions at night (low visibility). Technologies must be able to tackle darkness, offer a large spatial coverage of at least several kilometres, ideally be insensitive to wind, surface temperatures and other weather conditions, and provide information on migration parameters, including flight direction, speed and altitude as well as migration intensity. Species identification is not (yet) feasible with today's remote-sensing technologies.

In the course of the history of migration studies, a variety of techniques have been tested. Already in the 19th century lunar observations were used to quantify nocturnal migration around full moon (Lowery 1951). Nowadays, various temporally more flexible remote-sensing technologies, such as radar or thermal imaging, are available to shed light on the darkness. Radar technology and thermal imaging have proved to be efficient to study behavioural patterns at geographical barriers and/or in a variety of weather conditions (Liechti et al. 1995, Bruderer 1999). In particular radar technology offers many advantages in ornithology in comparison to other investigational methods such as visual counts or ringing. Less expenditure of time and effort, superior visibility and detectability (e.g. at higher altitudes or in the dark), as well as better applicability for large-scale monitoring (Shamoun-Baranes et al. 2014) are some of the obvious advantages, which have made radars a preferential tool in nocturnal migration studies.

LOCAL SETTINGS

A vertically pointing wind profiler situated in the outskirts of Bilbao at the Basque coast has seasonally exhibited signs of biological targets ever since its installation in 1996. Radar data quality was most severely affected during nights in early spring. Literature suggested birds as a possible source (Maruri 2001). Based on previous ringing data and visual daytime observations the region has been known for its pronounced migratory passage in autumn and low activity in spring (Lack and Lack 1953, Arizaga et al. 2014). However, the migration patterns observed in this radar indicated strong spring migration and weak autumn migration (Maruri pers. comm.). Therefore, the question arouse if these radar echoes stemmed from birds, and if so, if this radar and its extensive database could provide complementary new data on migration dynamics that have remained unappreciated by previously employed monitoring techniques.

OBJECTIVES

The aim of this PhD thesis is to investigate nocturnal migration patterns at the Bay of Biscay. The main focus consists in (1) complementing the aforementioned scarce knowledge on migration dynamics at the Bay of Biscay and its potential role as a geographical barrier by employing established technologies particularly suitable for nocturnal studies (radars, thermal imaging and moon watching); and (2) to assess the radar wind profiler as a new observation tool for ornithological purposes by establishing reproducible objective criteria to extract qualitative and quantitative measures of migration.

Nocturnal thermal-imaging recording at Cape Higuer camping site.

METHODOLOGY

STUDY SITES

Data was obtained from 10 sites situated around the Bay of Biscay (Fig. 1 [Map-ALLSites.jpg], Table 1): (1) At the Punta Galea station (PG; 43.37°N, 3.04°W), which is operated by the Directorate of Emergency and Meteorology of Euskalmet (Basque Meteorology Agency), wind profiler, thermal imaging and moonwatching data was collected. The site is situated at the brink of a cliff at the Basque coast in the outskirts of Bilbao, Spain. Its exposed location close to the sea makes it a perfect place to study behavioural patterns at a geographical barrier. (2) At Cape Higuer (CH; 43°23′N, 1°47′W), a coastal campsite situated 100 km east of Punta Galea, at the innermost part of the bay. The site lies close to the local ringing station Txingudi which had so far provided data on diurnal migration, and was chosen as a comparative site for thermal imaging

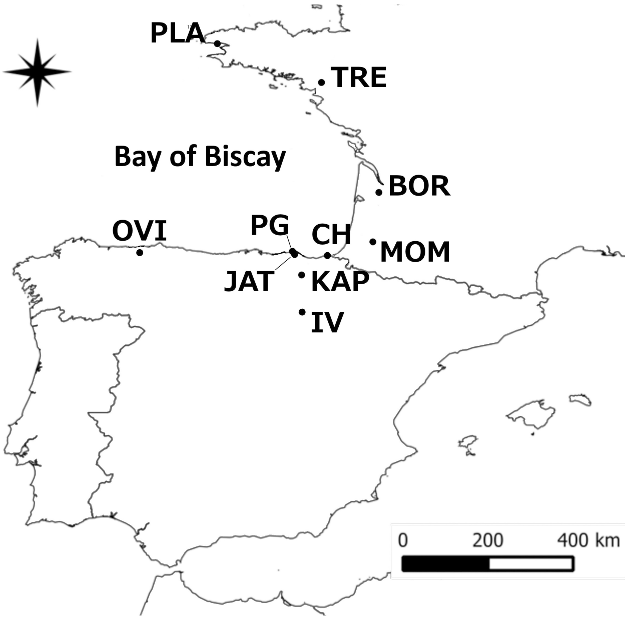

FIG. 1 *The Bay of Biscay with the locations of a) the radar wind profiler at Punta Galea (PG); b) thermal-imaging/moonwatching sites PG, Cape Higuer (CH) and the Iregua Valley (IV) and c) the weather radar sites Oviedo (OVI), Jata (JAT), Kapildui (KAP), Momuy (MOM), Bordeaux (BOR), Tréillères (TRE) and Plabennec (PLA).*

TABLE 1. *Use of remote-sensing devices per site: Punta Galea (PG), Cape Higuer (CH), Iregua Valley (IV), Oviedo (OVI), Jata (JAT), Kapildui (KAP), Momuy (MOM), Bordeaux (BOR), Tréillères (TRE) and Plabennec (PLA).*

	PG	CH	IV	OVI	JAT	KAP	MOM	BOR	TRE	PLA
Wind profiler	X									
Thermal imaging	X	X	X							
Moonwatching	X	X	X							
Weather radar				X	X	X	X	X	X	X

FIG. 2 *Wind profiler site at Punta Galea, Bilbao, Spain.*

and moonwatching data in order to check for an east-west gradient in migration intensity. (3) The Iregua Valley (Ebro river basin) at Villoslada de Cameros (IV; 42°04’N 2°41’W) served as a more southern and inland reference site for thermal imaging and moonwatching in autumn only. (4) Oviedo (OVI; 43°27’N 6°18’W), (5) Jata (JAT; 43°24’N 2°50’W), and (6) Kapildui (KAP; 42°45’N 2°32’W) were the weather radar sites in Spain, and French weather radar data was obtained from (7) Momuy (MOM; 43°37’“N 0°36’W), (8) Bordeaux (BOR; 44°49’N 0°41’W), (9) Tréillères (TRE; 47°20’N 1°39’W) and (10) Plabennec (PLA; 48°27’N 4°25’W). These weather radars were selected because of their close proximity to the Bay of Biscay.

INSTRUMENTATION TO STUDY MIGRATION AT A BARRIER

The presence of the sea as a geographical barrier with challenging meteorological conditions (high and frequent precipitation, variable winds) sets logistic and methodological constraints besides low visibility at night. Therefore, all remote-sensing and observation tools available in the study region were employed which could cope with local settings and which would be suitable to study nocturnal migration as per literature and own experience: radar (radar wind profiler and weather radars), thermal imaging and moon-watching. The different systems are described below. An initial review of the available literature also took findings from previous bird ringing campaigns and visual observations into account, which provided an overview over the current state of knowledge on diurnal migration in the region.

WIND PROFILER

The RWP at Punta Galea (Fig. 2) is a boundary layer wind profiler operating at a frequency of 1290 MHz. It is a phased-array Doppler radar with nine microstrip patch antenna panels which make use of the Doppler Beam-Swinging technique. The radar provides continuous, real-time vertical profiles of three-dimensional winds and virtual temperature by means of five beams, one vertically pointing and four tilted orthogonally by 15.5 degrees towards the four cardinal points, with an opening angle of 6 degrees. The RWP operates with two alternating resolutions with two different electromagnetic pulses, a low mode with a 60-m pulse length (corresponding to a 417-ns pulse) for measurements up to about 2 km in good meteorological conditions and a high mode with 400-m pulse length (corresponding to a 2833-ns pulse) for measurements up to about 4-8 km high in favourable conditions (Alonso et al. 1998). Sampling each of the five beam directions with both short and long pulse defines a measurement cycle of 5 minutes.

Wind profilers use refractive index irregularities as tracers in the wind. The backscatter registered by the receiver is converted to a complex I-Q signal and a signal processing chain is run consisting of coherent integration, spectral analysis, incoherent integration of a Doppler spectra, estimation of the moments. Finally a consensus algorithm is applied to calculate the final product, the three-dimensional wind vector. The operational parameters to archive data are configured in a way to store time series (raw data) and filtered spectral, moment, and consensus data. The data is visualized by means of the manufacturer's software: graphXM for consensus data (typically a wind barb plot depicting speed, SNR, vertical velocity in colours according to user-specified parameters), lapMom for the moments (time-height plot), LapXM-Console for spectral and time series, (stacked-contour-tabulated plot). For a detailed description of the system see the Vaisala User's Guide (2007).

THERMAL-IMAGING CAMERA

A long-range thermal-imaging camera (LORIS, IRTV-445L, Inframetrics, Massachusetts, U.S.A.) was used with an opening angle of 1.45° degrees. Thermal-imaging systems are based on the detection of differences in thermal radiation emitted by objects. Birds as endotherms differ therefore clearly from ambient air temperature and are visualized as contrasting objects in the sky passing the screen. From direct comparisons with tracking radar it is known that the camera is able to detect small-sized passerines up to 3000 m above ground level in clear skies (Liechti et al. 1995). Thermal imaging provides various migration parameters, such as migration intensity, direction and spatial arrangement of migrants (e.g. dense flocks vs. individuals). Flight altitudes can be estimated based on size classification of targets (Zehnder et al. 2001a). Identification of species is not possible, but it can be assumed that the majority of nocturnal migrants are passerines migrating alone or in loose not distinguishable flocks, while distinct flocks are indicators for non-passerines (e.g. waterfowl, waders). Larger flocks and many non-passerines (e.g. soaring species) tend to be more common in diurnal migration (Bruderer 1971, Alerstam 1990). Therefore, a rough classification between passerines vs. non-passerines can be implemented based on individual vs. flocking targets.

MOON WATCHING

Moon watching is probably the most ancient method to study nocturnal migration - it implies observing the lunar disc from two nights prior to until two nights after full moon by a visual aid such as a telescope and counting all the birds that pass in front of the moon

(Lowery 1951). The method is inseparably intertwined with cloudless skies which can be challenging in areas of typically instable weather conditions such as the Bay of Biscay. Watching the moon by naked eye would have irritated the eyes after a short while because of the intense moonlight. For that reason, migration in front of the lunar disc was "videoscoped" (video recording through telescope) by means of a telescope (Swarosvki ATS 65 HD, Zoom 20-60x) and a digital camera (Canon, Power Shot SX220 HS). In addition, this approach also allowed reviewing the moonwatching sequences, if necessary.

WEATHER RADARS

Horizontal-scanning operational weather radars mainly provide continuous and spatially comprehensive data on hydrometeors. Their ability to register biological targets such as birds and insects has attracted the attention of the ornithological and entomological community which has recently started to make increasingly use of this valuable data source (Koistinen 2000, Shamoun et al. 2014). The COST action ENRAM (European Network for the Radar surveillance of Animal Movement) is dedicated to the development and improvement of an automatic bird algorithm to extract information on bird migration from weather radar data which can then be used for ornithological research (Dokter et al. 2010). In the present study, this bird algorithm was used to extract migration traffic rates, flight directions and flight altitudes. Horizontal information was collected from all C-band weather radars of the OPERA network at or as close as possible to the coast of the Bay of Biscay. The radars provide four (six for Kapildui) measurements of radial velocity and reflectivity per hour for 20 elevations between 0-4000m above ground level yielding an altitudinal resolution of 200m.

APPROACH FOR DATA COLLECTION AND ANALYSIS

In contrast to weather radars, wind profilers have not raised much biological interest, even though they have been known to register bird movements as well (Wilczak et al. 1995). Research efforts have been focused on removing the biological signals rather than studying them. Therefore, in a first step of the thesis, available knowledge on wind profilers in conjunction with birds was reviewed, presented in **PAPER I**. Based on this review, it can be concluded that wind profilers have so far not been used in purely ornithological studies. The origin of the biological signals was never scrutinized and there was no objective method available to quantify bird targets and to finally calculate migration parameters.

In a second step, the radar database from the local wind profiler was examined and three years (2010-2012) of a good quality dataset were selected to gain an overview over seasonal and diurnal occurrence of biological signals at the radar site. This analysis was based on filtered consensus, moment and spectral data, which allowed identifying two annual peaks of nights with biological presence, i.e. March/April and August/September. (The findings were included and published in a later context in **PAPER IV.**) Based on these findings, the first step of a thermal imaging campaign in combination with moon-watching was set up to verify the origin of the presumed biological signals in the radar data and to compare migration intensities at different locations on a regional scale. Fieldwork took place at three sites during four hours from sunset at Punta Galea (Mar-May and Aug-Oct 2014, and Mar-Apr 2015), Cape Higuer (Aug-Oct 2014, Mar-Apr 2015) and in the Iregua Valley (Aug-Oct 2014). Data was recorded on videotapes for posterior digitalization and analysis to calculate migration traffic rates, flight altitudes and flight directions from the bird tracks. Results are detailed in **PAPER II**. Thermal imaging data revealed high migration intensity in spring in Punta Galea and Cape Higuer and low migration intensity in autumn at Punta Galea, though high intensity at Cape Higuer and in the Iregua Valley. Flight altitudes were generally high at about 2 km for all three sites and the Iregua Valley exhibited a more southward flight direction compared to the coastal sites.

Moon watching was carried out during thermal-imaging sessions at the three study sites in the same study periods in 2014 and 2015. The aim was to complement information on nocturnal bird composition from radar and thermal imaging data. No estimation of migration intensity was targeted. Details are presented in **PAPER III**. Overall, findings coincided with other studies showing predominance of passerines at night.

Once the origin of the seasonal signals had been confirmed as birds, the validation campaign of the wind profiler radar went over to the next phase, which was aimed at evaluating if a objective reproducible and robust methodology could be established that would allow calculating migration parameters (such as flight altitude or migration intensity) from wind profiler data. From the initial review of the filtered data products (spectral, moment and consensus data) it was clear that quantitative and qualitative criteria could only be obtained from raw time series data, which would require the development of a pioneer approach. In order to guarantee the success of this undertaking, expert knowledge on wind profiler signal processing was sought from Dr. Volker Lehmann at the Meteorological Observatory in Lindenberg, Germany. The COST action ENRAM approved a scientific mission at the meteorological observatory supporting this collaboration. The study was based on the calibration campaign in March 2015 combining wind profiler, thermal imaging and moonwatching data. The resulting successful qualitative and quantitative assessment of wind profiler data for the use as an ornithological research tool is provided in **PAPER IV**.

In order to complement the vertical data from the wind profiler and thermal imaging in March 2015, i.e. to set the local data into a broader geographical framework, horizontal information from the seven C-band weather radars was collected. The study period was limited to March 2015 in order to match the spring calibration campaign involving the wind profiler and thermal imaging. Data was processed by means of the algorithm developed by Dokter et al. (2010) and findings are discussed in **PAPER V.** Results indicate decreasing migration intensity from south to north in spring with general NE directions, with a potential funnelling effect in the southeastern edge between the sea and the foothills of the Pyrenees involving partial sea crossing. Unfortunately, it was not possible to obtain any information on a possible east-west gradient on the southern edge of the bay beyond Punta Galea because of an unfavourable degree of filtering in the respective weather radar data from Jata and Oviedo. Such more western data and preferably also more southern data would be needed to clarify the funnelling hypothesis.

CONCLUSIONS

The exhaustive selection of technologies employed in this project proved suitable to obtain novel insights on nocturnal migration dynamics at the Bay of Biscay. The main findings are as follows.

1. Historical wind profiler data and current thermal-imaging data revealed concordantly high nocturnal migration activity in early spring (March-April) and low activity in autumn at Punta Galea.

2. Comparison between the thermal imaging study sites indicated migration on a broader front in spring, compared to autumn, when migration concentrated closer to the Pyrenees, suggesting avoidance of the sea during this period.

3. Moon-watching identified the majority of the bird targets at night as passerines.

4. The qualitative and quantitative analysis of the wind profiler data allowed identifying reproducible criteria to extract migration parameters, such as flight altitudes and migration intensity, independent of weather conditions.

5. Weather radar data permitted to identify a north-south gradient along the French coast in spring. These patterns support the hypotheses that spring migration does not evolve on a broad uniform front across the entire bay, but rather concentrates in the southeastern edge.

It was not possible to characterize migration dynamics across the bay as the detection range of the technologies in combination with the applied methodology was not enough to reach beyond the coastline. Furthermore, constraints arose from heterogeneous filtering of weather radar data by the different providers. Generally, the degree of filtering can either be due to the technical infrastructure of the operational system or due to specifications defined by the operator. In biological studies, the degree of filtering is crucial as birds and other biological targets are usually considered as contamination to be removed. Through operator-specified filtering and storage, data from the two westernmost Spanish radars (Jata and Oviedo by AEMET) did not fulfil the requirements for the bird algorithm analysis and had to be excluded from the study. As a consequence, the migration patterns at the northwestern coast of Spain remain unknown.

Future work should extend the nocturnal measurements towards the northwestern coast of Spain in order to complement current findings on the migratory dynamics. Furthermore, measurements covering the actual sea area should be taken into account, as well as applying the same set of nocturnal measurements to autumn migration along the entire coast of the Bay of Biscay. As to the wind profiler data, more work is required to further explore the information available in time series data, both in regard to birds and potentially other biological targets in order to max out the benefits from the data of these types of operational radars.

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SPANISH SUMMARY - RESUMEN EN CASTELLANO

La migración de las aves incluye el desplazamiento de millones de individuos entre sus área de cría e invernada. Este fenómeno ha dado lugar a múltiples estudios científicos con el objeto de analizar los diversos factores que influyen en los patrones y dinámicas relacionados con la migración de las aves.

Durante sus migraciones, a menudo las especies migratorias recorren grandes distancias. Como consecuencia, la dinámica poblacional y la conservación de estas especies se ve afectada no sólo por las circunstancias en las áreas de reproducción, sino también por aquellas en las rutas migratorias e invernada. En este escenario, el conocimiento de las estrategias migratorias es capital, tanto desde un punto de vista biológico y ecológico como de la conservación.

A lo largo de las rutas migratorias de las aves terrestres existen varios factores que pueden tener un impacto sobre la supervivencia, tales como las condiciones meteorológicas extremas (vientos fuertes, precipitación...) y las barreras geográficas como desiertos, grandes cordilleras y mares. Los riesgos asociados a estas barreras geográficas son generalmente la falta de posibilidades de parar para descansar y reponer la energía consumida durante el vuelo.

El Mar Cantábrico está ubicado en el extremo occidental de la ruta del Atlántico oriental, una de las principales rutas migratorias de aves en Europa, que arranca en el sur de Escandinavia y recorre la costa del continente hasta el suroeste de la península ibérica, para de allí dar el salto a África. Diversos trabajos aportan datos a favor de la hipótesis de que las aves terrestres europeas tienden a evitar cruzar el mar Cantábrico durante sus migraciones, pero también existen observaciones de aves terrestres en migración activa diurna a través del Cantábrico, obtenidas bien desde barcos situados en alta mar, bien desde la costa. Así pues, el papel del mar Cantábrico como barrera geográfica para la migración de aves terrestres y de los sitios costeros como áreas de descanso y reposición está aún por ser determinada. También queda por investigar la influencia de la meteorología o estación del año en los patrones de migración; esto es, determinar bajo qué condiciones las aves cruzan, o no, el Cantábrico.

Para investigar la migración nocturna, los radares se han utilizado con éxito en muchos estudios. Esta tecnología nos permite acceder a información que no sería asequible con otras técnicas, como muestreos nocturnos o muestreos en otras condiciones de visibilidad reducida y a gran escala.

Otras tecnologías para investigar la migración nocturna son las cámaras térmicas y observaciones lunares. En estudios previos las cámaras térmicas permitieron recaudar datos sobre flujo, dirección y distribución altitudinal de aves y para verificar los datos de radares. Y por último, en las observaciones lunares se observa el disco lunar con un telescopio registrando la aves que pasan enfrente de la luna. Este método se limita a unos pocos días antes y después de la luna llena.

Para este estudio se utilizaron datos de dos tipos de radares (un perfilador y 7 radares meteorológicos, 3 de España, 4 de Francia), así como una cámara térmica y observaciones lunares (los sistemas se detallan en la parte en inglés). Los puntos de muestreo están indicados en Fig. 1. Los datos de la cámara térmica y las observaciones lunares se colectaron en los años 2014 (marzo-mayo, agosto-octubre) y 2015 (marzo-abril). Los datos del perfilador abarcan una base de datos histórica del 2010-2012 y datos recientes de marzo-abril 2015. Los datos de los radares meteorológicos también son de marzo-abril 2015.

Para aproximarse al tema de los radares y en particular al papel de perfiladores en la ornitología, se ha hecho una revisión **(ARTICULO I)** de los conocimientos existentes sobre el particular hasta el desarrollo de esta tesis doctoral.

En un segundo paso, se analizaron los datos del perfilador del 2010-2012 para determinar la presencia de migración en el Golfo de Vizcaya. Luego, se inició la campaña con la cámara térmica en los meses de actividad máxima, marzo-mayo y agosto-octubre para verificar que las señales del radar provinieran de aves. Para complementar los patrones obtenidos por la cámara térmica y verificar un posible gradiente de migración en la costa vasca, se muestrearon dos sitios adicionales (Cabo de Higuer y La Rioja) en otoño 2014 y uno (Cabo de Higuer) en primavera 2015. Los resultados de esta campaña se presentan en el **ARTICULO II.** Los resultados indican altitudes de vuelo siempre altas en los tres sitios y direcciones parecidas de vuelo en la costa (dirección suroeste), pero más orientadas hacia el sur en el sitio de La Rioja. En general, las intensidades de la migración variaron mucho de una noche a otra en los tres sitios de muestreo. En Punta Galea, el flujo más grande se observaba en marzo-abril, mientras que en otoño casi no había movimiento. En Cabo de Higuer, el flujo de primavera y otoño era parecido. De La Rioja solo hay datos de otoño y las cantidades se asemejan a las de Cabo de Higuer. En los mismos periodos se realizaron observaciones lunares siempre y cuando las condiciones meteorológicas lo permitían **(ARTICULO III)**.

En marzo-abril de 2015 se hizo también una campaña de calibración con el perfilador. Se seleccionaron 10 días de muestreos simultáneos con la cámara térmica. Estos datos luego se analizaron en colaboración con Dr. Volker Lehmann, del instituto meteorológico de Lindenberg, Alemania, en una estancia facilitada por la Acción COST ENRAM. Los resultados se presentan en el **ARTICULO IV.** Se han establecido por primera vez una metodología reproducible para la cuantificación y cualificación de las señales de las aves en las series temporales del perfilador que permite calcular y determinar alturas de vuelo e intensidad de migración, sin sesgo por señales atmosféricas, biológicas o de otra naturaleza.

Como último capítulo de la tesis se analizaron los datos de los radares meteorológicos de marzo 2015 a lo largo del Golfo de Vizcaya **(ARTICULO V)**. Estos radares sirvieron para complementar la información vertical del perfilador y de la cámara térmica con información horizontal a una escala geográfica más amplia. El análisis de estos datos se ha llevado a cabo por otra estancia facilitada por la Acción COST ENRAM, en colaboración con científicos de la universidad de Amsterdam, en particular con Dr. Adriaan Dokter, que han desarrollado un algoritmo para automatizar la extracción de las aves de los datos de estos radares. Durante los preparativos, se ha visto que los datos de los diferentes servicios meteorológicos se habían sometido a diferentes niveles de procesamiento y filtrado, sea por el mismo sistema de almacenamiento o sea por los parámetros y filtros establecidos por el propio operario. Como consecuencia, solo los datos del radar de Kapildui de Euskalmet y de los radares franceses contenían información biológica y se podían incluir en el estudio. Los resultados indican un gradiente decreciente de migración desde Kapildui hasta el norte de Francia.

En conclusión, las diferentes herramientas utilizadas en el presente proyecto permitieron la obtención de nuevos hallazgos sobre las dinámicas de la migración nocturna en la costa del Golfo de Vizcaya:

1. Alta actividad nocturna en primavera (marzo-abril) y poca actividad en todo otoño en Punta Galea.

2. Migración de frente más amplia en primavera que en otoño, concentración de la migración otoñal más hacia los Pirineos evitando posiblemente el cruce del mar.

3. Paseriformes predominan como migrantes nocturnos según las observaciones lunares, con solo un menor porcentaje de aves acuáticas entre otros.

4. Cualificación y cuantificación validada de los datos brutos del perfilador que establece por primera vez criterios reproducibles para medir parámetros de migración, independientemente de las condiciones meteorológicas.

5. Gradiente norte-sur en primavera a lo largo del golfo sugiriendo que la migración se desarrolla más bien al interior de la bahía y no esta uniformemente distribuida por el mar. Sin embargo haría falta comprobar este patrón por medidas desde la costa española noroccidental donde de momento no había datos disponibles.

Trabajos futuros deberían extender los muestreos nocturnos hacia la costa noroccidental y hacia el interior de España para aclarar los patrones espaciales y también investigar las dinámicas en otoño. Por parte del análisis de las señales del perfilador sería preciso profundizar la parte de las frecuencias por si fuera posible sacar más información acerca de la composición de las aves. Además queda por determinar si el perfilador es capaz de detectar otras señales de origen biológico y, en caso afirmativo, caracterizar los ecos de la misma manera como en el presente estudio para poder maximizar el uso de los datos disponibles.

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PAPER I

THE USE OF RADAR WIND PROFILERS IN ORNITHOLOGY: A REVIEW.

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SUMMARY

In the past 70 years radar technology has been increasingly applied in ornithological research in various geographical areas worldwide and contributed greatly to better understand avian migration. Many different radar types have been used such as tracking, ship or weather radars. However, wind profilers have been largely neglected in actual avian research. Wind profilers measure horizontal winds continuously and despite their low frequency range birds have been registered in many areas. So far the potential of wind profilers in avian research has not been fully explored and studies deal predominantly with birds in the context of clutter removal. However, based on their broad implementation in networks (e.g. E-PROFILE in Europe) situated in areas that are strategically important for bird migration, they could offer a valuable complement to already established or planned large-scale bird monitoring schemes by radar.

The objective of this review is to provide an overview over the evolution and establishment of operational radar wind profilers as well as over their mode of operation, in order to depict their role in meteorology and to evaluate their potential in ornithology. The assessment of this radar type is based on available literature on wind profilers and radar ornithology to outline potential complementary benefits of radar wind profilers in relation to other radars which are and have been more commonly used in avian research.

KEYWORDS

Birds, radar, clutter removal, ground truth

BIRD MIGRATION

Bird migration describes the annual movement of millions of birds between their breeding and wintering grounds (Alerstam 1990). During these journeys, birds pass through a variety of geographical areas. Areas that represent particularly challenging environments for migrating birds, e.g. based on adverse meteorological conditions and/or lack of stopover opportunities, are so-called geographical barriers, such as deserts (e.g. the Sahara), mountain ranges (e.g. the Alps) or seas (e.g. the Mediterranean Sea). Depending on the type of birds, their required resources and the type of barrier, different migration strategies have evolved and have been adapted to optimize energy consumption and ultimately survival (Newton 2008).

Examples of adaptations include nonstop migration vs. migration with many stopovers, migrating singly vs. migrating in flocks or the preference for nocturnal and/or diurnal migration (Alerstam 1990, Hedenström 2010). For example soaring species such as raptors or storks migrate almost exclusively during the day and preferably over land to make use of thermals (Kerlinger 1984, 1985, Meyer et al. 2000), while most small passerines take advantage of darkness to avoid predators and overheating (Pennycuick 1969, Kerlinger & Moore 1989, Alerstam 1990).

Other important factors during migration of both nocturnal and diurnal migrants concern adaptations in response to weather conditions (Richardson 1978). In unfavourable weather (e.g. head wind, rain) birds can make detours, add or prolong stopovers or even reverse migration (e.g. Alerstam 1978, Lindström & Alerstam 1986, Liechti & Bruderer 1998). Depending on wind force and direction, birds have been found to adapt their flight altitudes to fly in tailwinds to minimize energy consumption (Dokter et al. 2013b), but they are also able to cope with head or crosswinds, for example in areas with generally unfavourable wind conditions (Chapman et al. 2016).

All these aspects combined make up for the geographical, seasonal and temporal patterns that characterize bird migration across the world – as a consequence some areas represent key passage zones, such as the Strait of Gibraltar between Europe and Africa, while others are of minor importance.

From an ecological, ornithological and conservation perspective and also for air traffic safety it is important to have appropriate technology to monitor and study such highly complex large-scale movements of birds. Radar technology has proven particularly useful therein (Bruderer 1999). Besides the dedicated bird radar systems, operational radar networks are increasingly and successfully used for ornithological purposes (Shamoun-Baranes et al. 2014).

RADAR HISTORY AND OUTPUT IN ORNITHOLOGY

Radars offer many methodological benefits in comparison to other investigational approaches in ornithology such as visual counts or ringing. Desholm et al. (2006) and Beason et al. (2013) emphasize the reduced expenditure of time and effort, superior visibility and detectability (e.g. at higher altitudes or in the dark) as well as overall enhanced research productivity through the employment of radars. Shamoun-Baranes et al. (2014) highlight the better applicability of radars for large-scale monitoring. A wealth of radar studies has been performed in various regions worldwide e.g. Casement (1966) and Bruderer & Liechti (1999) in the Mediterranean, Biebach et al. (2000) and Schmaljohann et al. (2007) in the Sahara desert, Gudmundsson (1993) on Iceland or Gauthreaux (1970, 1971), Richardson (1976, 1982) and Cabrera et al. (2013) in America. Many ornithological studies employed adapted „on-off" radars - such as military tracking or marine radars with only a limited distance range. However, to understand long- and short-range migratory patterns, it is necessary to tap into networks of operational atmospheric radars, which can help fill this gap.

There are two basic types of atmospheric radars, those horizontally scanning and those vertically pointing. The horizontally scanning variety uses almost exclusively X-, C-, and S-band, while the vertically directed radars use mainly L- to VHF-band. In ornithological studies, predominantly horizontally scanning weather radars have been used (Gauthreaux 1971, Gauthreaux & Belser 1999, Dokter et al. 2010). These radars are organised in large networks worldwide, such as NEXRAD in the US and OPERA in Europe. Operational weather radars run continuously and provide large spatial and temporal coverage. In connection with weather radars, the COST action ENRAM (European Network for the radar surveillance of animal movement) was launched in 2013 to "establish the basis for a coordinated network of monitoring radars for the provision of real-time spatio-temporal information on animal movement through the air on a continental scale" for the benefit of both the environment and humans (Memorandum ENRAM). To the best of the authors' knowledge, the ENRAM network represents the only platform in the world to foster collaborations and research among radar biologists. In Gürbüz et al. (2015) ENRAM members provided a recent overview over the state-of-art of radars used in studies on airborne organisms.

In contrast to the efforts related to horizontal weather radars, vertically pointing atmospheric radars, such as wind profilers, play only a marginal role in biology, if any, even though they have been known to detect biological targets (Wilczak et al. 1995).

The aim of this review is to provide an overview over the evolution and establishment of operational radar wind profilers as well as over their mode of operation, in order to depict their role in meteorology and to evaluate their potential in ornithology. The assessment is based on available literature on wind profilers and radar ornithology to outline potential complementary benefits and shortcomings of radar wind profilers in relation to other radars which are and have been more commonly used in avian research.

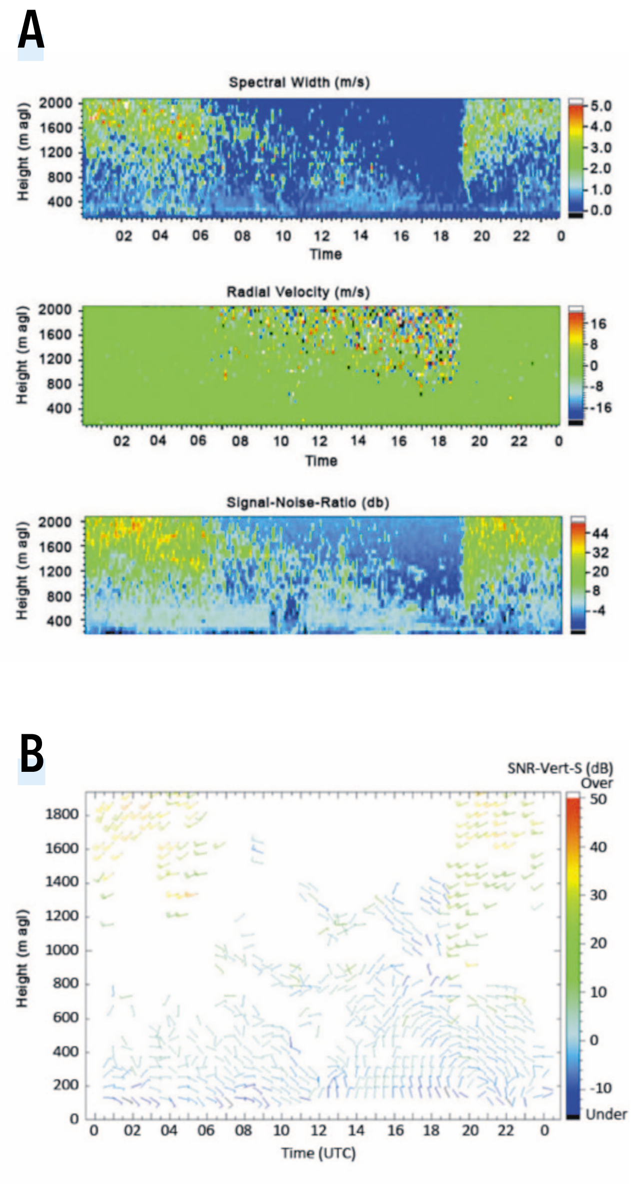

FIG. 1 *Examples of bird migration patterns in moment (A) and consensus (B) data.*

WIND PROFILER SYSTEMS

EVOLUTION OF TECHNOLOGY

The growing importance of understanding atmospheric dynamics and making accurate weather and climate predictions in today's globalized world has led to the development of a variety of different remote-sensing systems. One surface-based option is provided by radar wind profilers.

The discovery by Atlas et al. (1966) that radars can detect air turbulences paved the way to the first wind measurements by Doppler radars (Dobson 1969, Browning et al. 1973, Woodman and Guillén 1994). The first wind profilers were introduced in Europe (Czechowsky et al. 1976) and in the US (Green et al. 1975) shortly thereafter. From the 1980s onwards wind profilers were widely adopted for a variety of operational applications in weather forecasting (Balsley & Gage 1982, Strauch et al. 1984). In his review on the history and development of wind profilers Van Zandt (2000) highlighted the capability of measuring vertical winds as a unique feature of wind profilers. In addition to wind measurements, wind profilers have been used to measure precipitation (Ecklund et al. 1995a). As optional add-on, virtual temperature is provided through the Radio Acoustic Sounding System (RASS) which merges radio and acoustic techniques (May et al. 1989).

Once the wind profilers had become operational for atmospheric measurements, it soon became clear that these radars also register non-atmospheric targets (Ecklund et al. 1990). The quality of wind measurements was heavily affected in nights during bird migration season (Fig. 1), so it was concluded that these signals originated from migrating birds (Wilczak et al. 1995). Since then, many studies have dealt with clutter removal and provided different approaches based on spectral (Merritt 1995, Pekour & Coulter 1999 and Kretzschmar et al. 2003) or time series level (Lehmann & Teschke 2008a, b) to clean the radar data. However, none of these filters has been able to cope successfully with high bird densities and birds have remained a qualitative challenge in wind measurements.

As a result of the extending implementation, networks have been founded such as the NOAA profiler network (NPN) (active from 1992-2014) and the Cooperative Agency Profilers (CAP) derived thereof in the US, WINDAS in Japan (Ishihara et al. 2006) or E-PROFILE in Europe (Fig. 2a, Fig. 2b, Fig. 2c). In Europe, networking activities were initiated by two COST actions, COST-74 and -76, dedicated to

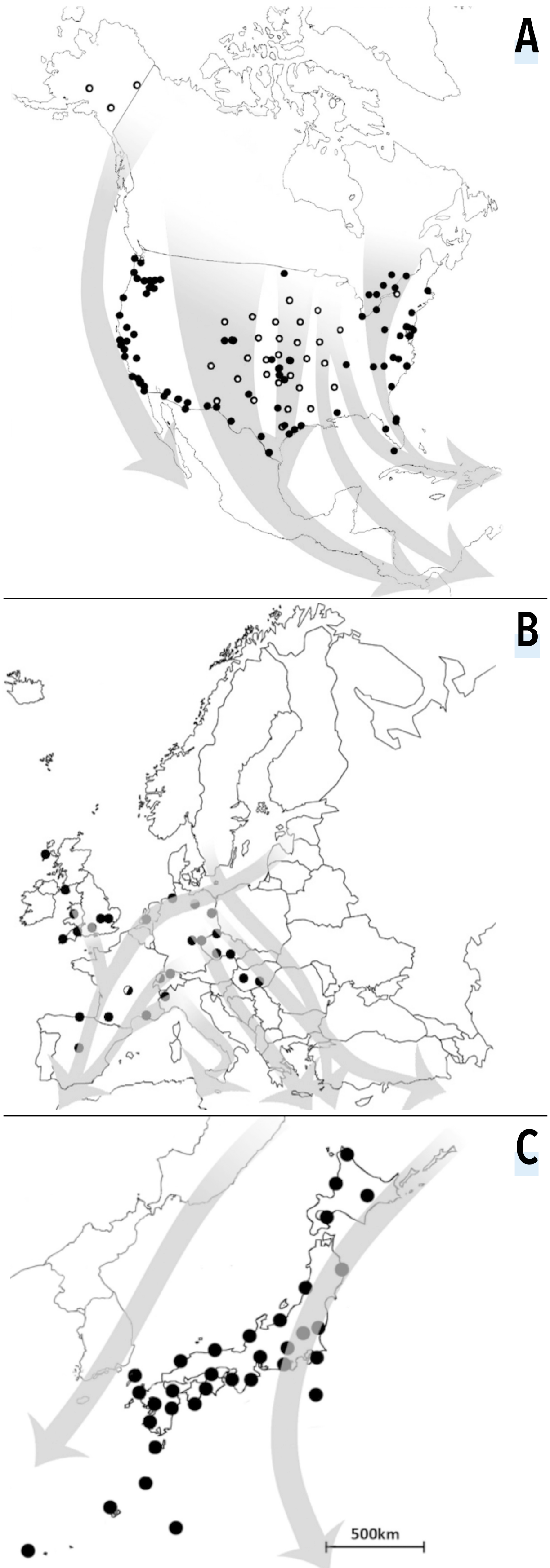

FIG. 2. *Wind profiler networks in (A) the US (filled dots: Cooperative Agency Profilers; circles: NOAA Profiler Network [1992-2014]) (B) Europe (E-Profile) and (C) Japan (WINDAS) with overlaid migratory flyways.*

research on operational aspects of radar wind profilers to improve data quality (Dibbern et al. 2003). Two campaigns linked with COST-76 (CWINDE-97 and -99) demonstrated that networking between various wind profiler systems was feasible despite their differences in design and purpose and the different operators (Oakley & Turp 2005). After COST-76, the WINPROF programme was created by the European Meteorological Services Network (EUMETNET) to proceed with the operational network and it continues today as E-PROFILE. The general aim of these networks is to coordinate and improve the quality and usability of meteorological information and to provide support and expertise to both profiler operators and users to render the use of this resource more efficient. According to Met Office (http://www.metoffice.gov.uk/) there are currently 29 wind profilers installed in 19 European countries, and more than 150 worldwide (Dibbern et al. 2003).

HOW DOES A RADAR WIND PROFILER WORK?

In the following we will briefly summarize the mode of operation and data output of wind profilers.

Generally there are two types of radar wind profilers - boundary layer and tropospheric wind profilers. Boundary layer wind profilers typically emit electromagnetic waves in the L-band and UHF range and tropospheric wind profilers operate in the VHF range. These are optimal ranges to detect irregularities of the refractive index of particle-free clear air which can span from a few centimetres to many meters in size (Wright 1998). In comparison, weather radars focused on the detection of hydrometeors (precipitation) rather than air itself and operate in the frequency range of S- and C-band.

Wind profiler specifications are customized based on site-specific requirements and conditions. In operation, the system typically produces wind profiles by one (or two different) electromagnetic pulse(s). If two pulses are specified, independent wind profiles for two height ranges will be calculated, with two different vertical resolutions (low vs. high mode). If a pulse encounters a target, the electromagnetic energy is scattered and a fraction of this so-called backscatter is registered by the radar. Based on the time lag between the transmission of the pulse and the reception of its backscatter, the distance of the target can be computed. This information is obtained for many levels (range gates) in the sampled vertical air column above the radar and finally represented as wind profiles (Vaisala 2007).

Wind profiles are obtained by three to five Doppler swinging beams emitted by phased array antenna panels (Fig. 3). One of the beams is directed vertically and the others are slightly inclined by 15°, pointing to the four (two) cardinal points. Data from at least three directions is needed to calculate the three-dimension-

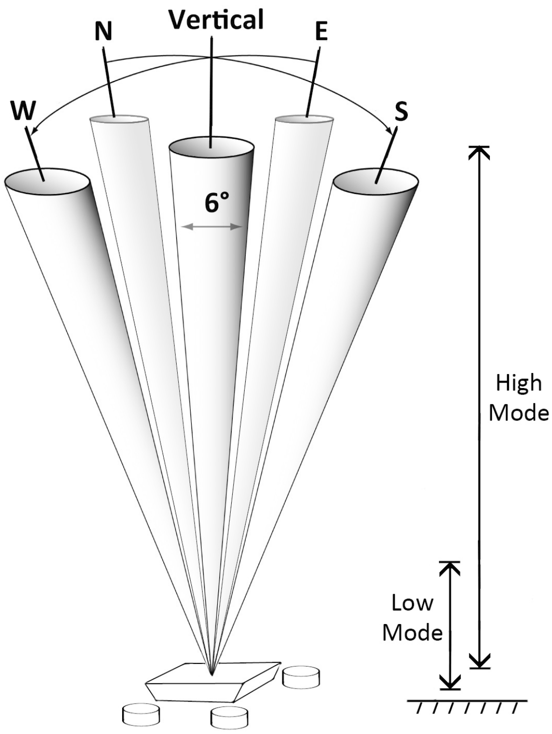

FIG. 3. *Scheme of a radar wind profiler with four RASS (Radio Acoustic Sounding System) containers and two sampling heights (low and high mode).*

al vector wind (wind direction, signal-to-noise ratio and speed) from the radial wind velocities. Just like in other Doppler radars, only objects with radial velocity are detected, i.e. objects moving away from (skywards) or towards (earthwards) the wind profiler.

Signal processing of the collected data is divided into two main parts, the time-domain stage and the frequency-domain stage. In the time-domain stage, a time series of the reflected signal is received during a specified dwell time for each range gate and each beam. From these time series, Doppler velocity spectra are estimated in the frequency-domain stage as a first output in the signal processing chain (Strauch et al. 1984). In the subsequent spectral averaging process, several consecutive spectra are used to calculate a mean spectrum. The product of this averaging step is the moment data consisting of signal-to-noise ratio (SNR), radial velocity, and spectral width, which represent the second processed output (Fig. 4). Applying the consensus algorithm (Fischler & Bolles 1981, Vaisala 2007), the wind vectors for each gate are calculated for each detection height, resulting in the final product, the consensus data, depicted as time-height plots with 3D wind barbs. These measurements run continuously.

A more in-depth account can be found e.g in Balsley & Gage (1980), Strauch et al. (1984) or Vaisala (2007).

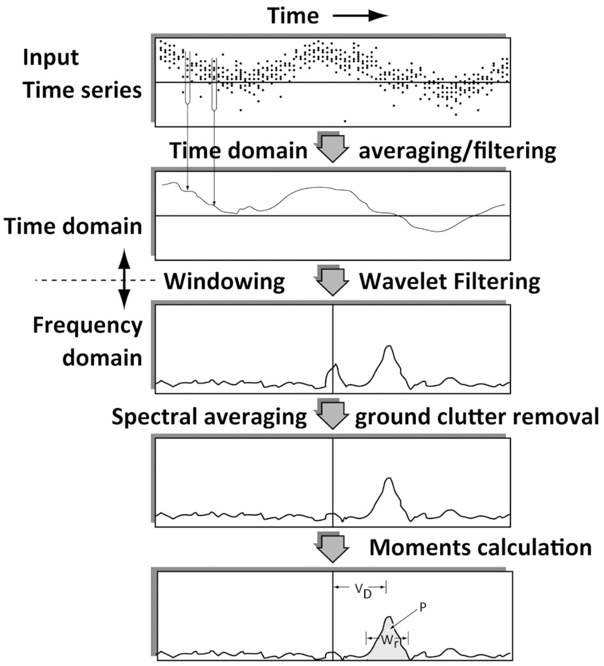

FIG. 4. *Data processing: moments calculation from time series data (Vaisala 2007).*

RADAR WIND PROFILERS IN ORNITHOLOGY

Presence of birds has been reported from a variety of wind profiler sites, e.g. in the US (Wilczak et al. 1995, Locatelli et al. 1998), Japan (Ishihara et al. 2006) and Europe (Kretzschmar et al. 2003, Lehmann & Teschke 2004). A general description of signals was provided by Wilczak et al. (1995). Bird presence has been described as extensive patterns between sunset and sunrise up to about 4 km, with high spectral width, high signal-to-noise ratio, variable radial velocities and resulting wind errors of about 10m/s (Wilczak et al. 1995, Weisshaupt et al. 2014). Examples of radar plots during bird migration are given in Fig.1.

When using radars for biological purposes, target verification by means of a secondary system, such as thermal imaging or visual observations, is essential, because target identification by radar alone is only insufficient (Schmaljohann et al. 2008). Otherwise the biological content of the sampled volume remains ambiguous given the fact that not only birds can migrate in high numbers, but also insects and bats (Larkin 1991, Gauthreaux et al. 2008, Chapman et al. 2011). The unknown content of the sampled volume could potentially bias the study outcomes and affect their reliability. For example in ecological impact studies this might have major consequences (Schmaljohann et al. 2008).

Four types of ornithological involvement can be found in wind profiler literature. (1) The majority of wind profiler studies in connection with ornithology is represented by research recognizing birds as contamination to be removed and proposing some filtering procedure without target verification (e.g. Merritt 1995, Wilczak et al. 1995, Pekour & Coulter 1999, Pekour 2002, Lehmann & Teschke 2004). (2) Studies recognizing birds as contamination to be removed and proposing some signal processing approach based on target verification by a secondary system. To the best of the authors' knowledge, this category includes one study, i.e. Kretzschmar et al. (2003). (3) A third category includes studies with an ornithological focus, but without target verification, also one study (Locatelli et al. 1998). (4) The fourth category comprises studies with an ornithological focus and target verification. There is one ornithological contribution by Weisshaupt et al. (2015) who employed a thermal-imaging camera as a verification tool.

The general lack of target verification could be explained by the minor interest in the biological content of the clutter per se in meteorology, if the focus lies on improving the quality of wind measurements and not on obtaining biological data. Overall, birds are considered the major biological cause of deteriorated wind profile quality based on their ability to fly actively against the wind (Wilczak et al. 1995). However, it has been suggested that insects are presumably also detected by wind profilers and probably have an impact on wind measurements (Ecklund et al. 1995b, Angevine 1997).

While insect presence and its characteristics has been treated by several studies in connection with weather radars (e.g. Achtemeier 1991, Wilson et al. 1994), there is no such information available from wind profilers, even though insects and birds can occur simultaneously. The only insect study involving marginally wind profiler data was executed by Rennie et al. (2010) who used a wind profiler as a reference tool for wind measurements when looking into insect echoes in weather radars in the UK. Even though insect activity might be considered a rather diurnal source of clutter, there are also considerable nocturnal movements at heights where birds migrate, i.e. up to 1 km or more (Chapman et al. 2003). Thus, it remains unknown to what extent the "birds" observed in wind profiler studies might be mixed with insects or other.

So, overall current literature has only shown presence/absence of birds, but detailed studies on biological signal characteristics are missing and potential artefacts and effects from filtering procedures are poorly understood. Recently, a promising approach was elaborated within the COST action ENRAM (Weisshaupt 2015) showing promising preliminary results on bird echo signature characteristics and derived measurements of the biological content in wind profiler data, both as to target identification and the extraction of migration parameters. These findings would encourage further efforts to scrutinize the wind profiler data pool in a biological context.

EXPERIMENTAL CAMPAIGNS WITH RADAR WIND PROFILERS AND OTHER RADAR

As stated previously, it is important to verify the radar signatures and to establish a reference to identify echo sources by means of a complementary second sampling technique, i.e. by so-called ground truth.

To validate and calibrate X- to S-band radars, various devices and methods have been used: moonwatching (Lowery 1951, Gauthreaux 1970, Liechti et al. 1995, Bruderer et al. 2012, Mateos & Bruderer 2012), thermal imaging (Liechti et al. 1995), ceilometers (Able & Gauthreaux 1975), mist-netting (Desholm et al. 2014, O'Neal et al. 2010) and visual observations (Hofmann 1956, Gauthreaux 1970, 1971, Dokter et al. 2013a).

All of these methods provide simultaneous measurements of bird numbers of which migration traffic rates can be calculated (Lowery 1951, Schmaljohann et al. 2008), a quantitative reference value for comparing different measurement systems and methods.

Moonwatching, mist-netting and visual observations additionally deliver information on bird composition, while thermal imaging and visual observations provide migration directions. This entire information can then be used in combination with the observed radar patterns to aid interpreting echo signatures.

Once a radar system has been validated it can be further used as a validation tool (Dokter et al. 2010). As to wind profilers, the two existing studies mentioned earlier (Kretzschmar et al. 2003 and Weisshaupt et al. 2015) employed thermal imaging for target verification. Other studies involving wind profilers compared the outputs of various non-validated wind profilers, such as Wilczak et al. (1995), and therefore cannot be counted as validations since comparing several volumes of unknown content will not help clarify the origin of any targets. Therefore, at a biological level, there are still many open questions related to wind profilers.

CONCLUSIONS

Wind profilers are highly sensitive remote-sensing systems which were originally designed to measure clear-air echoes. They have been implemented globally and are partly organised in networks, such as E-PROFILE in Europe. Just like other radar systems, wind profilers also register airborne biological targets. Available literature on radar wind profilers provides information on presence/absence of biological targets (birds) in L-band to VHF radars, however, recent data indicates that the potential of this data source has not been fully exploited and that more detailed information could be gained on biological targets. So far, seasonal and diurnal patterns as well as the altitudinal extent of migration have been identified, i.e. parameters generally of interest in bird migration research as well as related topics (e.g. flight safety). Furthermore the existing wind profiler systems sample data in areas of potential ornithological interest, which would enhance the value of wind profiler data. The availability of networks could facilitate data provision to biologists in a coordinated way.

In contrast to studies with other radar systems, only two studies verified the sampled wind profiler data and at the time of writing there were no further studies specifically on the content of biological clutter. Therefore it remains open if wind profilers could also be of interest to other areas in biology, e.g. entomology, but the records on diurnal clutter could be an interesting first indicator.

The findings encourage further exploration of the wind profiler data in a biological context. In particular, the authors see a great potential in further analysing raw data (time series) in order to optimize the extraction and level of details of migration-specific data. This type of radar could potentially provide a complementary continuous vertical data source to available horizontal weather radar data. It would be thus useful to identify the system specifications (e.g. wavelength, sampling height, range resolution etc.) that correspond best to the needs in avian research so that the interests of both the meteorological and biological community could be synchronized. In a future step, it could be consequently interesting to automatize the collection of biological data from wind profilers as is currently done for weather radars in Europe. For these purposes, a close collaboration between the existing radar networks and ornithologists (or also other biologists) could prove fruitful in order to use the wind profiler data also in a non-meteorological context.

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PAPER II

NOCTURNAL BIRD MIGRATION AT THE SOUTHEASTERN BAY OF BISCAY AS OBSERVED BY THERMAL-IMAGING CAMERA

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SHORT TITLE: Nocturnal migration at the Bay of Biscay

KEY WORDS: Basque coast, geographical barriers, migration strategies, infrared, tailwind, SW-Europe

SUMMARY

CAPSULE Bird migration was recorded by an infrared device at three sites in the southeastern Bay of Biscay, indicating seasonal east-west differences in migration flow.

AIMS The main aims of this study were (1) to quantify and describe nocturnal migration dynamics in proximity of a sea barrier, and (2) to assess seasonal and geographical drivers of migration patterns.

METHODS To achieve these goals a thermal-imaging camera was used at two coastal study sites (Punta Galea [west], Cape Higuer [east]) in spring and three study sites (coast: Punta Galea, Cape Higuer; inland: Iregua Valley) in autumn during four hours from sunset in overall 90 nights in 2014 and 2015.

RESULTS Spring migration was strong at both coastal sites in early spring. Autumn migration was weak at the western coast, but strong at the eastern coast and inland. Tailwind had no significant effect on migration intensity, but migration ceased during strong cross- or headwinds despite clear skies. The majority of the targets were passerines.

CONCLUSIONS The patterns observed suggest spring migration occurs on a broader front, potentially involving sea-crossing further to the west, while autumn migration concentrates more eastwards over land. In both seasons, there was no significant response to wind conditions.

INTRODUCTION

The East-Atlantic flyway represents one of the principal migration routes in Europe, comprising the Bay of Biscay as a geographical barrier for migratory landbirds. Few studies have been published concerning the role of the Bay of Biscay in bird migration. In their study on diurnal autumn migration through the Pyrenees, Lack & Lack (1953) observed great numbers of birds coming in from the Bay of Biscay as well as travelling along the coast and then continuing inland. They concluded that migration was proceeding on a broad front. In another study, which was based on passerines ringed at several coastal stopover sites along the Bay of Biscay, Arizaga et al. (2014) reported much weaker passage in spring compared to autumn. By contrast, a coastal operational radar located in the southeastern Bay of Biscay revealed high nocturnal activity in spring and low activity in autumn (Weisshaupt et al. 2014).

It is well known that variations in migration strategies found in short- and long-distance migrants cause changes in the spatial and seasonal flow of migration (Bruderer & Liechti 1999) resulting in different routes in spring and autumn (e.g. Klaassen et al. 2010, Agostini et al. 2011, Willemoes et al. 2014). For instance, in Iberia some migrants select more western (Atlantic) flyways in autumn, but more eastern (Mediterranean) flyways in spring (Bairlein 2001).

Also prevailing seasonal meteorological conditions could have an impact on migratory routes, e.g. when crossing geographical barriers (Thorup et al. 2003, 2006). Adverse weather (e.g. headwinds, precipitation) halts or delays the crossing of barriers, as it could entail excessive energy costs or increase mortality risk (e.g. Richardson 1978, Liechti & Bruderer 1998). Prevailing conditions over a given barrier could then eventually determine if migrants decide to cross or to make a detour. So basically, tailwinds (north- to north-easterly in autumn; south- to south-westerly in spring) both in autumn and spring would be expected to promote migration over the open sea of the Bay of Biscay. However, as the study region is characterized by a highly variable meteorological environment dominated by westerlies, the anticipated high numbers of autumn migrants would be faced with headwinds which might prevent them from flying over water. Interestingly, some studies suggest that birds also travel under suboptimal conditions, i.e. in head- or cross-winds, because waiting for optimal conditions would result in a major delay (e.g. Bruderer 1999, Karlsson et al. 2011, Chapman et al. 2016). Thus, alternatively, it is also possible that tailwinds have a minor impact on migration intensity at the bay given the overall challenging weather setting.

A large proportion of migratory movements occur at night (Alerstam 1990). Studying active nocturnal migration per se excludes certain sampling methods based on its very nature such as ringing and visual counts. One available technique to study nocturnal activity is thermal-imaging (Liechti et al. 1995, Zehnder et al. 2001a, Gauthreaux & Livingston 2006). Such infrared devices are highly sensitive to even small temperature differences. Depending on the camera model and meteorological conditions, objects can be registered in distances of up to several kilometres (Liechti et al. 1995). General pros and cons of thermal imaging are reviewed in McCafferty (2013). One of the advantages is that thermal imaging allows us to obtain various migration parameters, such as migration intensity, direction and spatial arrangement of migrants (e.g. dense flocks vs. individuals). Flight altitudes can be estimated based on size classification of targets (Zehnder et al. 2001a). A further benefit is the ease of use and quick start-up of such cameras. Their relatively small size and weight permit swapping easily between study sites within short time. A disadvantage is that thermal-imaging cameras alone cannot be used to identify species (Gauthreux & Livingston 2006). However, it can be assumed that the major proportion of nocturnal migration concerns passerines migrating alone or in loose flocks, while larger flocks and many non-passerines (e.g. soaring species) tend to be more common in diurnal migration (Bruderer 1971, Alerstam 1990). Finally, as a consequence of temperature sensitivity, thermal imaging devices strongly depend on thermally uniform environments for optimal data collection, i.e. completely clear (or alternatively overcast) skies, because thermal radiation from moving cloud layers could hamper the detection of birds (Zehnder et al. 2001a, Gauthreaux & Livingston 2006). Also humidity has been observed to affect thermal imaging negatively.

The aim of this study is to characterize and quantify nocturnal migration along the coast of the south-eastern Bay of Biscay (northern Iberia) in order to (1) characterize migration phenology, (2) determine the potential impact of wind conditions on the spatial and temporal variations in migration intensity, and (3) identify what kind of migrants pass primarily (e.g. based on flight patterns, singly flying passerines or flocks).

Based on available data, we would expect to find broad-front migration in spring including sea crossing, i.e. comparable migration intensities and directions along the coast. In autumn, a more easterly concentration of migration is anticipated, with a pronounced coastal east-west gradient, with superior migration intensity in the innermost bay area and inland, and generally higher numbers of migrants compared to spring. Overall, wind assistance would be expected to favour migration, but it might play a secondary role based on the challenging nature of overall weather situations.

MATERIAL AND METHODS

DATA COLLECTION

A long-range thermal-imaging camera (LORIS, IRTV-445L, Inframetrics, Massachusetts, U.S.A.) was used with an opening angle of 1.45°. From direct comparisons with tracking radar it is known that the camera is able to detect small-sized passerines up to 3000 m above ground level in clear skies (Bruderer & Liechti 1994, Liechti et al. 1995).

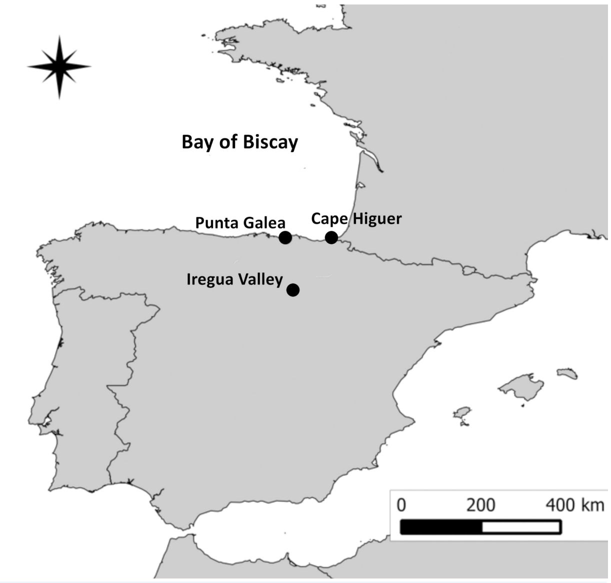


FIG. 1 *Locations of the three sampling sites used to quantify bird migration across the Bay of Biscay: Punta Galea, Cape Higuer and Iregua Valley (Northern Spain).*

Data were collected at three sites in Northern Iberia: two on the Basque coast [Punta Galea, Bilbao (43°22'N, 3°02'W); Cape Higuer, Hondarribia (43°23'N, 1°47'W)] and one inland in the Iregua Valley (Ebro river basin) at Villoslada de Cameros (42°04'N 2°41'W) (Fig. 1). The two coastal sites were selected to account for a possible East-West gradient in migration intensity, while the third site served as inland reference point with a possible North-South gradient. The sampling was designed as follows: (1) in spring 2014, 10 nights were sampled each in March, April and May at Punta Galea [west]; (2) in autumn 2014 (from August to October), 15 nights were sampled each at Punta Galea [west] and Cape Higuer [east] and 10 nights in the Iregua Valley [inland]; (3) in spring 2015, 10 nights were sampled each at Punta Galea [west] and Cape Higuer [east] from March to April.

The number of sampling days was chosen in a way to obtain a representative temporal coverage of migration at each site, switching between sites every second day, if weather permitted. Sampling took place only in nights with no rain and as clear skies as possible to minimize a potential bias resulting from precipitation and cloud cover and to enhance detection of targets in the camera. The camera was positioned vertically and oriented to the north with the aid of a compass to facilitate posterior extraction of the migratory directions. Passing migrants were observed on a TV screen and video-taped during 4 h from sunset. Subsequently, the videotapes were digitalized for further analysis.

METEOROLOGICAL DATA

Wind data for the three sampling sites were collected from NOAA, National Oceanic and Atmospheric Administration, U.S. Department of Commerce. Particularly, both u and v wind components were used for pressure levels of 700, 850 and 925 mb, roughly corresponding to an altitude of 3250, 1500 and 775 m above sea level, respectively, at 18:00 hours and 00:00 hours. The mean tailwind from 18:00 and 00:00 hours was included as an additional variable accounting for possible fluctuations in wind parameters in the course of this six-hour interval. Based on this wind data, tailwind components were calculated as $V_w \cos(\varphi_T - \varphi_W)$, where V_w was the wind velocity, φ_T was the mean preferred track direction (in this case, 225° for the autumn migration period, and 45° for the spring migration period), and φ_W was the wind direction (Åkesson & Hedenström 2000).

DATA ANALYSIS

FLIGHT DIRECTIONS

For the extraction of flight directions the software Kinovea was used. All tracks were time stamped and classified by hour (hour 1 to 4, starting at sunset). All those targets which did not follow a straight trajectory (e.g. curves, sudden reversions) or which might have originated from bats or insects ("bubbles" as described in Zehnder et al. (2001a)) were excluded. Flight tracks were analysed by means of the R package "circular" and Oriana. Mean directions were calculated for each site and season. Following Zehnder et al. (2002a, b), directions were classified as "forward migration", if they fell within the site- and season-specific mean migration direction [mean direction ± 60°], or as "reverse migration", if they fell within the range of directions ± 60° around mean+180°. A Rayleigh test was applied to test for the variance associated with the site- and season-specific circular distributions (i.e. uniform vs. concentrated). A Watson-Williams test was used to test for variations in mean directions. Flight tracks were not corrected for possible wind drift.

FLIGHT ALTITUDE

Targets were assigned to 7 size categories, corresponding to flight altitudes from 0.3 km (Class 7) to 2.1 km (Class 1) (sensu Zehnder et al. 2001a). However, the camera can detect birds at higher levels of up to at least 3 km (Liechti et al. 1995). Therefore the scale of the size categories is only to be considered an approximation, reflecting mainly altitudinal distribution rather than exact flight altitude levels. Gauthreaux & Livingston (2006) criticized the use of thermal imaging as stand-alone method pointing out to the potential errors when dealing with differently sized birds and any resulting effect on flight altitude estimation. However, this very camera was tested and calibrated previously by tracking radar by Liechti et al. (1995), and findings indicated size bias in nocturnal songbirds to be negligible.

MIGRATION INTENSITY

The migration traffic rates (MTR) were computed to account for the conical sampling in which the surveyed volume increases with distance of the target to the recording device (Lowery 1951). The MTR represents the number of birds passing a line of one kilometre perpendicular to the flight direction in one hour (birds*km^{-1}*h^{-1}). For each site the mean MTRs were calculated per night, month and season (for details see Zehnder et al. 2001a). The effect of factors potentially driving migration intensity was tested by Generalized Linear Models (GLMs) in the program R [R Development Core Team (2004)]. The analyses were conducted with three separate data sets: 1) Punta Galea [west] in spring 2014, 2) Punta Galea [west] and Cape Higuer [east] in autumn 2014 and spring 2015, and 3) Punta Galea [west], Cape Higuer [east] and Iregua Valley [inland] in autumn 2014. The purpose of conducing three separate analyses was to better disentangle seasonal and geographical patterns. Log-transformed (log transformation plus 1 to account for 0 values) hourly MTR values were set as the response variable and the independent explanatory variables were: site (only in analysis 2 and 3), hour, month (only analysis 1), season (only analysis 2) and tailwind components. Site, hour, month, and season were included as discrete control factors, while tailwind components were included as linear (quantitative) variables. The tested models included all combinations of one of the six tailwind variables (for three heights and two instants of time, see above) and the other variables, as well as double interactions, though not the full model because of the many types of tailwind variables and potential confounding effects. All models were ranked according to their small-sample size corrected Akaike values (AICc) by means of the function "model selection" of the R package "MASS" and "MuMIn" (Burnham et al. 1998, Johnson et al. 2004). Models differing in less than 2 AICc values were assumed to support the data equally well. B-parameters with P-associated values >0.05 were considered to be non-significant.

RESULTS

Overall, 11804 bird tracks of 420 h of video recordings were included in the analysis: 6144 tracks for Punta Galea [west] (4249 in spring 2014, 292 in autumn 2014, 1603 in spring 2015), 4657 for Cape Higuer [east] (2217 in autumn 2014, 2440 in spring 2015) and 1003 for the Iregua Valley [inland] in autumn 2014. Overall, 698 tracks were excluded from analysis, i.e. 116, 542 and 40 in spring 2014, autumn 2014 and spring 2015, respectively, which belonged to potential insects or other objects, or tracks without clear heading (e.g. curves or reversion). Only 0.6 % of all the flight tracks belonged to visually distinct flocks of 2-15 individuals.

FLIGHT DIRECTIONS

The Rayleigh test showed that circular data in each season and site were not uniformly distributed, but exhibited a preferential migratory direction ($P < 0.001$). Overall, flight directions tended to be more concentrated in spring (mean percentage of

TABLE 1. *Mean (± se) migratory direction per site and season. Column captions: Mean, mean migration direction; proportion of forward migration (%FM) within ± 60° around mean directions; proportion of reverse migration (%RM) ± 60° opposite to mean directions.*

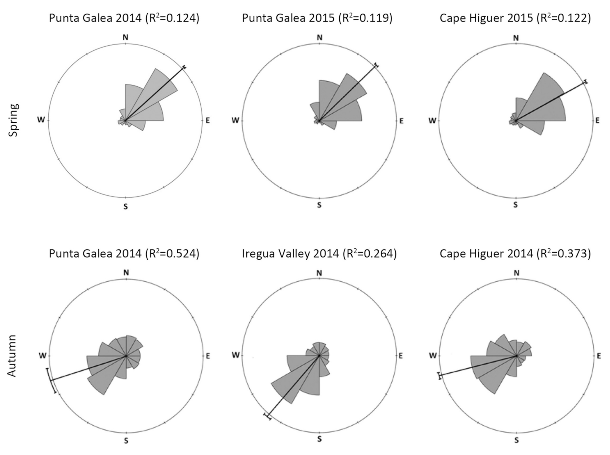
Site/Season	Mean ±se	%FM	%RM
Punta Galea [west]			
Spring 2014	47.9° ± 0.5°	95.2 %	1.6 %
Autumn 2014	251.6° ± 4.7°	63.6 %	19.9 %
Spring 2015	45.9° ± 0.7°	96.3 %	0.7 %
Cape Higuer [east]			
Spring 2015	61.1° ± 0.6°	95.9 %	1.6 %
Autumn 2014	255.7° ± 1.2°	78.6 %	9.5 %
Iregua Valley [inland]			
Autumn 2014	220.6° ± 1.4°	85.6 %	7.4 %

APPENDIX 1. *Mean directions per altitude class and per site; PG = Punta Galea [west], CH = Cape Higuer [east], IV = Iregua Valley [inland].*

Site/Season	Class 1	Class 2	Class 3	Class 4	Class 5	Class 6	Class 7
PG Spr 2014	46.9	51.3	55.2	104.0	40.5	–	289
PG Spr 2015	46.2	44.8	52.6	–	–	322[a]	–
PG Aut 2014	248.2	267.0	253.0	249.5	199.3	358[a]	–
CH Spr 2015	70.4	53.9	54.8	47.6	42.9	98.4	52.9
CH Aut 2014	256.1	253.9	249.8	204.1	292.3	327.9	316.1
IV Aut 2014	218.8	226.4	209.9	76.2	–	–	176.5

[a] *Only one track*

tracks falling within ±60° around the mean site- and season-specific directions, 95.8 %) than in autumn (Table 1). Overall, tracks were more unidirectional in the three highest levels, i.e. class 1-3, than in lower levels. Mean directions in the three upper height levels concentrated within ± 10° around the seasonal mean, while in the lower levels mean values deviated between 2-144 degrees (Appendix 1). Reverse migration occurred overall less frequently in spring (<2 % of tracks) than in autumn (7.4-19.9 % of tracks). The highest nightly MTR of reverse migration occurred at Cape Higuer [east] in October 2014, with 303 birds*km^{-1}*h^{-1} moving towards NE. A chi-square test showed no significant differences in the proportion of forward and reverse migration between Punta Galea [west] and Cape Higuer [east] in spring ($\chi^2 = 3.62$, $P > 0.05$) or between spring 2014 and spring 2015 at Punta Galea [west] ($\chi^2 = 4.64$, $P > 0.05$). The proportion of reverse and forward migration between sites differed significantly in autumn (χ^2 [Punta Galea [west] and Cape Higuer [east]] = 9.35; χ^2 [Punta Galea [west] and Iregua Valley [inland]] = 20.05; χ^2 [Iregua Valley [inland] and Cape Higuer [east]] = 8.03; $P > 0.05$), with the highest rate of reverse migration at the western coastal site (Punta Galea) and lowest at the inland site (Iregua Valley).



APPENDIX 2. *Migration directions (arrow: mean directions) of birds at Punta Galea [west], Cape Higuer [east] and the Iregua Valley [inland] in spring (upper row) and autumn (lower row).*

Mean directions between the two coastal sites differed significantly in spring ($F_{1,\,4041} = 270.9$, $P < 0.001$) (Appendix 2), pointing more eastwards in the east, compared to more northern directions in the west. In autumn, there were also significant differences between each coastal site and the Iregua Valley [inland] (Iregua Valley [inland] and Punta Galea [west], $F_{1,\,1292} = 63.811$, $P < 0.001$; Iregua Valley [inland] and Cape Higuer [east], $F_{1,\,3219} = 323.89$, $P < 0.001$) which showed more southward directions, but not between the two coastal sites ($F_{1,\,2507} = 1.033$, $P = 0.3$) (Appendix 2).

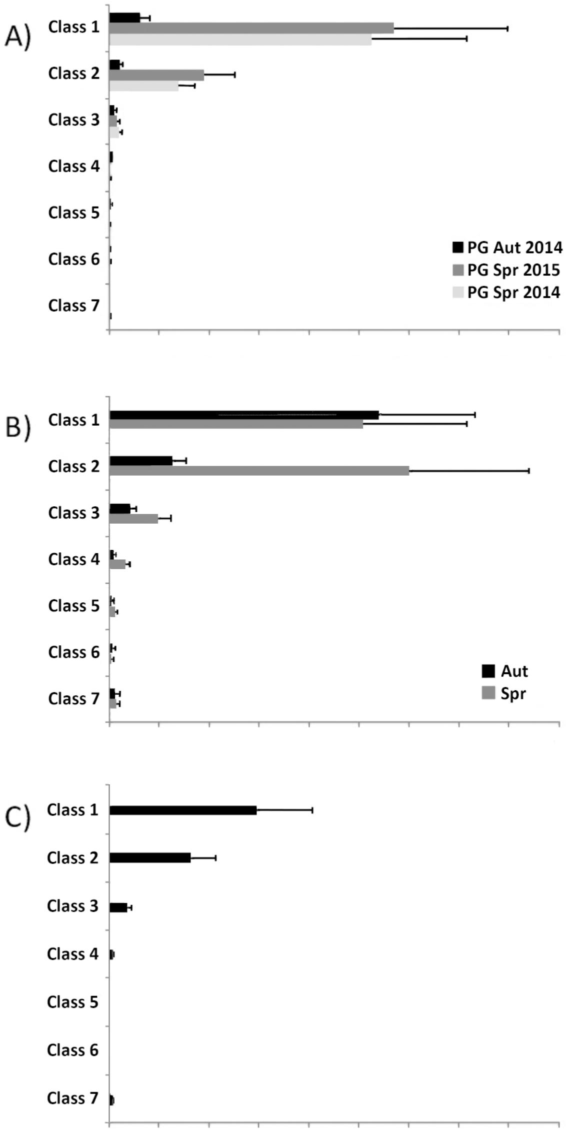


FIG. 2 *Migration altitudes in relation to the site and season determined by means of a thermal-imaging camera operating during a period of 4 h starting at sunset. (A: Punta Galea [west]; B: Cape Higuer [east]; C: Iregua Valley [inland])*

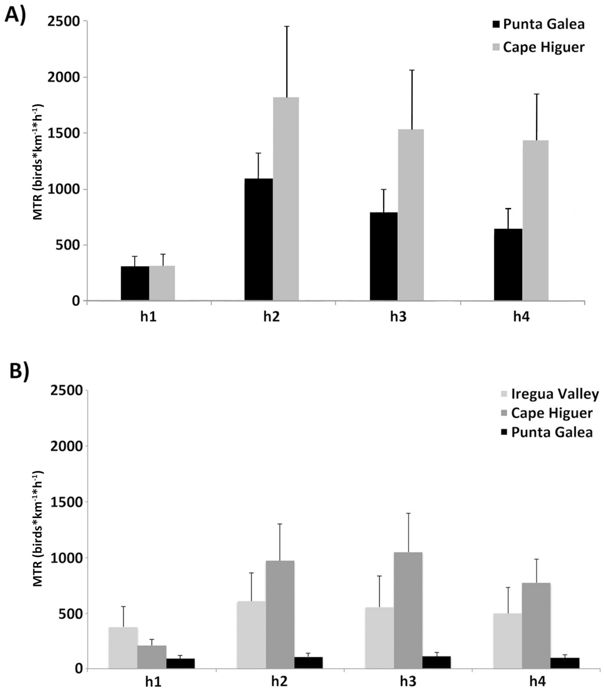


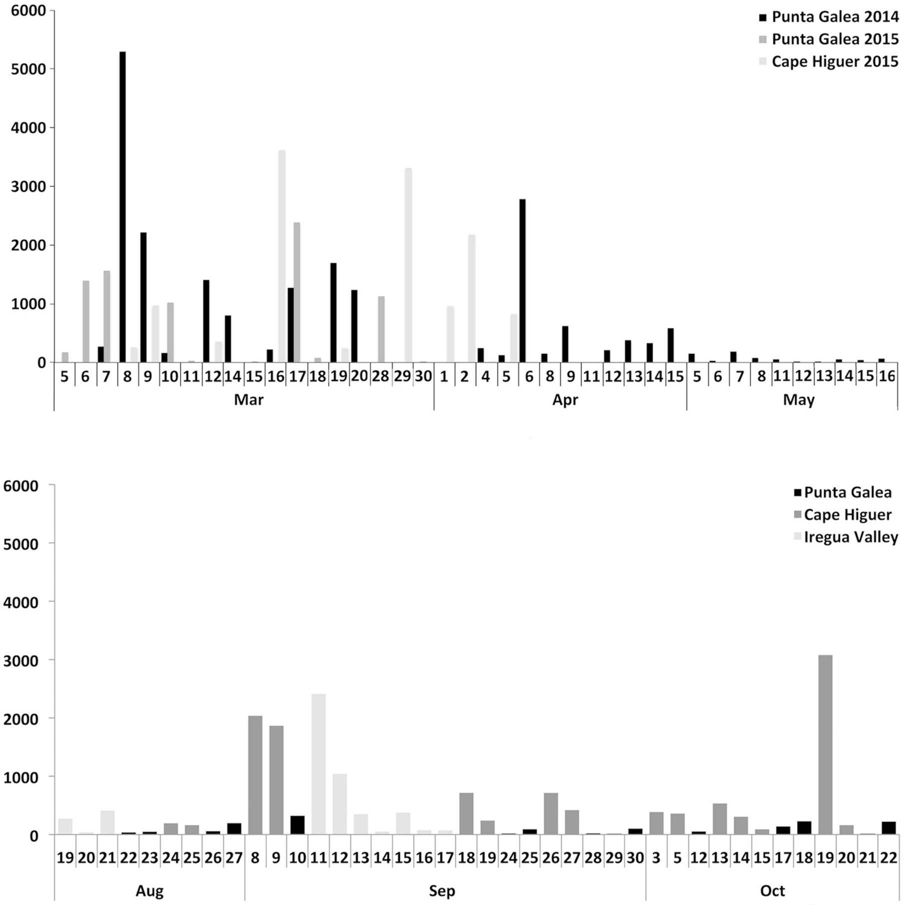
FIG. 3 *Mean (±se) hourly migration intensity in relation to site and season (A: spring; B: autumn). Years have been pooled for the analysis.*

FLIGHT ALTITUDE

Most (80-100 %) of the tracks concentrated at high altitude in class 1 and 2 (corresponding to an estimated altitude of 2.1 and 1.9 km, respectively), with only marginal activity in the lower levels (classes 3 to 7; (Fig. 2) . Overall, tracks were more unidirectional in the three highest levels, i.e. class 1-3, than in lower levels.

MIGRATION INTENSITY

The general migration pattern observed during each four-hour sampling was unimodal, with an activity peak either during the second or third hour after sunset (Fig. 3). Migration intensity varied considerably between nights. Hourly MTRs ranged from



APPENDIX 3. *Nightly migration traffic rates per site and season (above: spring; below: autumn).*

0 to 6713 birds*km-^{1}*h-^{1} and nightly mean MTRs from 0 to 5290 birds*km-^{1}*h-^{1} with only a small proportion of high-traffic nights of more than 3000 birds*km-^{1}*h-^{1} (Appendix 3). At Punta Galea [west] in spring 2014, migration intensity declined steeply from a monthly mean of 1458 birds*km-^{1}*h-^{1} in March to 483 birds*km-^{1}*h-^{1} in April and finally 53 birds*km-^{1}*h-^{1} in May. At Cape Higuer [east] a similar, though less pronounced tendency could be observed with 1461 birds*km-^{1}*h-^{1} in March and 995 birds*km-^{1}*h-^{1} in April. In autumn, August was the month of least activity at all sites. September was the peak month at Cape Higuer [east] (996 birds*km-^{1}*h-^{1}) and in the Iregua Valley [inland] (623 birds*km-^{1}*h-^{1}), while Punta Galea [west] exhibited a small peak in October (128 birds*km-^{1}*h-^{1}).

For Punta Galea [west] in spring 2014, only one model fitted the data better than the rest (Table 2). This model showed that MTR varied between months and along the four hours from sunset. The analysis of B-parameters revealed that the MTR peaked in the second hour after sunset, and reached its highest values in March (Table 3; Fig. 4).

TABLE 2. *Rank of the model with lowest AIC and the null model (birds~1) used to identify the variables determining the intensity of nocturnal bird migration at Punta Galea [west] during spring 2014. Other candidate models were ranked within a position of >2 AICc values from the model one. Abbreviations: AICc, small sample sizes-corrected Akaike values; ΔAICc, difference in AICc values in relation to the top model.*

Models	AICc	ΔAICc	AICc weight	No. parameters
1. Month + Hour	271.8	0.0	0.99	7
2. Null	335.2	63.3	0.00	1

TABLE 3. *B-parameter estimates obtained from the model with lowest AIC of Table 2.*

Parameters	B	se (B)	P
(Intercept)	+2.16	0.17	<0.001
Month: Apr.^{a}	-0.30	0.17	0.086
Month: May^{a}	-1.37	0.17	<0.001
Hour 2b	+1.00	0.20	<0.001
Hour 3b	+0.65	0.20	0.001
Hour 4b	+0.55	0.20	0.007

Hour 1, 2, 3 and 4 refer to hours after sunset; Hour 1= first hour from sunset. ^{a}Reference values (B = 0): Month = Mar. ^{b}Reference values (B = 0):

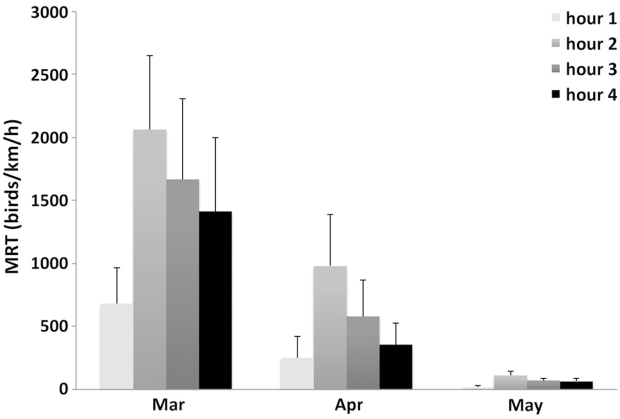


FIG. 4 *Mean (±se) migration intensity by month at Punta Galea [west] during spring 2014.*

TABLE 4. *Rank of the model with lowest AIC and the null model to identify the variables determining the intensity of nocturnal bird migration at Punta Galea [west] and Cape Higuer [east] in autumn 2014 and spring 2015. Other candidate models were ranked within a position of >2 AICc values from the model one.*

Models	AICc	⊿AICc	AICc weight	No. parameters
1. Site × Season	550.4	0.0	0.52	5
2. Site + Season	551.8	1.3	0.27	4
3. Null	587.0	36.6	0.00	1

TABLE 5. *B-parameter estimates obtained from model averaging of the models 1 and 2 of Table 4.*

Parameters	*B*	*se (B)*	*P*
(Intercept)	+2.06	0.16	<0.001
Season: Autumn[a]	– 0.55	0.21	0.010
Site: Cape Higuer [east][b]	+0.59	0.24	0.012
Season × Site	+0.33	0.32	0.308

[a]*Reference values (B = 0): Season: Spring.* / [b]*Reference values (B = 0): Site: Punta Galea [west].*

TABLE 6. *Rank of the models with ΔAICc <2 and the null model to identify the variables determining the intensity of nocturnal bird migration at Punta Galea [west], Higher Cape and Iregua Valley [inland] in autumn 2014. Tailwind refers to values at 775 m and 1500 m above sea level at 18:00 h.*

Models	AICc	ΔAICc	AICc weight	No. parameters
1. Site × Tailwind 775	411.7	0	0.53	7
2. Site × Tailwind 1500	413.1	1.4	0.27	7
3. Null	451.5	39.8	0.00	1

TABLE 7. *B-parameter estimates obtained from the model averaging of the models 1 and 2 of Table 6. Tailwind refers to values at 775 m and 1500 m above sea level at 18:00 h..*

Parameters	*B*	se *(B)*	*P*
(Intercept)	+1.46	0.11	<0.001
Site: Cape Higuer [east] [a]	+1.14	0.18	<0.001
Site: Iregua Valley [inland] [a]	+0.68	0.21	0.001
Tailwind 775	-0.01	0.02	0.67
Cape Higuer [east] × Tailwind 775	+0.05	0.05	0.29
Iregua Valley [inland] × Tailwind 775	+0.09	0.08	0.22
Tailwind 1500	+0.00	0.01	0.86
Cape Higuer [east] × Tailwind 1500	+0.02	0.03	0.56
Iregua Valley [inland] × Tailwind 1500	+0.04	0.05	0.51

[a] *Reference values (B = 0): Site: Punta Galea [west]*

The comparison between Cape Higuer [east] and Punta Galea [west] in autumn and spring showed a significant relationship of site and season on MTR (Table 4). The interaction between site and season was not significant (Table 5), but migration intensity in autumn was significantly lower than in spring and higher at Cape Higuer [east] than at Punta Galea [west] (Table 5).

Autumn analysis of the three sampling sites also yielded two models which fitted the data better than the rest (Table 6). These models included the interaction between site and tailwind at 775 m and 1500 m above ground level, respectively, at 18:00 h. However, in model averaging, only the site variable was significant (Table 7).

DISCUSSION

This is the first thermal-imaging study to determine nocturnal bird migration phenology at the Bay of Biscay. Migration altitude, direction and intensity at three sites at or close to the Bay of Biscay, within the East-Atlantic flyway, exhibited large inter-night fluctuations, but also in relation to the site and season, indicating spatio-temporal variations. The majority of registered tracks stemmed from singly flying birds, indicating predominance of passerines, as found in other regions (e.g. Bruderer 1971, Alerstam 1990). The small fraction of birds in compact flocks or line formations can be probably ascribed to passing waterfowl or waders, based on findings from a parallel moonwatching study (Weisshaupt et al. 2016).

Even though clear skies were preferably selected for sampling, interference from small-scale and large-scale weather changes still occurred given the highly variable meteorological conditions in the study area. In connection with this, a detection bias cannot be excluded through cloud layers and/or wind conditions, which might have prompted the birds to fly at higher/lower altitudes within or beyond the scope of the camera. However, this effect, if any, would be expected to affect all sites more or less equally in each season and thus the fluctuations cannot be solely attributed to weather, but do actually reflect variable numbers of migrants.

FLIGHT DIRECTIONS AND ALTITUDE

Mean directions in both spring and autumn were in line with the main migratory axis (NE in spring, SW in autumn) through western Europe (Zink 1970, Hilgerloh 1989, Trösch et al. 2005). The significant statistical difference at the two coastal sites Punta Galea [west] and Cape Higuer [east] in spring remains unclear. It could be due to a possible divide in migration flow between birds of more western vs. eastern breeding grounds or an influence of topography at a local-scale. Interestingly, however, we did not detect any significant difference between the two coastal sites in autumn, but only between the coastal sites and the inland site (Iregua Valley). This difference suggests a shift to a more southern direction towards the interior of Iberia compared to the coast, which might be the beginning of the "Zugknick", a pronounced migratory directional shift southwards found in various species in southwestern Europe (e.g. Gwinner & Wiltschko 1978, Beck 1984, Hilgerloh 1985, Liechti et al. 2012). This scenario would also be supported by the low MTR values at the western site and more similar MTRs between the eastern and the inland site. Alternatively, it could be argued that birds simply followed the direction of the valley in which sampling took place. However, this conclusion seems less likely given the complex topography of the mountainous area with short, rather high valleys of varying alignments, surrounded by the extensive Ebro valley. Furthermore, on a more local scale, the valley in question extends on a more southerly axis of roughly 190-205°, compared to the mean migration direction of 220.6° (±1.4°).

Flight directions were highly unidirectional in spring with only a negligible proportion of reverse migration (<2 %). In contrast, autumn showed a significantly higher scattering with the highest rate of reverse migration at Punta Galea [west] (ca. 20 %). It is unlikely that this pattern is due to weather conditions only, because abrupt weather changes occur both in autumn and spring. A plausible explanation would be the higher proportion of juvenile birds in autumn (Zehtindejiev & Liechti 2003, Nilsson et al. 2014).

Considering the seasonal patterns and the geographical setting, the mean migration direction suggests migration on a broader front including sea crossing in spring. In principle, the mean direction can be interpreted in two ways, 1) migrants follow the coast and do not cross the open sea of the bay, as directions at Punta Galea [west] coincided well with the coastline both in spring and autumn; or 2) the parallel direction is by chance and birds fly well out across the sea at Punta Galea [west]. The actual strategy could be a combination of the two hypotheses. While passing the study site, birds still follow the coastline until reaching the northernmost point and then fly out to the sea. This interpretation is supported by both the seasonal patterns and the mean direction at Punta Galea [west] in spring pointing to the region of Bordeaux, France. Such a trajectory would coincide with an air-line distance of ca. 250 km which based on Bruderer and Bolt (2001) could be covered by a songbird in a single nonstop flight. Taking into account the observed southern directions at the autumn inland site, it seems reasonable to conclude that birds would perceive the western site as an unnecessary detour when heading south over land in autumn, but not in the face of the time pressure in spring.

Another indicator of sea-crossing is the predominance of high flight altitude, as reported in this study, while low nocturnal altitudes are associated with coasting or landing (Bruderer & Liechti 1998, Nilsson et al. 2014). Studies in other similar coastal areas, e.g. in southern Scandinavia, found a similar pattern (Zehnder et al. 2001a, Nilsson et al. 2014). The mountainous region around the Iregua Valley [inland] with peaks of about 2000 m above sea level could account for a similar effect. Zehnder et al. (2001b) reported flight altitudes <3500 m in the Alps, stating that birds avoid climbing/descending flights between valleys and mountains by choosing high flight altitudes in mountains. More research is needed to answer this question conclusively.

MIGRATION INTENSITY

The overall migration intensity peaked during the second or third hour after sunset, independent of the site and season. This is in agreement with findings from earlier studies (e.g. Alerstam 1976, Dolnik 1990, Bruderer 1997), and has been linked to the main take-off period in the first hour after sunset. Local radar data (Weisshaupt et al. 2014) indicates a similar pattern with clutter (i.e. bird migration) extending 1-2 hours after sunset across the entire height profile (i.e. to be interpreted as a peak) and then signals continue (or are absent) in a slightly narrower, but uniform altitudinal extension throughout the night. Therefore, the low autumnal intensity observed at Punta Galea [west] in the first half of the night cannot be explained by the hypothesis that migrants potentially crossing the sea have not reached the area yet, even though such a pattern would remain unappreciated in measurements during the first four hours after sunset. It rather reflects actual absence of migration in the area. It seems more reasonable that spring migration occurs on a broad front, whilst autumn migration is concentrated more eastwards with migrants entering Iberia over the continent and potentially avoiding sea crossing. This explanation would be also supported by the observed steep east-west decrease of MTRs between the two coastal sites Punta Galea [west] and Cape Higuer [east] as well as findings based on ring-recovery analyses for northern Iberia (Galarza & Tellería 2003). Diverging spring and autumn migration routes have been shown for various species (e.g. Klaassen et al. 2010, Willemoes et al. 2014) and have been attributed to higher time pressure to reach the breeding grounds in spring (Kokko 1999). Concentration over land in autumn could be also explained by a higher proportion of juvenile birds choosing a safer route.

At the two coastal sampling sites the migration intensity in spring was characterized by several extreme migration events (nightly migration traffic rates between 3500-6000 birds*km^{-1}*h^{-1}) alternating with nights of low and medium migration intensities (nightly migration traffic rates between 0-1500 birds*km^{-1}*h^{-1}). A certain bias on intensities is possible given the fact that only one camera was available and no simultaneous measurements were possible. However, it can be assumed that all sites underlie the same probability of missing low or high intensities based on the study design (sampling intervals of 1-3 days per site), so the bias is expected to be negligible. The inter- and intraseasonal decrease at Punta Galea [west] fits with radar findings obtained by Weisshaupt et al. (2014) at the same site. Spring MTRs from Punta Galea [west] (1458 birds*km^{-1}*h^{-1} in 2014 vs. 778 birds*km^{-1}*h^{-1} in 2015) indicate that data from one season may be insufficient to properly reflect the typical numbers of a site. External drivers like weather conditions can probably have a strong impact on migration dynamics. February 2015 brought severe winter weather with snow down to the coastline and low temperatures prevailing until March. Furthermore, there were long periods of northerly and partially easterly winds. So it cannot be ruled out that these adverse large-scale weather conditions possibly influenced the observed lower migration intensity at Punta Galea [west] compared to the previous year.

Overall, however, a decreasing number of migrants in the course of spring is in accordance with the idea that spring migration in this region is mainly shaped by short-distance migrants, probably overwintering in Iberia or northern Africa, rather than long-distance migrants spending the winter in tropical Africa (sensu Finlayson 1992). This interpretation is also compatible with the fact that Reed Warblers Acrocephalus scirpaceus, a long-distance migrant captured in the study region, were caught in very low numbers during ringing campaigns on the Basque coast in spring (Arizaga et al. 2014).

Interestingly, tailwind did not have any significant effect on migration intensity. Fact is, however, that migration in spring ceased completely during strong easterly or northerly winds (i.e. direct or lateral headwinds) even though skies were clear. Thus, migrants may not show a clear preference for one particular wind direction, but simply for winds that would offer some tailwind component, and which may remain unappreciated in some of the analyses because of the wide range of wind directions (Nisbet & Drury 1967, Steidinger 1972).

CONCLUSIONS

In conclusion, thermal imaging allowed providing novel insights on nocturnal migration phenology at the southeastern coast of the Bay of Biscay, complementing previous data from diurnal studies. Flight directions, flight altitude distribution, as well as seasonal and geographical variations in migration intensity, indicate that spring migration occurs on a broader front than autumn migration, potentially involving sea crossing. In autumn, there is a pronounced east-west gradient, indicating a more eastern migration flow. Tailwind assistance did not have any significant impact on the spatial and temporal evolvement. The majority of the tracks originated from singly flying birds, indicating a predominance of passerines. It would be interesting to further investigate the observed patterns based on simultaneous data from long-range remote sensing technology (e.g. weather radars) to improve our understanding of migratory dynamics and patterns on a larger geographical scale.

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PAPER III

PRELIMINARY ASSESSMENT OF NOCTURNAL BIRD MIGRATION AT THE BAY OF BISCAY AS OBSERVED BY MOON-WATCHING.

Short title: Moon-watching at the Bay of Biscay

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ABSTRACT

The East-Atlantic flyway represents one of the main bird migration routes worldwide, comprising the Bay of Biscay as a geographic barrier. So far, the significance of the Bay of Biscay for and its impact on migrants and their routes has not received much attention. The main goal of this study is to characterize the composition of nocturnal bird migration along the coast of the Bay of Biscay in northern Iberia. For this purpose, moon-watching was carried out at two study sites (Punta Galea, Cape Higuer) during spring and autumn 2014. The vast majority of observed migrants consisted of singly flying passerines, with some interspersed groups of non-passerines such as waterfowl, waders or swifts.

KEY WORDS: Atlantic flyway, Basque coast, passerines, spring and autumn migration.

RESUMEN EN CASTELLANO

La ruta del Atlántico Oriental es una de las rutas de vuelo migratorio mas importantes en el mundo e incluye el golfo de Vizcaya como barrera geográfica. La importancia y el impacto del golfo de Vizcaya para las aves migratorias y sus rutas no han recibido mucha atención en la investigación. El objetivo principal de este estudio es caracterizar el ensamblaje de las aves que migran de noche por la zona del golfo de Vizcaya en el norte de la Península Ibérica. Para ello, se han efectuado observaciones lunares en dos sitios de muestreo (Punta Galea, Cabo de Higer) en primavera y otoño 2014. La mayoría de las aves registradas eran paseriformes volando individualmente, y algunos grupos de no-paseriformes como aves acuáticas, limícolas o vencejos.

LABURPENA

Atlantiko ekialdeko ibilbidea munduko migrazio bide garrantzitsuenetako bat da eta Bizkaiko golkoa barrera geografiko bezala barne hartzen du. Hegazti migratzaileengan Bizkaiko golkoak duen garrantziak eta eraginak ez dute arreta handirik jaso ikerkuntzan. Ikerlan honen helburu nagusia Bizkaiko golkoko eremuan, Iberiar penintsulako iparraldean, gauez migratzen duen hegazti multzoaren karakterizazioa egitea da. Horretarako ilargi betearekin behaketak egin dira bi laginketa puntuetan (Galea eta Higer lurmuturrak) 2014ko udaberri eta udazkenean. Erregistratutako hegazti gehienak banaka hegan egiten zuten paseriformeak ziren, eta baita paseriforme ez diren talde batzuk ere, hegazti urtarrak, zangaluzeak edo sorbeltzak esaterako.

Studying active nocturnal bird migration entails various challenges, such as reduced (or no) visibility, and requires appropriate measuring techniques. One technique to quantify this type of migration is moon-watching, probably the oldest of all as it was applied already in the 19th century (e.g. Scott 1881, Chapman 1888 and Libby 1889 in Lowery 1951). Birds passing in front of the lunar disc are observed and counted through a telescope. Depending on the flight and silhouette characteristics, it is possible to identify bird families, but practically no species (Liechti et al. 1996). Even though very simple to implement, data collection by moon-watching is restricted to a few cloudless nights around full moon. This method is described in detail by Lowery (1951) and has been widely used in various studies, also in more recent times [e.g. Kiepenheuer and Linsenmair (1965), Nisbet and Drury (1969), Liechti et al. (1995), Liechti 2001].

Bird migration studies along the coast of the Bay of Biscay have focused on ringing data from landed migrants mainly from autumn campaigns, or also on daytime observations of active migration (e.g. Lack and Lack 1953, Grandio and Belzunce 1987, Mendiburu et al. 2009, Arizaga et al. 2014). Thus spring data per se and overall knowledge on active nocturnal migration is scarce. The aim of this note is to contribute to the characterization of nocturnal bird migration, and in particular bird assemblage, along the coast of the southeastern Bay of Biscay (northern Iberia), based on preliminary results obtained from a moon-watching study.

To gain more information on the nocturnal migrant composition, moon-watching was carried out at two study sites on the Basque coast: Punta Galea, Bilbao (43°22'N, 03°02'W) in the west, and Cape Higuer, Hondarribia (43°23'N, 01°47'W) in the east, close to the French border. If cloud cover allowed, two nights prior to until two nights after full moon (sensu Lowery 1951) were sampled from March to May 2014 at Punta Galea, and in September 2014 at both study sites (no simultaneous observations). A telescope (Swarosvki ATS 65 HD, Zoom 20-60x) and a digital camera (Canon, Power Shot SX220 HS) were used to "videoscope" (video recording through telescope) the lunar disc to facilitate posterior analysis. Like this, each suitable night yielded samples of 30-60 min. The sampling time per night was restricted by the battery life of the camera and the limited personnel on site (1 person), as well as by meteorological conditions (clouds in front of the lunar disk). However, as the lunar samples should serve as a complementary measurement of bird composition (no bird flux or directions) for a simultaneous thermal-imaging study only, the sampling effort was not extended, but rather adapted to what was observed in the thermal-imaging camera at the same site, i.e. if the camera recorded no activity, no moon-watching was performed (e.g. in particular in May). Passing birds were counted and assigned to the categories passerines vs. non-passerines or, if possible, also down to family levels, e.g. larids, swifts, thrushes, etc. Migration traffic rates or directional calculations as detailed in Lowery (1951) were not targeted in this study, still a descriptive account of migrants flow is provided.

In spring 2014, overall 4.8 h of moon-watching were recorded in 4 nights in March (2:53 h), 3 nights in April (1:42 h) and 1 night in May (00:15 h) at Punta Galea. 66 (88 %) birds were identified as passerines, apparently thrushes or thrush-like species, and 9 (12 %) were ducks. We observed decreasing migration intensity in the course of spring, with a mean flow of 22.2 birds/h in March, 1.5 birds/h in April, and 0 birds/h in May. Further occasional unrecorded observations included also a small flock of four waders. In autumn, overall 35 birds were recorded in 2.25 h: 34 birds in 2 nights at Cape Higuer, equivalent to 1.8 h, and one night at Punta Galea with one bird, equivalent to 0.5 h of recordings. 32 (94 %) migrants at Cape Higuer were singly flying passerines with some swifts interspersed; the remaining 2 (6 %) were larids (gulls or terns). Mean flow was 19.31 birds/h. At Punta Galea, in contrast to spring observations (especially in March), autumn migration was nearly zero and only one gull/tern was observed, i.e. the mean flow was 2 birds/h.

FIG. 1. *Snapshot of 9 waterbirds passing in front of the lunar disk on March 13, 2014, at Punta Galea, Spain.*

Moon-watching provided data allowing us to have an overview over migrants' assemblage in the southeastern Bay of Biscay. The vast majority of these birds consisted of singly flying passerines, with some interspersed groups of non-passerines such as waterfowl, waders or swifts (Fig. 1); a short moon-watching sequence is available at http://www.aranzadi.eus/fileadmin/videos/Moonwatch_Videoteil_kuerzer2.avi, which was recorded on March 13, 2014, at Punta Galea, (Spain), showing two single passerines [00:15 and 00:17] and 9 ducks [00:28]). The predominance of passerines is in line with findings based on radar and moon-watching from nearby regions such as the western Mediterranean or southern England (e.g. Parslow 1968, Liechti et al. 1995). Interestingly, migration activity at Punta Galea seemed to be higher in spring than in autumn. Overall, the effort of this exploratory study, which principally targeted bird composition, is insufficient to deduce any further migratory patterns like directions and migration intensity (i.e. "migration traffic rates" sensu Liechti et al. 1995). In order to obtain such migration parameters, which allow for comparisons with data from other areas, and to draw any robust conclusions on a potential seasonal variability, a more ample moonwatching study would be needed, i.e. standardized simultaneous observations as detailed in Lowery (1951) and Liechti et al. (1995), at various sites along the Bay of Biscay, in both spring and autumn. Ideally, such a study should include observations in clear skies of at least 30 minutes per night, once the moon has risen up to at least 14° above the horizon (if the moon is lying lower, directional and quantitative estimations become inaccurate) (Nisbet 1959). However, given the highly variable meteorological conditions prevailing at the Bay of Biscay, which also reduced and affected the presented effort in the field considerably, other sampling methods with less limited sampling requirements (not only during full moon and in clear skies), such as radar or thermal imaging, could be worthy alternatives for further nocturnal studies in the area.

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PAPER IV

RADAR WIND PROFILERS AND AVIAN MIGRATION - A QUALITATIVE AND QUANTITATIVE ASSESSMENT VERIFIED BY THERMAL IMAGING AND MOON WATCHING.

SHORT TITLE: Wind profilers used to study bird migration.

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ABSTRACT

1. Radars of various types have been used in ornithological research for about 70 years. However, the potential of radar wind profiler (RWP) as a tool for biological purposes remains poorly understood. The aim of this study is to assess the suitability of RWP for ornithological research questions.

2. A 1290 MHz RWP at the southeastern coast of the Bay of Biscay has been known to exhibit seasonally occurring nocturnal signals attributed to migrating birds. As a first step to verify the origin of these seasonal patterns, historical radar data from 2010-2012 were analysed, and both bird patterns and temporal occurrence were identified in processed consensus, moment and spectral data. A thermal-imaging (TI) camera in conjunction with moon watching was used as verification systems at the radar site to confirm the ornithological origin of the radar echoes. The simultaneous data on spring migration served as a basis for the identification of biological signatures (qualitative parameters) on time series level (raw data) and to derive quantitative migration parameters (flight altitude, migration traffic rates) thereof. Finally the quantitative measurements of the TI camera and the radar were compared considering meteorological conditions.

3. The approach allowed identifying reproducible criteria based on time series to calculate migration traffic rates and altitudinal flight distribution. General flight directions were only available in consensus data. In clear weather conditions the calibration methods coincided well with the wind profiler data.

4. Findings show that wind profiler raw data offers reliable information on migration intensity, flight altitudes and flight directions in a variety of meteorological conditions. The method presented can be applied as a complement to present efforts to use weather radars for large-scale bird monitoring. Furthermore it is also interesting for the meteorological community to refine signal-processing methods.

KEY WORDS: ornithology, wind profiling, calibration, thermal imaging, remote sensing

INTRODUCTION

Radars offer many advantages in ornithology in comparison to other investigational methods such as visual counts or ringing because of less expenditure of time and effort, superior visibility and detectability (e.g. at higher altitudes or in the dark), as well as better applicability for large-scale monitoring (Shamoun-Baranes et al. 2014). Lack and Varley (1945) were the first to describe the detection of seabird movements by radar at the southern British coast. An overview over the wealth of ornithological radar studies in Europe and the Middle East was provided by Bruderer (1999). Detailed bird-radar studies have mainly used X-band tracking or ship radars (e.g. Bruderer 1999, Gauthreaux and Belser 2005, Karlsson et al. 2012). However, it has also been known from weather radar networks, such as NEXRAD or OPERA, that these remote-sensing systems register bird movements (Gauthreaux et al. 1998, Koistinen 2000, Holleman et al. 2008, Dokter et al. 2010). In connection with weather radars, the COST action ENRAM (European Network for the Radar surveillance of Animal Movement) is dedicated to "establishing the basis for a coordinated network of monitoring radars for the provision of real-time spatio-temporal information on animal movement through the air on a continental scale", potentially benefitting both the environment and humankind (ENRAM Memorandum of Understanding 2013). In contrast, in RWPs great efforts have been undertaken to remove the biological signals rather than to study them (e.g. Wilczak et al. 1995). RWPs measure clear air echoes, which are generally weaker than non-atmospheric echoes, and require very long dwell times to be detectable. If non-atmospheric signal components are present, the atmospheric signal component is likely to be masked and thus atmospheric data quality is deteriorated (Merritt 1995). So appropriate signal processing plays a decisive role. To remove so-called "biological contamination", Merritt (1995) presented an approach based on a statistical averaging method (SAM) on the spectral level. Other signal processing approaches proposed by Pekour and Coulter (1999) and Kretzschmar et al. (2003) were also based on the spectral level, while Lehmann and Teschke (2008), Lehmann (2012) and Bianco et al. (2013) worked on time series level. All these studies regarded birds as contamination to be removed, however, the potential of RWP for actual ornithological purposes remains poorly understood. In particular the continuous vertical profiles, covering the entire air column up to several kilometres, i.e. where bird migration takes place, paired with the widespread use of these radars in networks such as E-Profile (Europe) (Fig. 1a) or for air quality monitoring as the Cooperative Agency Profilers (CAP, US) (Fig. 1b) could potentially be an interesting complement to the horizontal scanning method of weather radars. Therefore RWPs are of potential ornithological interest and worth undergoing a closer evaluation.

As a first approach in such an evaluation process, the

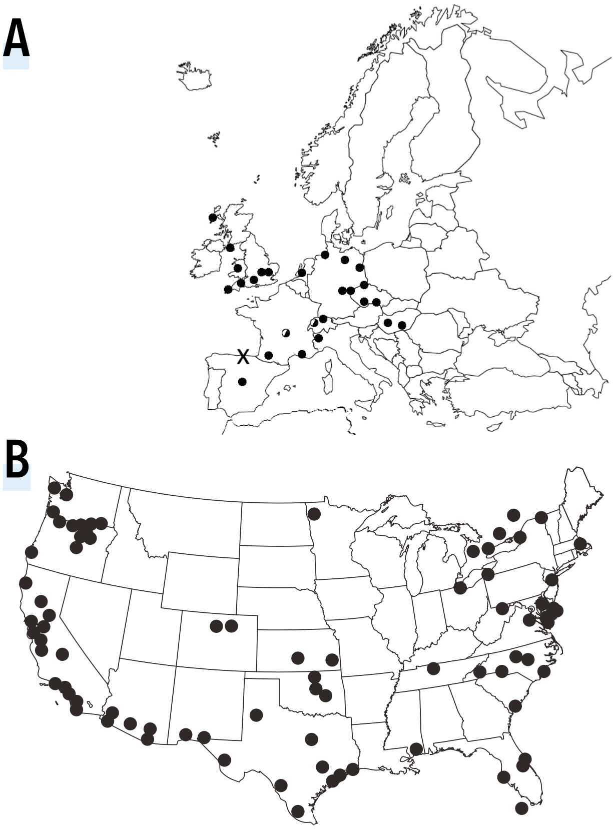

FIG. 1 *An overview over the RWP sites from (A) the European network (E-Profile) including the Punta Galea WRP (x) (filled dots: 1 RWP, half-filled dots: 2 RWP); and (B) the Cooperative Agency Profilers (CAP) in the US.*

source of the radar signals needs to be verified by a secondary system such as visual observations or thermal imaging if the characteristics of bird signatures in a radar type are unknown, because target identification by radar alone is only insufficient (Schmaljohann et al. 2008). Otherwise, considering migration, the content of the sampled volume remains ambiguous given the fact that not only birds can migrate in large numbers, but also insects and bats (Chapman et al. 2011). When using two or more systems simultaneously in calibration field studies, it is important to be aware of the potential limitations of each. For example, meteorological conditions can have a major impact on target detection in case of thermal imaging. Increased humidity (e.g. precipitation or fog) or cloud movement can be a limiting factor as it decreases detectability of targets (Zehnder et al. 2001). In contrast, in RWP, low relative humidity has been known to decrease data quality (Vaisala 2007). Otherwise no bias is to be expected from atmospheric echoes because they are always greatly inferior to bird echoes (Merritt 1995).

In order to evaluate the potential of RWP for providing qualitative and quantitative information on bird migration, year-round data from a wind profiler on the Basque coast (Spain) was analysed in combination with thermal imaging data. Since its installation in 1996, the radar has registered biological signals in particular during bird migration season.

The aim of this study is to provide an in-depth characterization of bird signals versus other biological and atmospheric signals in order to (1) explore the capacity to obtain quantitative and qualitative wind profiler data for ornithological purposes; (2) to compare RWP data with thermal imaging and moon-watching data and to discuss discrepancies and similarities considering technological and meteorological factors; (3) to discuss advantages and disadvantages of "raw data" (time series) vs. further processed (spectral, moment and consensus data) RWP data. The results will not only help the ornithological community harness a new observation tool, both at a local scale to study migratory behaviour in an ecological context (e.g. close to a geographical barrier), as well as at other RWP sites, but they will also support future improvements in signal processing in meteorology.

DESCRIPTION OF THE SYSTEMS

THERMAL-IMAGING CAMERA & MOON-WATCHING

A long-range thermal-imaging camera (LORIS, IRTV-445L, Inframetrics, Massachusetts, U.S.A.) was employed with an opening angle of 1.45 degrees. Data was recorded on videotapes for posterior digitalization and analysis. Thermal-imaging systems are based on the detection of differences in thermal radiation emitted by objects. Birds as endotherms differ therefore clearly from ambient air temperature and are visualized as contrasting objects in the sky, i.e. passing the screen. From these trajectories, migration directions are derived. Direct comparisons with tracking radar have shown that the camera is able to detect small-sized passerines up to about 3000 m above ground level in clear weather conditions (Bruderer and Liechti 1999, Liechti et al. 1995, Zehnder et al. 2001). High-flying birds are typically seen as smaller objects than lower flying birds, a principle which can be used to establish altitude classes and estimate the flight altitudes. Size differences between passerines are considered negligible (Zehnder et al. 2001) and no size bias on altitude classes is to be expected. The camera is preferably used in clear skies as cloud interference and humidity potentially affect the detection of birds aloft.

In addition to thermal imaging, moon watching was carried out in spring 2014 and 2015 to complement information on nocturnal bird composition. Observing the lunar disc from two nights prior to until two nights after full moon is a way of studying nocturnal migration and is detailed in Lowery (1951). A telescope (Swarosvki ATS 65 HD, Zoom 20-60x) and a digital camera (Canon, Power Shot SX220 HS) were used to "videoscope" (video recording through telescope) the lunar disc to facilitate posterior analysis. This method was used as an additional approximation for bird identification in this study, no estimation of migration intensity was targeted.

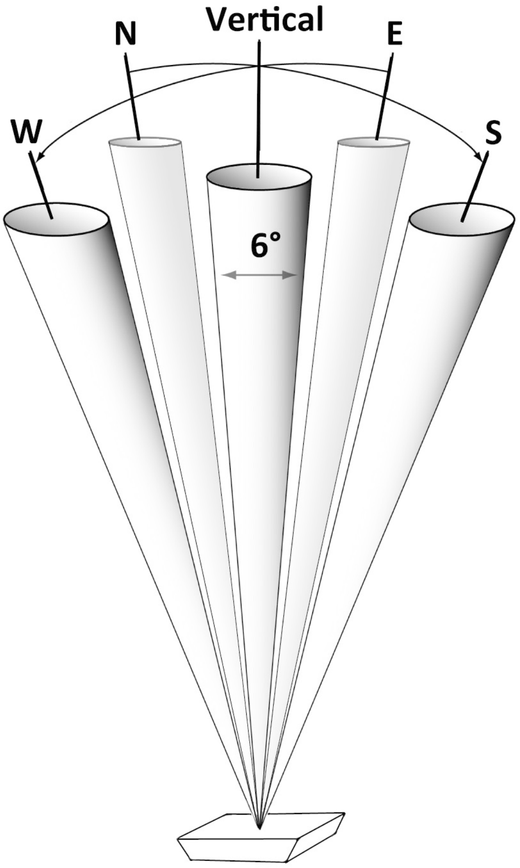

FIG. 2 *Beam configuration of the boundary layer wind profiler radar at Punta Galea, Spain.*

RADAR WIND PROFILER

RWP SPECIFICATIONS AND TERMINOLOGY

Radar data for this study was retrieved from the 1290-MHz LAP 3000 boundary layer wind profiler with integrated Radio Acoustic Sounding System (RASS) owned by Euskalmet (Basque Meteorology Agency). The radar site is situated at the northeastern side of the estuary of Bilbao, Spain, on a cliff top (43.37°N, 3.04°W) (Fig. 1a). The RWP is a phased-array Doppler radar with nine microstrip patch antenna panels providing continuous, real-time vertical profiles of three-dimensional winds and virtual temperature by means of five beams, one vertically pointing and four tilted orthogonally by 15.5 degrees towards the four cardinal points, with an opening angle of 6 degrees. (Fig. 2). For a detailed description of the system see Carter et al. (1995) and the Vaisala User's Guide (2007).

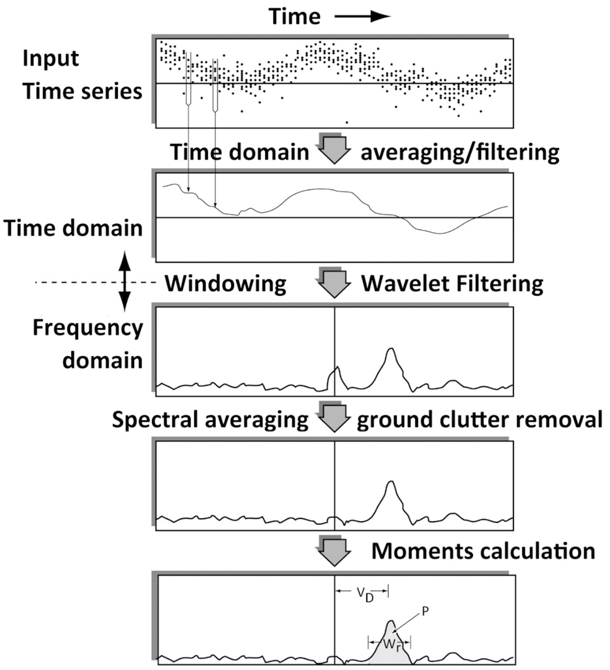

FIG. 3. *Data processing: moments calculation from time series data (Vaisala 2007).*

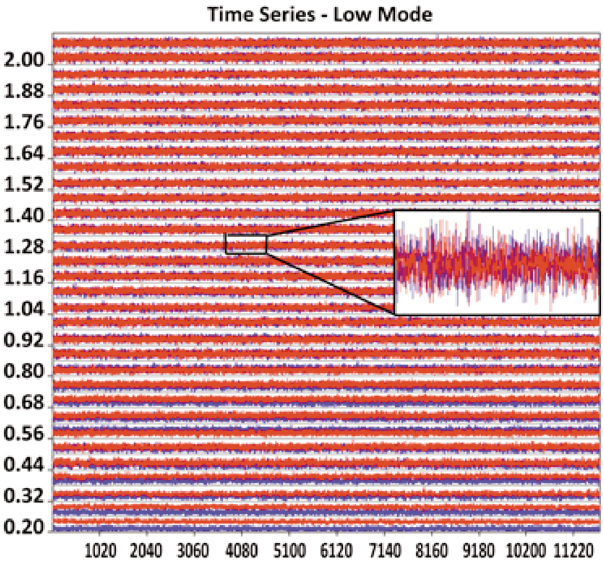

FIG. 4 *Example of clear air in time series presented as normalized signal-to-noise ratio plots for each gate in low mode.*

OPERATIONAL PARAMETERS

The RWP operates with two alternating resolutions with two different electromagnetic pulses, a low mode with a 60-m pulse length (corresponding to a 417-ns pulse) allowing to detect clear-air echoes up to about 2 km in good meteorological conditions and a high mode with 400-m pulse length (corresponding to a 2833-ns pulse) which extends this range to about 4-8 km high in favourable conditions. The vertical resolution of the Punta Galea wind profiler is defined by the pulse width, and the received signal is sampled by the radar electronics at discrete range gates (32 gates in low mode, 20 gates in high mode). A time series, i.e. raw data, of the reflected signal is generated with a dwell time of 30 seconds per beam (for an overview over signal processing steps see Fig. 3). Scanning each of the five beam directions with both short and long pulse defines a scan cycle of 5 minutes. Time series

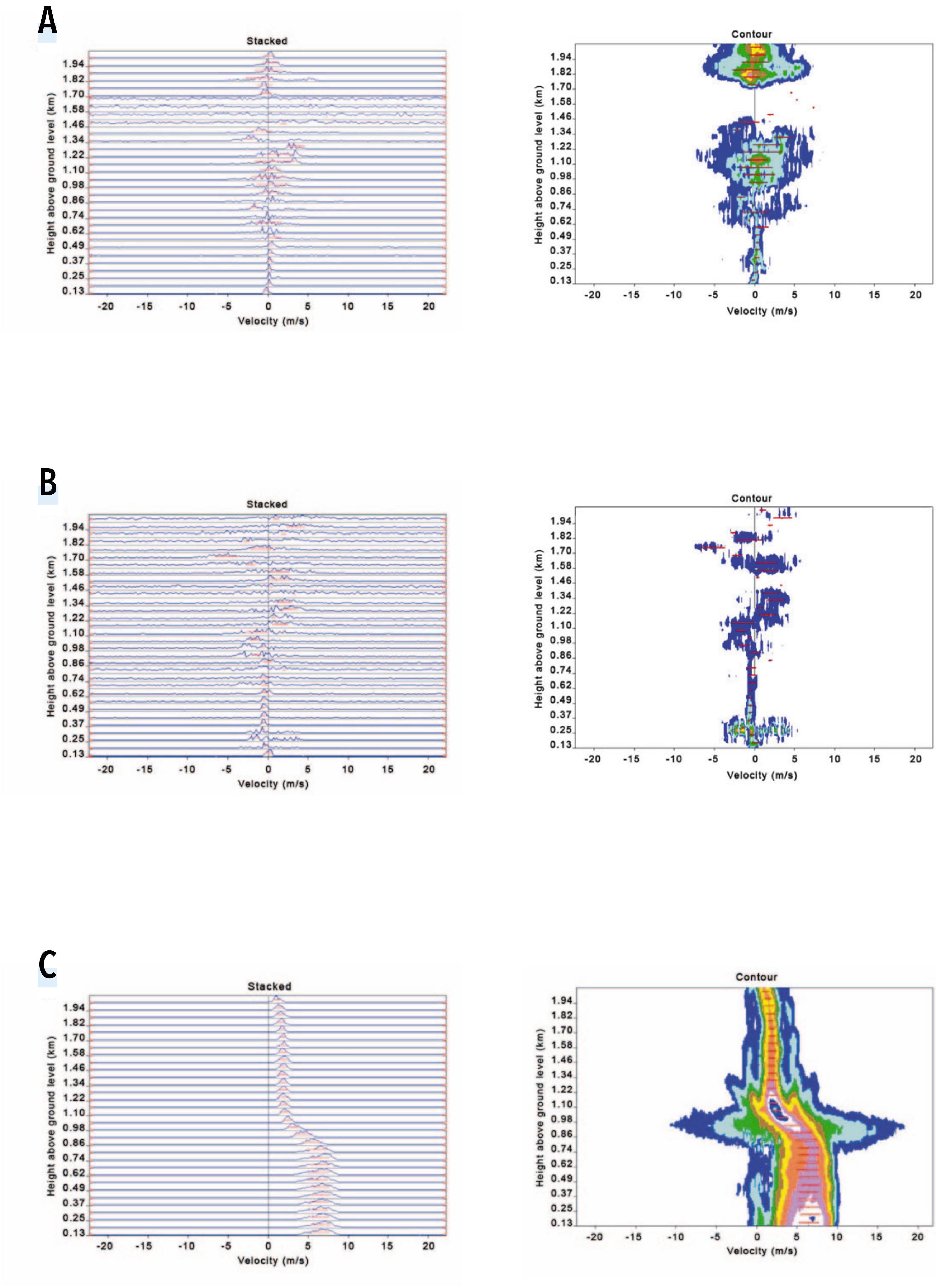

FIG. 5 *Time-height plots of spectral data - examples of (a) spectral data for strong migration; (b) low/moderate migration; and (c) precipitation, as depicted in stacked and contour mode.*

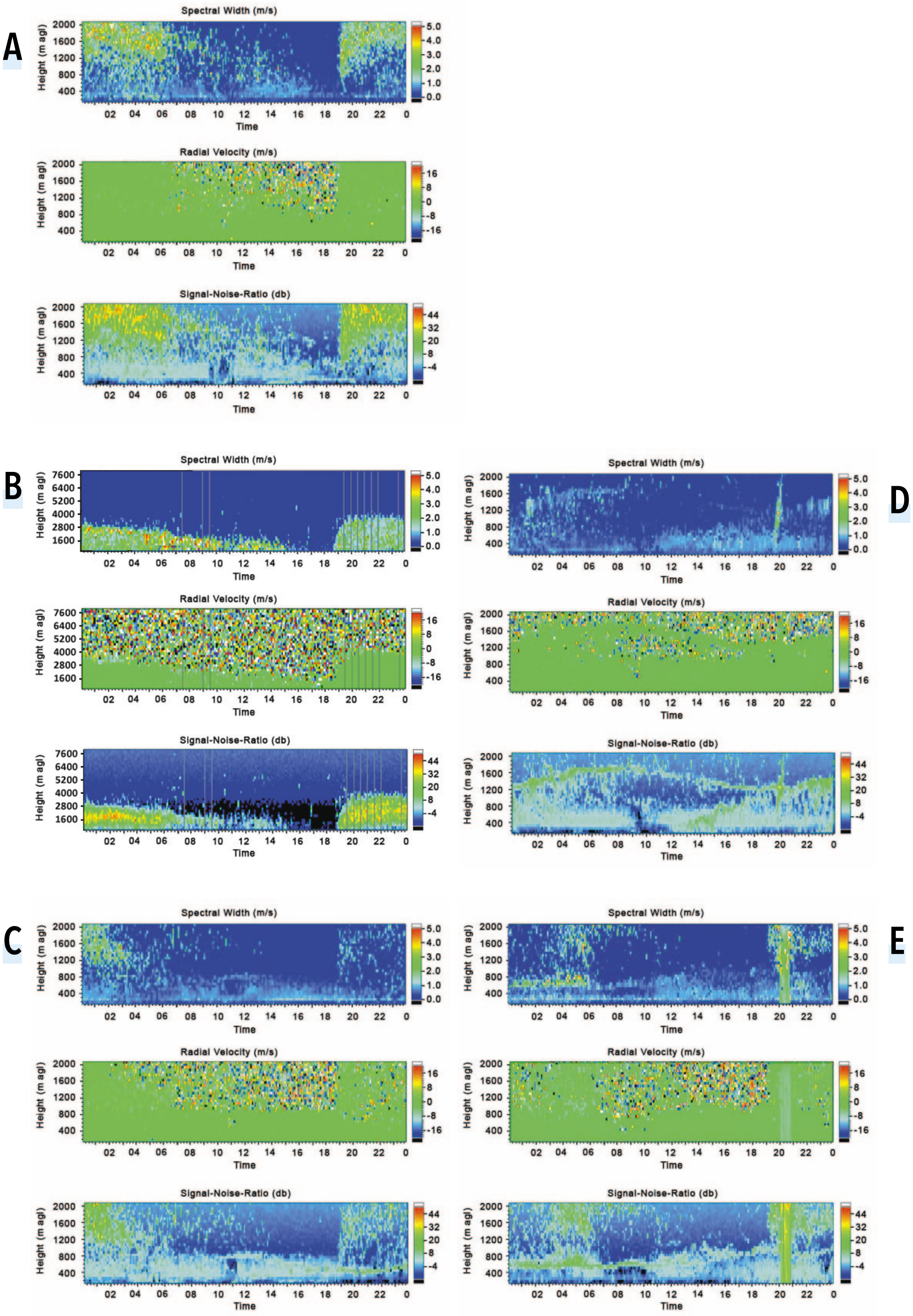

FIG. 6 *Time-height plots of moment data - strong (A: low mode, B: high mode) vs. light migration (C) events in spring; in summer/autumn (D); and migration with rain between 20:00-21:00 h (E).*

data is presented as normalized signal-to-noise ratio (SNR) plots for each gate (Fig. 4). Normalization means that the strongest echo determines the scale of a gate. (If strong and weak echoes are mixed, weaker ones could be indiscernible and visualization would require an analysis with a higher resolution.) Based on these time series, Doppler velocity spectra ("spectral data" hereafter) are estimated as the next output in the signal processing chain (Strauch et al. 1984). Spectral data can be visualized in plots either in normalized or non-normalized stacked and contour mode (Fig. 5).

In the subsequent spectral averaging process, several consecutive spectra are used to calculate a mean spectrum. The product of this averaging process is the moment data consisting of SNR, radial velocity, and spectral width, which represent the second processed output (Fig. 6 A-E).

Applying the consensus algorithm (Fischler and Bolles 1981, Vaisala 2007), the wind vectors for each gate are calculated for each detection height every 30 minutes, resulting in time-height plots with 3D wind barbs, named consensus data, the final product (Fig. 7). All SNRs displayed in this article were range-corrected.

METHODOLOGY

DESIGN OF CALIBRATION CAMPAIGN

The Euskalmet wind profiler database ranges from 1996-2015. Throughout this time period, data quality was observed to severely deteriorate in spring, i.e. during bird migration season in line with available literature (Maruri 2001).

In order to attain an overview over the temporal occurrence along the annual cycle and characteristics of bird migration in RWP data, spectral, moment and consensus data were analysed for the years 2010-2012 which offered uniformly good quality datasets.

The parameters to visualize moment and consensus data were chosen in a way to optimize the detection of migration patterns in the plots as described hereafter. In a first approach, the SNR ratio in both consensus and moment data was set to a range of -15 to 50 dB; in moment data, spectral width was set to 0 to 5 m/s

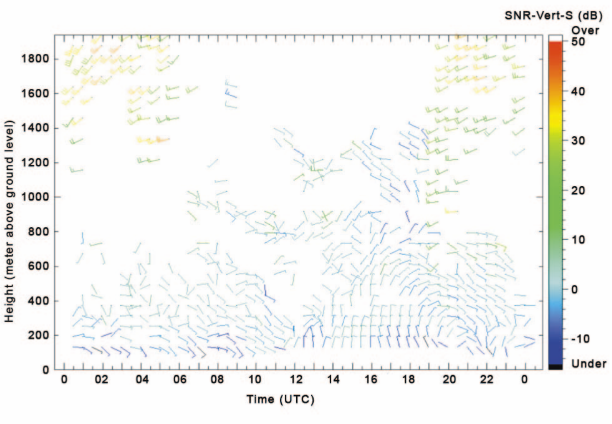

FIG. 7 *Horizontal wind vector (consensus) data from Punta Galea during strong migration event on March 13, 2012.*

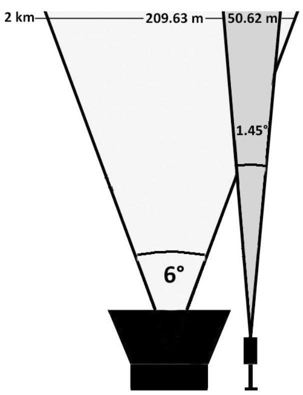

FIG. 8 *Lateral view of the set-up for calibration campaign at Punta Galea (Spain).*

and radial velocity to -20 to 20 m/s for all datasets from 2010-2012, which includes the entire range of both non-atmospheric and atmospheric signals. For the bird-specific visualisation of the calibration campaign data the range was later set to -10 to 30 dB for SNR, 0 to 3 m/s for spectral width and -8 to 8 m/s for radial velocity. In addition, results from an exploratory thermal-imaging and moon-watching campaign at the RWP site were also taken into account (Weisshaupt 2015, 2016). Thermal-imaging data recorded during 4 h from sunset on 45 nights from March to May and 15 nights from August to October 2014 and moon watching was carried out as a minor complementary sampling whenever possible in the same period. Thermal-imaging data was also videotaped for 4 h from sunset at the radar site. It has been known from previous studies in other areas that the first four hours of a night represent the main take-off period (Biebach et al. 1991, Åkesson et al. 1996) and that after the fourth hour migration intensity would generally decrease again. Therefore this time period was considered optimal to obtain a representative sample of migration activity.

The aim of this preparative data collection was to identify the settings for the calibration campaign in 2015 as described hereafter, i.e. optimal season, daytime, study period and flight directions, and to control and optimize data quality of both systems. Based on the findings from these previous studies, a shorter study interval of 10 nights was then chosen for the actual calibration campaign in March 2015, which was observed to be most intense as to migration activity (Weisshaupt 2015). No radar data was available for March 18, 2015 due to a system breakdown.
The camera was set up at the southern side of the RWP to align both systems on an approximate SW-NE axis, i.e. the observed spring migration direction, to increase the probability of recording the same birds in both systems (see Fig. 8). Sampling took place in as clear nights as possible to optimize the detection of birds.

DATA ANALYSIS OF CALIBRATION CAMPAIGN

THERMAL IMAGING & MOON WATCHING

All bird tracks were time-stamped and further classified according to flock size, target types etc., if applicable. Targets which did not follow a straight trajectory (e.g. curves, sudden reversions) and which might have originated from bats or insects ("bubbles" as described in Zehnder et al. (2001)) were excluded. Then the remaining tracks were assigned to 7 size categories corresponding to an altitude range from ground level (class 7) up to approximately 2-3 km (class 1) depending on meteorological conditions, based on previous calibration with tracking radar as established by Zehnder et al. (2001). Finally, the mean migration traffic rates (MTR) were computed for each continuous four-hour sampling period. MTRs provide a measure of number of birds passing a line of 1 km perpendicular to flight direction in one hour (for details see Lowery 1951, Zehnder et al. 2001).

On two nights, moon-watching sessions were carried out to account for potential variability in bird echo signatures.

WIND PROFILER

For reliable quantitative measurements it is very important to have a solid qualitative measurement of individual bird signatures and to consider the beam geometry (Schmaljohann et al. 2008).

Data from the vertical beam was selected to exclude as many potentially confounding factors as possible that might arise from beam geometry and asymmetrical positions of side lobes in the tilted beams (see Fig. 9 for beam geometry). Furthermore, the vertical beam provides the best measure of flight activity of a front (Lowery 1951). Of the two vertical beam options (low vs. high mode), the low mode was chosen as its sampling height coverage is more similar to the thermal-imaging range and because of the higher resolution in comparison to the high mode. The high mode was consulted for a general overview over altitudinal migration activity only.

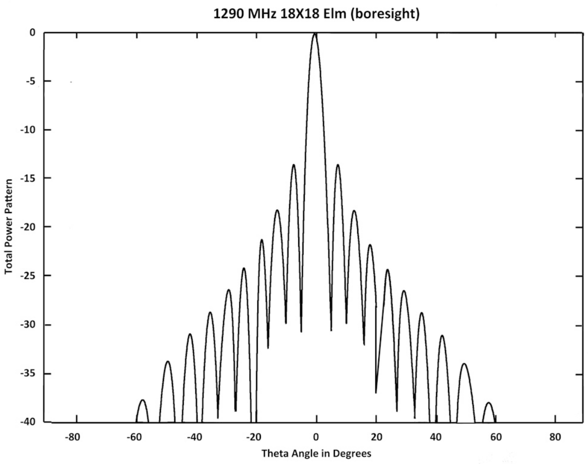

FIG. 9 *Theoretical antenna radiation pattern (beam geometry) of the vertical beam with vertical main lobe (peak) and inclined side lobes.*

QUALITATIVE AND QUANTITATIVE ANALYSIS OF TIME SERIES AND SPECTROGRAMS

In a first qualitative step, the signals were classified as bird echoes, atmospheric echoes and echoes of unknown origin. For a better understanding of the joint time-frequency structure of all possible signal components, Gabor spectrograms were calculated based on the time series data. This method is particularly useful for the analysis of nonstationary data and often allows for a clear separation of the various signal components in RWP data (Muschinski et al. 2005, Lehmann and Teschke, 2008)

Echoes from biological sources, i.e. birds, typically exhibit elliptical sinusoids (Fig. 10). In spectrograms, birds exhibit typically a regular "zigzag pattern" associated with flapping flight, representing the only radial movement of birds in perpendicular position, which is perceived by the radar.

The following aspects are important when analysing time series data: (1) Vertical multiplication of echoes: Signatures of birds (and other signals stronger than precipitation) can spread into two or more adjacent gates based on their very high reflectivity (Fig. 10). This spreading is described by the range-weighting function for a single range gate (Doviak and Zrnic, 1993). The nearest gate where a target is located is the one with the highest I/Q values, i.e. the one with

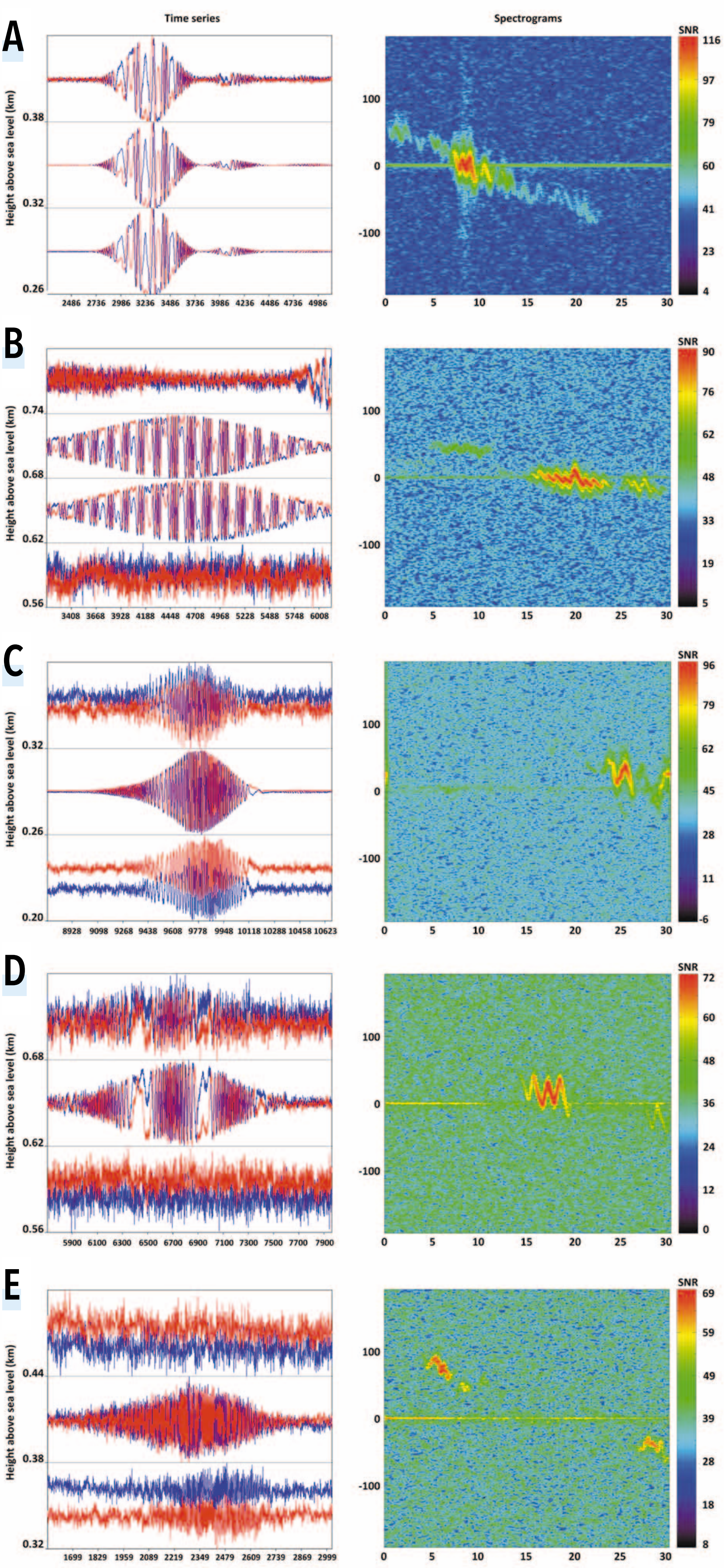

FIG. 10 *Time series (left) and spectrogram (right) plots for qualitative classification:*

A is "very good" (gate at 0.32 km),

B is "good through beam centre" (gate at 0.68 km);

C is "good marginal" (gate at 0.26 km);

D is "poor through beam centre" (gate at 0.62 km);

E is "poor marginal" (gate at 0.38 km).

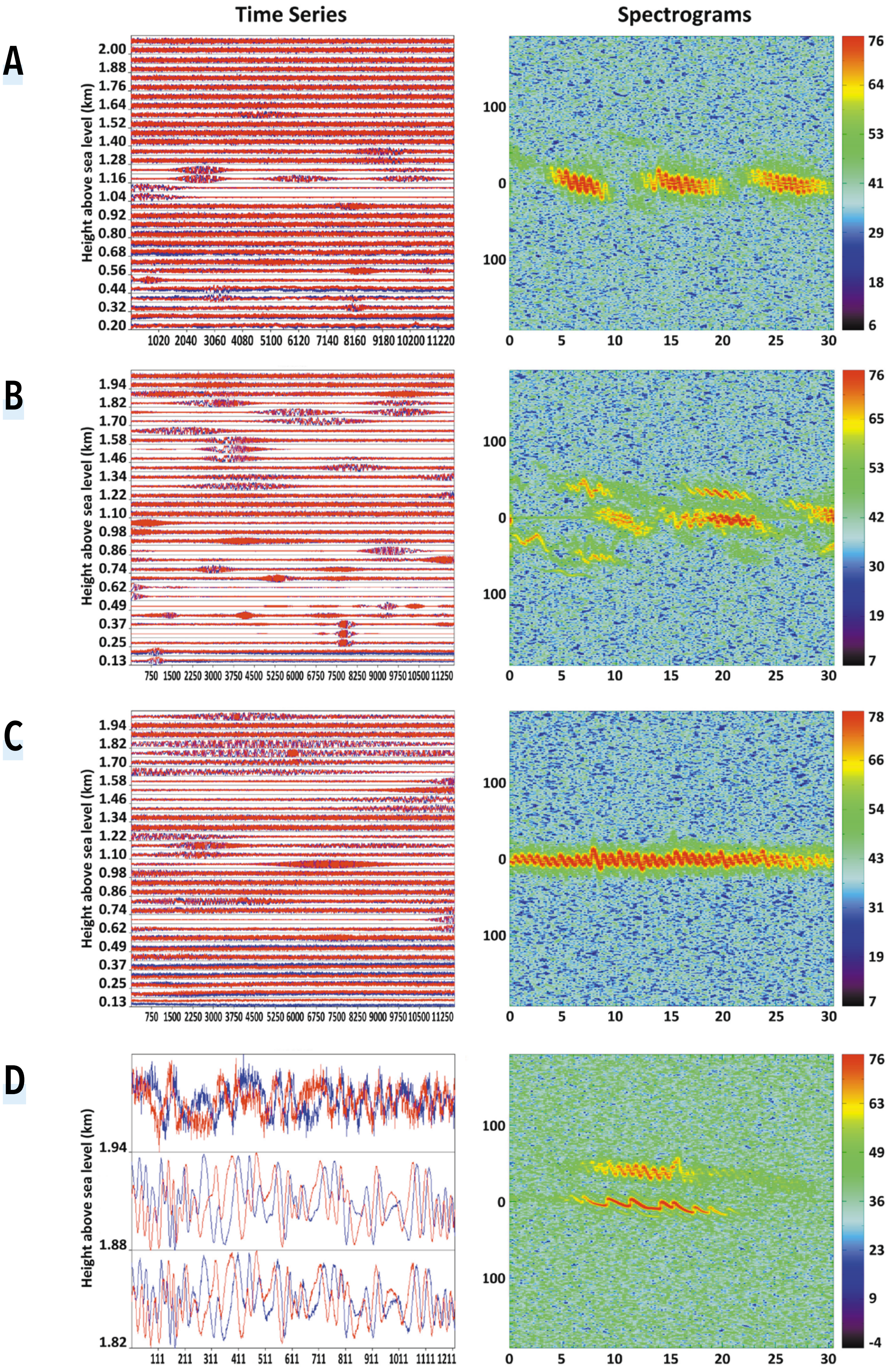

FIG. 11 *Various examples of birds in time series and spectrograms. A: three different birds in the gate at 1.16 km; B: high migration intensity, birds occurring simultaneously in the gate at 1.097 km; C: long bird echo in the gate at 1.82 km; D: overlapping echoes of two birds in the gate at 1.88 km.*

the "nicest" echo signature of all gates in question, together with the spectrogram of the highest SNR scale value. (2) Horizontal multiplication caused by the trajectory of a target across the radar beam: Targets passing both side and main lobe exhibit weaker horizontal copies closely before and/or after the main echo in the same gate in time series and one or more steeply diagonally aligned copies in spectrograms (Fig. 10A). In case of strong target echoes passing through main and side lobes, duplication can thus be both horizontal and vertical. (3) Shape of sinusoids: A target passing through the main lobe typically exhibits a distinct dense sinusoidal curve interspersed with gaps in time series and transiently a frequency of 0 Hz in the spectrogram, i.e. it passes through the zero line (based on its perpendicular position relative to the beam). All other targets, not passing through the centre of the main lobe, i.e. the zero line in the spectrogram, present a continuously dense sinusoidal curve without gaps. Additionally the quality of these marginal signals is poorer and the I/Q and SNR scale values lower. (4) Concurrently passing targets, be it bird-bird or bird-other target, cause a superposition of frequencies (beat frequencies, Fig. 11D).

This classification is crucial to clean data from duplicates, which would falsify any further analysis. Based on these qualitative features the bird echoes were ranked as "very good", "good" or "poor" and non-bird/non-atmospheric echoes as "fail". This classification was then applied as a basis for the quantitative analysis where only "good" and "very good" bird echoes were included to calculate MTR and altitudinal flight distributions, as described below.

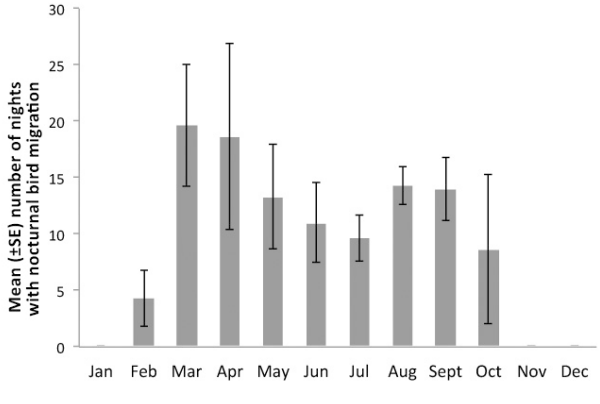

FIG. 12 . *Mean (±SE) number of days with nocturnal bird migration as derived from the wind profiler situated at Punta Galea, Northern Spain (years 2010 to 2012).*

COMPARISON THERMAL-IMAGING CAMERA VS. RWP

METEOROLOGY

As meteorological conditions can affect both systems (and thus the results) as described previously, meteorological data was taken into account and collected as follows. Cloud cover at the radar site was measured in oktas at sunset of each sampled night. Complementary data on wind direction and force, visibility and temperature were obtained from the nearby meteorological stations at the airport of Bilbao and Santander (Euskalmet, the Department of Atmospheric Science of the University of Wyoming [http://weather.uwyo.edu], Metar [http://www.ogimet.com]), as well as large-scale meteorological situations of Europe (Metoffice).

MIGRATION TRAFFIC RATES

MTR were calculated from both thermal imaging and RWP data in order to attain a comparable measure of migration intensity and to account for the conical sampling method of both systems. While the altitudes required for MTR calculations of the thermal-imaging camera were derived from target size classes, as described earlier, altitudes in the RWP were defined by the gates. MTRs were calculated from "good" and "very good" echoes of each 30s time series plot. Based on these 30s MTRs, mean MTRs were then calculated for each night. Flight altitude distribution was estimated based on the 30s MTRs which were converted into nightly MTRs per gate.

BIRD COMPOSITION

In thermal imaging passerines vs. non-passerines can be roughly differentiated based on individual tracks vs. well-defined groups, as passerines typically travel singly or in loosely dispersed flocks at night (Balcomb 1977).

RESULTS AND DISCUSSION

HISTORICAL DATA

In processed historical data from 2010-2012 bird echoes were observed from mid-February to end of October (Fig. 12). In all three years the frequency of nights with migration reached a first peak in March/April, and a second peak in August/September. In spring strong bird migration patterns consisted typically of a sudden and rapid onset of echoes about 0-60 min after sunset to 0-60 min before sunrise affecting the entire radar profile up to about 4 km (Fig. 6B). In autumn, however, intensity never approximated the intensity or the altitudinal extent of spring, which could be attributed to a broader migration front in spring than in autumn as found for example by Liechti et al. (1996).

SPECTRA

From spectral data onwards in the signal processing chain, bird migration is depicted as filtered data, i.e. it is not clear if the filter has removed/maintained actual birds or copies from side lobes which do not represent genuine bird echoes. Therefore it might represent a mixture of bird and non-bird echoes and is no longer valid for any qualitative or quantitative study, except for bird presence/absence only.

In the contour mode of the spectral data (Fig. 5A) strong bird migration was depicted as big patches similar to ink blots. In case of moderate or low activity, these patches were smaller (Fig. 5B). They clearly differed from clear-air or precipitation patterns as to spatial and temporal variation and continuity (Fig. 5C). In the stacked mode of spectral data, bird echoes exhibit multiple peaks forming a broad jagged pattern (Fig. 5A-B).

MOMENTS

Migration patterns were observed in spectral width, radial velocity and SNR. Spectral width was typically

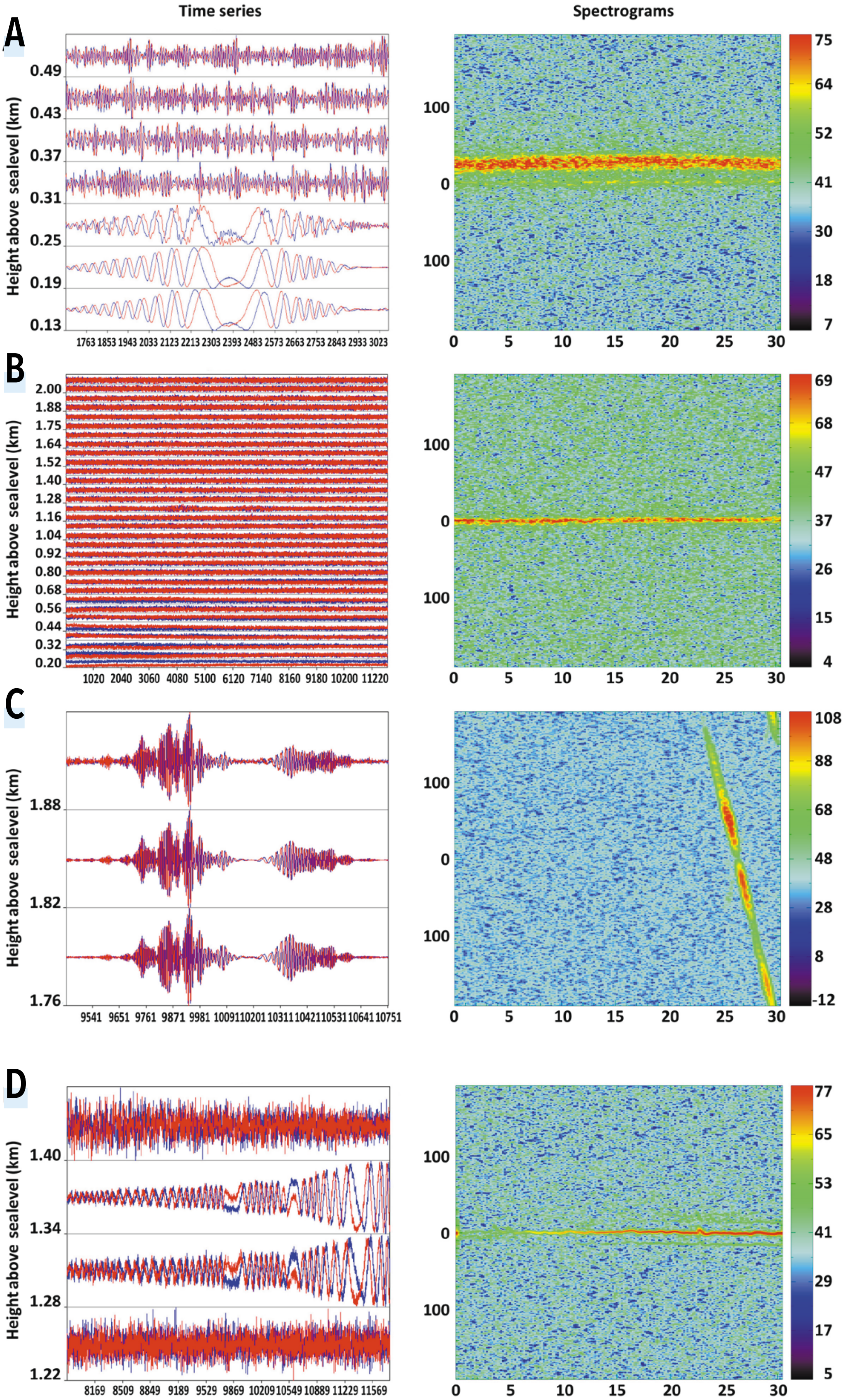

FIG. 13 *Examples of non-bird echoes in time series (left column) and spectrograms (right column). A: precipitation with bird in the gate at 0.190 km of the time series; B: clear air signal (same for all gates); C: airplane in the gate at 1.82 km; D: other biological source in the gate at 1.34 km.*

high and variable, while SNR was high and radial velocity greatly variable. These characteristics lead to a mottled pattern in the three plots, clearly differing from the uniform precipitation pattern (Fig 6E). Based on texture analysis (e.g. porous vs. filled areas) migration intensity could be classified as "strong", "moderate" and "weak" (Fig. 6A, 6C).

In spring, moment data exhibited nocturnal patterns of weak to strong intensity. The conspicuous increase in signals was characterized by a "wedge" at sunset at low altitude (Fig. 6A), best observed in the low mode between approx. 400-2000 m above ground level, which then extended across the entire plot area up to about 4000 m (high mode: Fig. 6B) throughout the night. Between about 0-500 m above ground level the actual onset of signals was often blurred by or mixed with clutter of non-biological origin. In summer and autumn, the nocturnal patterns in moment data consisted mainly in a thin "wedge" shortly after or at sunset alone and/or sprinkles during the night reaching about 2000 m (Fig. 6D), corresponding to weak intensity compared to spring. No differentiation between birds and other potential biological targets was possible.

CONSENSUS DATA

Bird migration in the final wind data based on consensus averaging is typically visible as wind barbs exceeding clearly the SNR ratio (> 30 db) and velocity of true winds of surrounding plot areas, with directions corresponding to migration directions (Fig. 7). Migration was only depicted in consensus data in peak migration events in early spring. This apparent lack of sensitivity to weaker migration can be attributed to the pathway of signal processing as discussed below.

THERMAL IMAGING AND MOON WATCHING

In spring 2014, between 0-1100 tracks were recorded per night, amounting to nightly MTRs of about 0-6000 birds/km/h (Weisshaupt 2015). In 2015, numbers ranged from 1 to 502 tracks and 5-2400 birds/km/h. Based on these two field seasons, four classes of migration intensity were established.

MTRs between 0-1000 birds/km/h were classified as "low", 1000-2000 birds/km/h as "moderate", 2000-4000 birds/km/h as "high" and more than 4000 birds/km/h as "very high". Thus in 2015, the TI database included 5 events of low, 4 events of moderate and 1 event of high migration intensity. These categories were used later in the analysis of both TI and radar data.

Based on own lunar observations (Weisshaupt et al. 2016) we can safely assume that the majority of nocturnal migrants are small passerine birds (singly flying birds), with only a low one-digit proportion of larger non-passerines, mainly waders or waterfowl (flocks).

ANALYSIS OF TIME SERIES

QUALITATIVE ANALYSIS OF RWP DATA

Differentiation between various types of targets proved to be most reliable in both time series and Gabor

spectrograms, compared to the other RWP outputs. Birds (as sinusoids in time series or zigzag in spectrograms) could be readily distinguished from precipitation, airplanes and non-bird echoes of potential biological origin (for comparison see Fig. 13).
Bird echoes typically appeared during up to 20 seconds (depending on the gate/altitude). In spectrograms each echo is slightly diagonally aligned from upper left to lower right, when a bird enters and exits the beam. Bird echoes at high altitudes, i.e. in gates 20-32, could extend considerably given the larger diameter of the beam. Temporally prolonged echoes could also result from head winds decelerating a bird's flight, as was verified by TI camera recordings. Airplane echoes affected several gates in time series and had a distinct short steep shape in the spectrograms (Fig. 13C). Precipitation depicted as weak homogenous pattern occurring uniformly in all gates in time series and as a horizontal line in the positive frequency area in spectrograms (Fig. 13A).
Overall, target classification (bird vs. non-bird) was easiest if migration intensity was low or moderate according to the TI classification, as the probability for overlapping echoes was low. In case of high bird densities care is needed not to confuse migrants flying close to one another with copies from side lobes in time series and spectrograms. The diagonal allocation of the individual echoes together with the shape of the echo signature in spectrograms facilitates differentiation (see Fig. 10/11), however, few ambiguous cases remain. There were various types of frequency patterns in spectrograms (see Fig. 11A-E), it was however not possible to assign them to particular groups of birds (family or genera level). Considering the thermal-imaging and moon-watching findings and previous literature (e.g. for an overview see Alerstam 1990), it can be assumed that the majority of the targets represent passerines. However, more specific verification devices would be needed to relate any frequency pattern to a specific type of bird.

Once duplicates were excluded from the time series dataset, all echo signatures were classified into four categories according to their quality and origin based on time series and spectrograms. Only targets with a spectrogram intensity of >60 dB were included because of strongly deteriorating quality of echo signatures below 60 dB. All non-bird echoes (e.g. airplanes, strong atmospheric (e.g. lightning) and unknown signals) and signals involving multiple overlapping birds were classified as "fail" and excluded from further analysis (for an overview see Fig. 13). Bird echoes were classified as "poor" if the signal was clearly ragged and/or irregular, typically with I/Q maxima of <10'000 a.u. (i.e. arbitrary units) and maximum spectrogram intensity of <75 dB; as "good" if the signal was clean and regular, but less ragged and stronger, with I/Q maxima of 10'000-20'000 a.u. and a maximum spectrogram intensity of 75-100 dB; and as "very good" if the signal showed a very clean and regular sinusoidal shape, with I/Q maxima of >20'000 a.u. and a maximum spectrogram intensity of >100 dB (for examples see Fig. 10A-E). "Very good" was only assigned to targets passing through the centre of the main beam. Slight deviations of the thresholds were possible. In cases of echoes of different quality in one gate, it was possible that a "poor" echo (e.g. from target present in a side lobe only) was assigned a (correct) low I/Q value, but a "(very) good" spectrogram intensity which was actually based on the "good" echo (from a target in the main lobe) coexistent in the same time interval and gate.

As a product between the time series and moment data, spectral data allowed obtaining a better understanding of signal processing. Comparisons with time series showed that signal processing could merge two signals from adjacent gates into one signal in an actually unoccupied gate, so that neither number nor altitude of a target would be accurate. This fact is important to consider when handling processed RWP outputs. However, in case time series data is not available, spectral data can support verification of moment data based on signal characteristics. No differentiation between birds and other potential biological targets is possible.

QUANTITATIVE ANALYSIS OF RWP DATA

MIGRATION TRAFFIC RATES IN RWP

Overall, 3610 echo signatures extracted from time series were included in the quantitative analysis. 14 % were classified as "fail", 58 % as "poor", 24 % as "good" and 4 % as "very good". So overall, 28 % of the echo signatures were incorporated in the MTR calculations. Nightly mean MTRs ranged from 3601-9932 birds/km/h (Fig. 14).

FLIGHT ALTITUDES IN RWP

Altitudinal flight distribution concentrated in most nights in the gates 1-16, i.e. up to 1 km, without any noteworthy activity in the highest levels at about

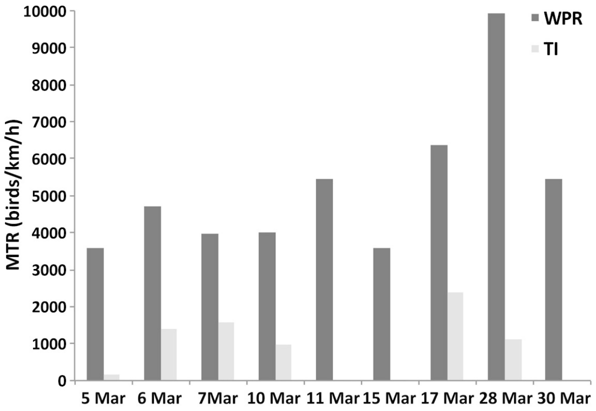

FIG. 14 *Comparison of nightly mean migration traffic rates (MTR) measured by wind profiler (RWP, dark grey) and thermal imaging (TI, light grey).*

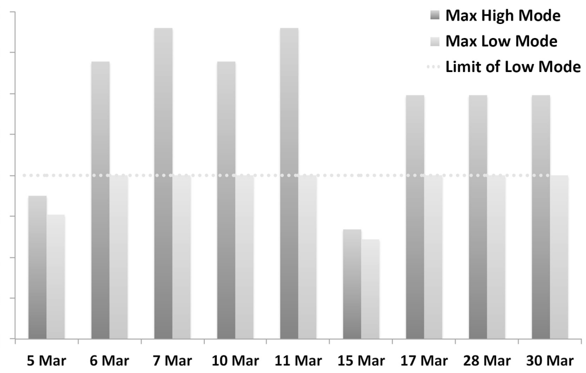

FIG. 16 *Comparison of observed maximum migration altitudes per day in the two operating modes (high mode: dark grey; low mode: light grey; maximum sampling range of low mode: dotted line)*

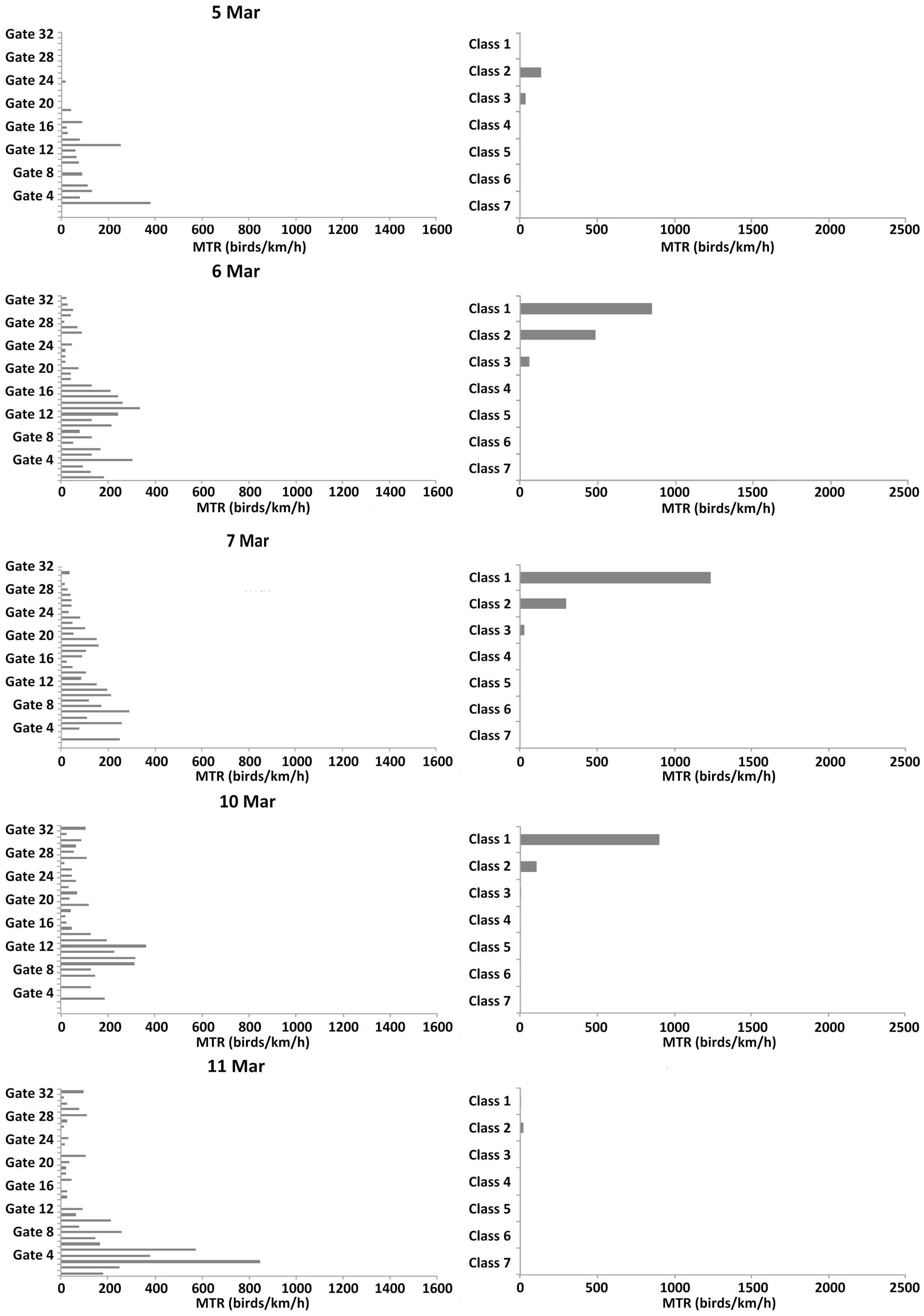

FIG. 15 *Comparison of altitudinal distribution of migration intensity measured by wind profiler (left column) and thermal imaging (right column).*

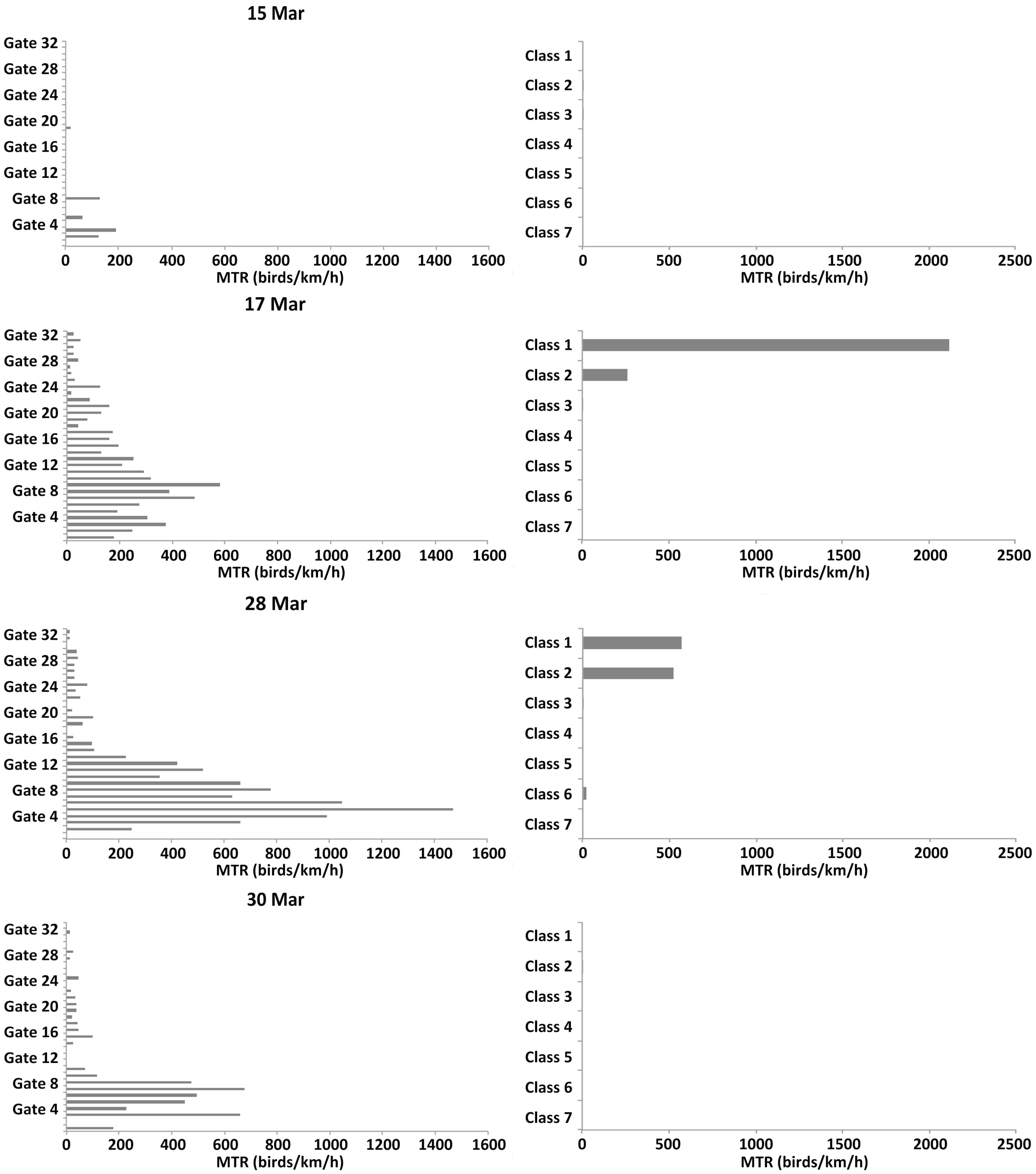

FIG. 15 *continued.*

2 km (Fig. 15). It could be argued that at this height, the probability of encountering mixed echo signatures is higher due to the larger sampling volume, but that they were removed because of the conservative selection approach of the study. However, the tentative inclusion of such unqualified echoes did not change the altitudinal pattern. A comparison with the maximum migration height in the high mode showed migration beyond 2 km in 7 of 9 nights (Fig. 16 [Fig), i.e. beyond the low mode sampling range. In the two nights of maximum migration altitudes below 2 km, the two modes exhibited similar values.

MIGRATION PARAMETERS IN RWP VS. THERMAL IMAGING

METEOROLOGICAL CONDITIONS

Overall, meteorological conditions (Table 1) were highly variable during the campaign and can be divided into four scenarios: (1) from 5 – 7 March with calm, dry and clear conditions with E/SE winds; (2) from 10 – 15 March warmer weather with increased humidity, fair visibility and E winds; (3) 17 (and 18) March with similar conditions as (1); and (4) 28 – 30 March with high humidity and W/NW winds.

MIGRATION TRAFFIC RATES

Generally, nightly mean MTRs of the RWP were between 2 – 1045 times higher than the TI MTR (Fig. 14). While MTRs of both systems correlated well in some nights, there were large discrepancies in other nights. During clear and dry conditions as on 5, 6, 7, 10 and 17 March, the MTRs of the TI camera and the radar correlated well (Fig. 14). In the camera, the highest activity was measured on March 17 (rank 2 in radar). During these five nights the radar showed 2-20 times higher MTRs than the camera which could be interpreted as an artefact of the different sampling volumes and intervals of the systems. However, there was a considerable mismatch during the nights of 11, 15 and 30 March with the radar showing migration intensities 200-1000 times higher than the camera. In addition, March 28 was the most intense night in the radar, while in the TI it was only the fifth most intense. These four nights were characterized by high humidity of around 80-95 % and continuous cloud cover or haze. Particularly striking is the practical absence of migration on 11, 15 and 30 Mar in the TI device (25, 12 and 5 birds/km/h, respectively), while the RWP registered similar numbers as on 6 March which would correspond to about 1400 birds/km/h in TI. The greatest discrepancy was recorded on 30 Mar (RWP MTR >1000 times than TI MTR), followed by 15 Mar (RWP MTR > 300 times than TI MTR).

Based on the increased mismatches between RWP and TI related to meteorological conditions, preference should be given to conditions with clear skies and low humidity when using thermal imaging, in particular in humid regions as the Basque Country, even though Zehnder et al. (2001) regard both completely overcast and clear skies as equivalent conditions for the detec-

TABLE 1.*Meteorological conditions at the radar site of Punta Galea, Bilbao, Spain.*

	5 March	6 March	7 March	10 Mar	11 Mar	15 Mar	17 Mar	18 Mar	28 Mar	30 Mar
Large-scale situation	Anticyclone over W France and Britain	Anticyclone across entire W Europe. Inversion closer to surface level	Inversion is now almost on surface level	Low-pressure front slowly pushing the anticyclone southwards	Low-pressure area has moved further south, but anticyclone does not cede	Low-pressure area has pushes the anticyclone southwards, occlusion zone at the Cantabrian coast	Low-pressure area over southern Iberia	Identical to 17 March	Low-pressure area disappeared from Iberia. Fronts approach despite anticyclone west of Portugal	Anticyclone over Atlantic Ocean influenced by fronts
Wind conditions	Very weak SE winds < 1000 m asl, inversion at 1000 m asl, >1000 m slightly stronger E winds	Weak ESE surface winds and the winds in altitude are weaker.	Calm conditions, faint N wind only at about 3 km asl.	Calm with weak eastern winds in altitude	Calm with slightly easterly winds below 900 m and westerly winds above 900 m	Calm	Weak E winds at surface level and SE winds > 1000 m asl	Weak SE winds < 3 km	W winds, increasing with altitude	Moderate SW/W winds < 1000 m asl, strong NW winds >1000 m
Visibility	good	good	good	fair	fair to poor	fair	Good	good	good	good
Cloud cover at radar site	0/8	1/8	1/8	6/8	8/8	7/8	4/8	7-8/8 at sunset, clearing up after 1 h	4-6/8	8/8
Humidity	65-80 %	60-81 %	62-87 %	80-93 %	87-93 %	81-93 %	51-62 %	54 % (at sunset) - 81 % (hour 4)	82-93 %	82 %
Temperature	6-8°C	8-11°C	8-12°C	10-11°C	11-12°C	5-7° C	12-14° C	11-14° C	11-13° C	14° C

tion of birds. In contrast, in the wind profiler, humid conditions would not impair detectability of targets (i.e. birds.

ALTITUDINAL FLIGHT DISTRIBUTION

The altitudinal distribution of the RWP diverged considerably from the patterns observed in the TI device (Fig. 15). While migration observed by TI evolved predominantly in the upper height classes corresponding to an estimated altitude of 2-3 km, the RWP profiles showed a concentration of migration at 1 km or lower. This divergent pattern remains unclear. Given the nature of the thermal imaging system based on temperature differences, it could be expected to find a negative bias towards higher flying and small targets as heat differences might not be registered equally well with increasing altitude and small targets might not emit enough heat to be registered (as it is the case with insects in higher altitudes). However, this would result in a dominance of large targets in thermal imaging, Also meteorological factors would lead to the same effect of favouring low-flying targets. Another reason could be the detection range of the camera, which is not as clearly delimited as in the radar. So birds registered in the upper height classes were possibly beyond the detection range of the RWP low mode. In the high mode migration was visible up to about 4 km. However, this does not explain the practical absence of low flying birds either.

BIRD COMPOSITION

The camera registered a low fraction (1.8 %) of dense bird flocks including 4-8 individuals, indicating presence of non-passerines. However, in the radar no suspicious patterns could be observed that would have been indicative of bird flocks of more than three individuals. Theoretically, the dwell time of 30 seconds per beam should suffice to record flocks. Expected patterns would be multiple echo signatures at close intervals in the same gate in both time series and spectrograms (if birds flew behind each other) or also beat frequencies in time series. Or alternatively, if birds flew side by side, it could be expected to see similar echoes passing in close temporal intervals in both main and side lobes, resulting in clustered echoes passing through and outside the zero line in spectrograms. However, the dataset did not present any such case. This could be theoretically explained by the RWP sampling method of recording 30 seconds vertically followed by a gap of 5 minutes – given the overall low proportion of bird flocks it can be concluded that they are not readily captured by the beam. Overall, more research is needed to evaluate the potential of identifying birds at a more specific level.

FLIGHT DIRECTIONS

Flight directions of targets can be readily analysed in TI data. Directional information of the RWP, in contrast, is accessible if data from various beams is taken into account, e.g. in consensus wind vector data. When extracting flight directions from consensus data some technical aspects must be taken into account. Wind (and flight) directions result from the measurements of the five beams, i.e. from subsequent, not simultaneous, measurements. Considering the flight speed of many migrants being between 10-20 m/s (Bruderer and Boldt 2001), a bird would need about 10-20 seconds to cross the beam at an altitude of 2 km and even less on lower levels. So a bird cannot be captured by all five beams to provide an individual wind vector. However, thermal-imaging data (N. Weisshaupt unpubl. data) has shown that spring migrants fly in a narrow directional range, i.e. within less than 10 degrees from the mean direction, with only a small fraction of reverse migration (<2 %). Therefore the differences between the directions measured by each beam, even if they stem from different birds, would be small. In case of high densities, all beams would be affected by birds and thus there would be consensus between the measurements and bird echoes are not removed. In contrast, increased variability of track directions per beam, as would be expected in autumn (Nilsson et al. 2014), could lead to more frequent removal of bird signals in the averaging process. Furthermore low bird densities as observed in the study region in autumn, would potentially reduce the number of the affected beams per measurement cycle. For example if only one out of five measurements contained a bird echo, this aberrant measurement, i.e. the bird, would be removed by signal processing. So both higher variability in track directions and low densities could explain the fact that wind barbs indicating presence of birds are hardly observed in autumn data.

CONCLUSIONS

Qualitative parameters were identified to successfully separate bird vs. non-bird echoes in time series and spectrograms and to derive quantitative measurements thereof, i.e. MTRs and flight altitude. This information was available for the entire vertical profile of 2 km of the low mode.

The calibration by thermal imaging substantiated the reliability of the radar as an observational tool in both humid and dry conditions. Migration traffic rates correlated well with thermal imaging in clear conditions. However, flight altitudes diverged considerably, possibly because of slightly different detection ranges of the systems or meteorological conditions. As opposed to the camera, it was not possible to extract any information on bird composition or directions on time series level.

Overall, clear advantages of the time series raw data over further processed data (spectra, moments, consensus data) were identified to acquire both quantitative and qualitative data. Quantitative information derived from processed data was restricted to general presence/absence. (Consensus) wind vector data was the only source of directional information and only accessible during high migration intensities for an unspecified number of birds.

More work is required to fully assess possible bird composition patterns in spectrograms, e.g. by exploring different frequencies and reflectivities. It would be also interesting to develop an approach to obtain directional information independent of migration flow.

Finally, we would like to stress that this study applies to this boundary layer RWP model. If RWP with other specifications (in particular height resolution) are used, possible effects on the data should be taken into account.

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PAPER V

EFFECTS OF A SEA BARRIER ON LARGE-SCALE MIGRATION PATTERNS STUDIED BY A NETWORK OF WEATHER RADARS

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ABSTRACT

During their migratory journey, birds pass through a variety of meteorological conditions and geographical areas with limited or inexistent possibilities to land and refuel. In this context it is important to evaluate the role of ecological barriers, such as mountain ranges or seas, from a conservation and ecological perspective. The present study investigates the bird migration patterns at a water barrier, the Bay of Biscay, bordering one of the main migration corridors in the East-Atlantic flyway. To evaluate the significance of the Bay of Biscay as an ecological barrier during bird migration would help assess the importance of coastal natural habitat potentially serving as stopover sites. Data from five Spanish and French operational weather radars, located along the Bay of Biscay, were processed for spring migration 2015 to calculate bird migration parameters (flight directions, altitudes and migration traffic rates [MTRs]) to obtain a spatial overview of the migration system around the bay.

Overall, the highest MTRs were registered by the radars at the southeastern edge of the bay, with a gradual decrease northwards. Migration had generally a NNE/NE direction and extended up to about 3-4 km in the south and about 1.5 km at the northern coast. The temporal pattern of nocturnal migration intensities within nights (bimodal vs. uniform flow) indicated migration over land in the south, sea-crossing until half way up the French coast and avoidance of the northernmost corner. Migrants readily undertake distances of about 250 km across water, while longer distances are less frequented. This pattern could indicate a potential bottleneck effect between the Pyrenees and the sea concentrating birds at the southeastern edge of the bay or is alternatively an artefact of the general NE direction of the main migration from southern Iberia. Findings highlight strong spatial structuring in nocturnal passerine migration at a large spatial scale.

INTRODUCTION

Throughout the annual cycle migratory birds transit different meteorological conditions and geographical areas with scarce or no availability of stopover sites, as in the case of ecological barriers such as deserts, mountain ranges or seas (Biebach 1990). Therefore birds have developed a variety of strategies to optimize energy expenditure and eventually survival, for example by avoiding barriers and travelling over safer areas (Alerstam 2001, Newton 2008).
Against the background of today's population declines of many migratory bird species (Sanderson et al. 2006), it is important to disentangle both small- and large-scale migration patterns and dynamics, in order to improve conservation measures at potential stopover sites, in particular in front of ecological barriers.

Several studies have observed various behavioural responses to water barriers, such as change of flight altitudes and directions in order to tackle or avoid the flight over water (e.g. Bruderer and Liechti 1998, Fortin et al. 1999, Sjöberg and Nilsson 2015). Diehl et al. (2003) found both crossing and avoidance of a water barrier during migration events. While birds could theoretically obtain a speed benefit from crossing, some chose a safer route over land instead. A similar spread of the migration flow at a water barrier was found by Gagnon et al. (2010) who observed both birds crossing an estuary and following the coast. In combination with such behavioural responses, meteorological conditions, such as precipitation or winds, have been identified as factors influencing the decision to cross barriers (Liechti 2006). Generally, migrants seem to prefer precipitation-free weather and tailwinds (Alerstam 1990). However, there are also studies showing evidence that birds also fly in unfavourable conditions in areas with frequent adverse winds (e.g. Karlsson et al. 2011). So depending on the meteorological setting of a particular area, birds might opt for a compromise and travel under suboptimal atmospheric circumstances.
In the end, the decision on whether to make a safer, though longer journey or to take risks in return for saving in time is in the end a balance between the overall benefits and downsides anticipated in a particular area (Bruderer and Liechti 1998).

The Bay of Biscay, as a part of the East-Atlantic flyway, represents a potential ecological barrier between Central Europe and the Iberian Peninsula. One of its particularities is its highly variable and harsh meteorological conditions (wind, precipitation) (Gangoiti et al. 2001, Maruri et al. 2014), which would also affect migratory birds trying to cross this sea. While extensive research on active nocturnal migration has been conducted in the Western Mediterranean by a series of techniques (e.g. Casement 1966, Bruderer 1999, Bruderer and Liechti 1999), a large-scale view on nocturnal migration dynamics (e.g. sea avoidance vs. crossing and consequences) is largely missing in Western Europe. The scarce literature available on bird migration along or across 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 (e.g. Lack and Lack 1953, Grandio and Belzunce 1987, Bruderer and Liechti 1999, Mendiburu et al. 2009, Arizaga et al. 2014). Lack and Lack (1953) observed passerines at the French-Spanish border flying apparently inland from the sea. Radar studies in southern England indicated a NNW/SSE migration axis of nocturnal migrants concentrating in the central to eastern English Channel in autumn (Parslow 1962). However, there is no information on nocturnal migration.

Given the typically vast extension of barriers, appropriate monitoring tools are required to resolve the large-scale movements across such surfaces. In ornithology, a variety of radar types have been employed, mainly marine or tracking radars, to measure flight altitudes, speed, directions and densities of migratory birds (Bruderer 1997). Nowadays, operational weather radar networks in the US (NEXRAD) and Europe (OPERA) are increasingly used to study bird migration on continent-wide scales (e.g. Gauthreaux et al. 2003, Shamoun-Baranes et al. 2014, Kelly et al. 2016). As part of OPERA, weather radars also cover the Bay of Biscay, which can provide information on geographical and seasonal migration patterns.

The aim of this study is to describe migration dynamics at an ecological barrier by means of multiple weather radars, using the specific case of the Bay of Biscay. The combination of challenging meteorological conditions and the imminent open sea, together with the foothills of the Pyrenees reaching the southeastern coastal edge, make for an interesting region to study the impact of a major ecological barrier on migratory flyways. Based on findings from the Basque coast (Weisshaupt et al. 2016), it would be expected to find sea crossing in spring which would show as variations in nocturnal migration intensities, e.g. 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 on sea during night, and with a morning peak indicating landing at the target shore. The general NE migration direction anticipated for spring migrants on the East-Atlantic flyway (Zink 1970) could furthermore lead to E-W and S-N gradients of MTRs along the coast. A preference for migration on days with wind assistance would be expected for spring, given the dominance of westerlies in the region.

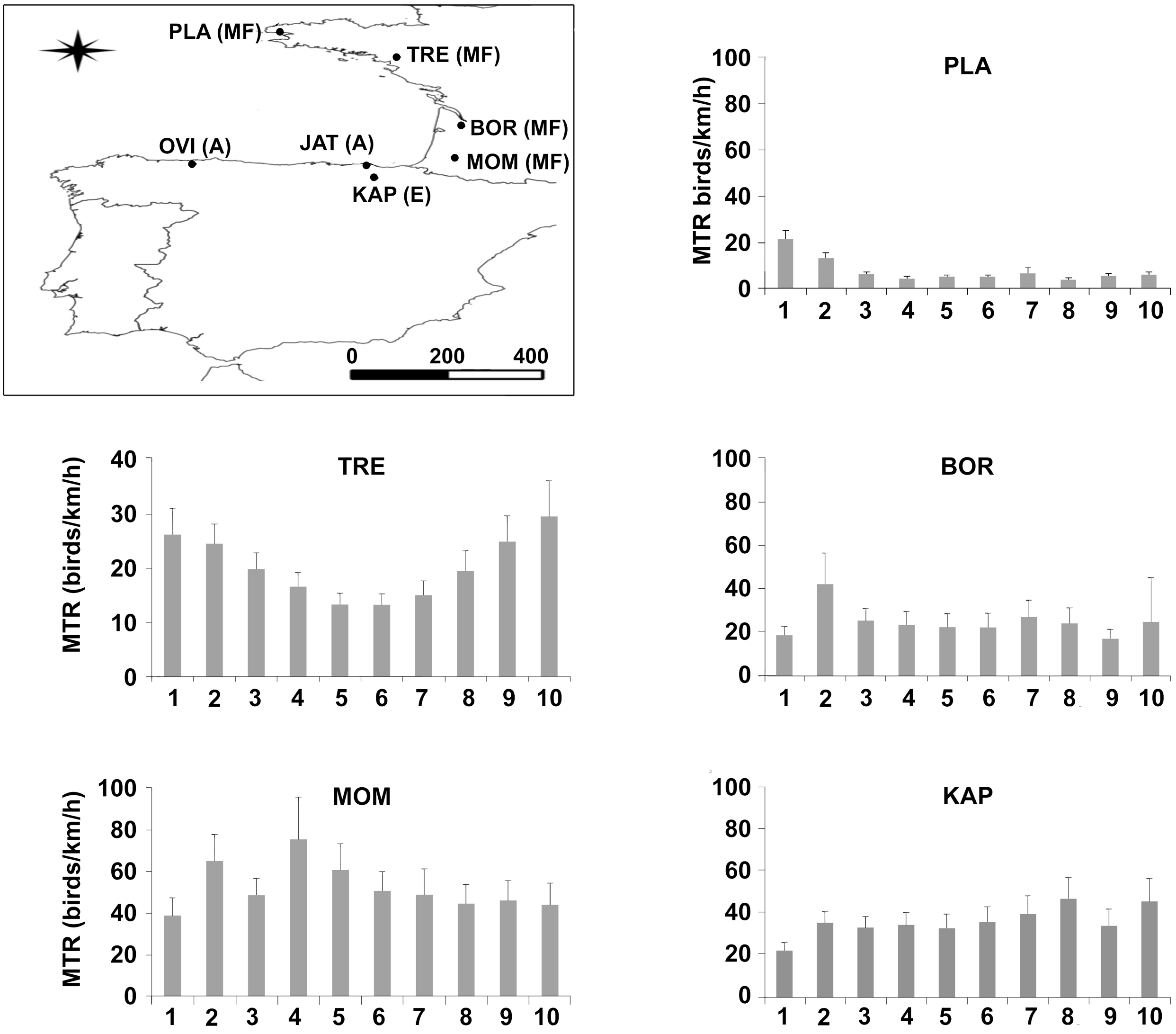

FIG. 1 *Map: Radar sites along the Bay of Biscay included in this study. Two radars from the Spanish State Meteorological Agency (AEMET, A): Oviedo [OVI], Jata [JAT]; one radar from the Basque Meteorology Agency EUSKALMET (E): Kapildui [KAP]; and four radars from the French national meteorological service (Météo-France, MF): Momuy [MOM], Bordeaux [BOR], Tréillères [TRE] and Plabennec [PLA]. Histograms: Comparison of hourly mean migration traffic rates (MTR; ±SE) at the available radar sites in nights without precipitation divided into decades.*

MATERIAL & METHODS

DATA INPUT

Reflectivity and radial velocity data was obtained from four C-band weather radars in France, i.e. 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) (Fig. 1). These radars were selected because of their proximity to the coast. Originally, also data from two coastal radars of the Spanish State Meteorological Agency (AEMET) were included to cover the 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, these radar data had been processed by a special filter that made them unsuitable for the analysis (see supplement).

The study period was restricted to 1 March to 6 April 2015 to coincide with other parallel studies by vertical observation systems in the study region and March to April was previously identified as peak migration period on the Basque coast, with a rapid decrease from mid April onwards (Weisshaupt et al. 2016). This early spring period coincides with migration of short-distance migrants, such as thrushes or finches, across the Iberian Peninsula (Finlayson 1992).

Data from the Bordeaux radar was unavailable from 1-15 Mar.

BIRD ALGORITHM

When dealing with large data sets of multiple radars, it quickly becomes impossible to screen all data manually, so overall efficiency of is greatly increased through fully automated data processing. Dokter et al. (2010) developed a specific bird algorithm to automatically separate birds from other targets registered by weather radars. This algorithm allows obtaining vertical profiles of flight altitude, speed, direction and densities based on data in a range of 5-25 km around a radar. The method is currently used for automated migration quantification in the COST research network ENRAM (European Network for the Radar Surveillance of Animal Movement, COST action ES1305).

The bird algorithm developed by Dokter et al. (2010) uses radial velocity data. It was employed to filter out atmospheric signals and extract information on flight direction, altitude and intensity of nocturnal bird migration for all available elevations at an altitudinal resolution of 200m (20 levels from 0-4000m) of the radar data. Birds were identified and separated from other echoes based on a radial velocity standard deviation of >2ms-1 (see Dokter et al. 2010 for details) in a range of 5-25 km around the radars. The limited distance was chosen to reduce range-dependent biases. These parameters had been established and verified previously in France, Belgium and the Netherlands by Dokter et al. (2010). In the present study, this predetermined radius covers movements over land until about 15-45 km from the coast in all selected radars, except for the Plabennec radar, where the radius covers the coastal sea (distance from coast: 18 km). For the Tréillères radar, the distance threshold was set to 40 km because the scan elevations were very low and only permitted a 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 extension of migration on most days.

As a result of the specific French radar processing scheme (triple PRT Doppler scheme), the radial velocity data was relatively noisy as compared to earlier studies (Dokter et al. 2013, Kemp et al. 2013). As a result, some precipitation contamination remained in all radar data despite the filter mechanism. These days were manually removed in order to minimize any potential bias in further analysis. The hours considered for analysis were restricted to the period between sunset and sunrise because this migration represents the most massive biological event observed in weather radars. For individual nights in which birds were particularly numerous and therefore filtered out (see supplement), the standard deviations were manually lowered to avoid any bias in MTRs and derived calculations.

METEOROLOGICAL DATA

Wind data for the five radar sites were collected from NOAA, National Oceanic and Atmospheric Administration, U.S. Department of Commerce. Particularly, both u and v wind components were used for pressure levels of 700, 850 and 925mb, roughly corresponding to an altitude of 3250, 1500 and 775 m above sea level, respectively, at 00:00 hours. Tailwind components were calculated as $V_w \cos(\varphi_T - \varphi_W)$, with wind velocity V_w, the mean preferred track direction φ_T (45° for spring migration period), and the wind direction φ_W (Åkesson and Hedenström 2000).

DATA ANALYSIS

Migration traffic rates (MTRs) were calculated as an average of the 4 hourly measurements (6 for Kapildui) per radar for each night and site using

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

with ρ being the bird density in birds/km^3, Δh the altitude bin width (0.2 km) and ground speed v in km/h. 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 (for details see Lowery 1951). The night duration was set to sunset to sunset, and then divided into decades. Average migration patterns were visualized using these decades as the time axis to line up each night with respect to sunrise and sunset.

Data was managed and analysed in the program R (R Development Core Team [2004]).
MTR values were log-transformed to attain a normal distribution and then normalized by dividing each nocturnal mean MTR through the sum of all mean MTRs per site to divide out day-to-day variations in overall migration intensity in between-radar comparisons. Then pairwise comparisons between neighbouring radars were tested for significance in 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.

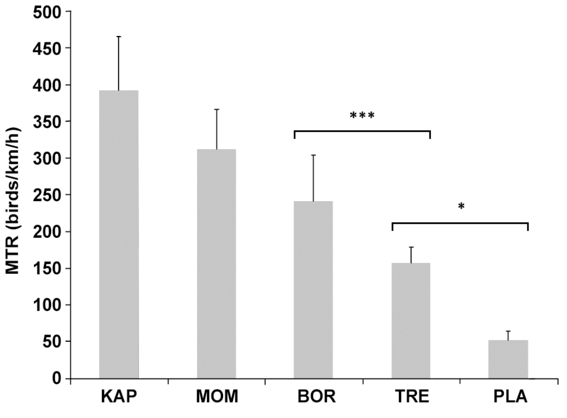

FIG. 2 *Comparison of nightly mean migration traffic rates (MTR; ±SE) at each radar site (Kapildui: KAP; Momuy: MOM; Bordeaux: BOR; Tréillères: TRE; Plabennec: PLA) with significant differences between Bordeaux-Tréillères (p<0.001), and Tréillères-Plabennec (p<0.05).*

The effect of wind on migration intensity was tested by Generalized Linear Models (GLMs). Absolute log-transformed nightly mean MTR values were set as the response variable and the independent explanatory variables were site and date as discrete control factors, and tailwind components as linear (quantitative) variables. The tested models included all combinations of one tailwind variable (for three heights) and the other variables, as well as double interactions. The full model was omitted to avoid potential confounding effects caused by the different tailwind variables. All models were ranked according to their small-sample size corrected Akaike values (AICc) by means of the function "model selection" of the R package "MASS" and "MuMIn" (Burnham et al. 1998, Johnson et al. 2004). Models differing in less than 2 AICc values were assumed to support the data equally well. B-parameters with P-associated values >0.05 were considered to be non-significant.

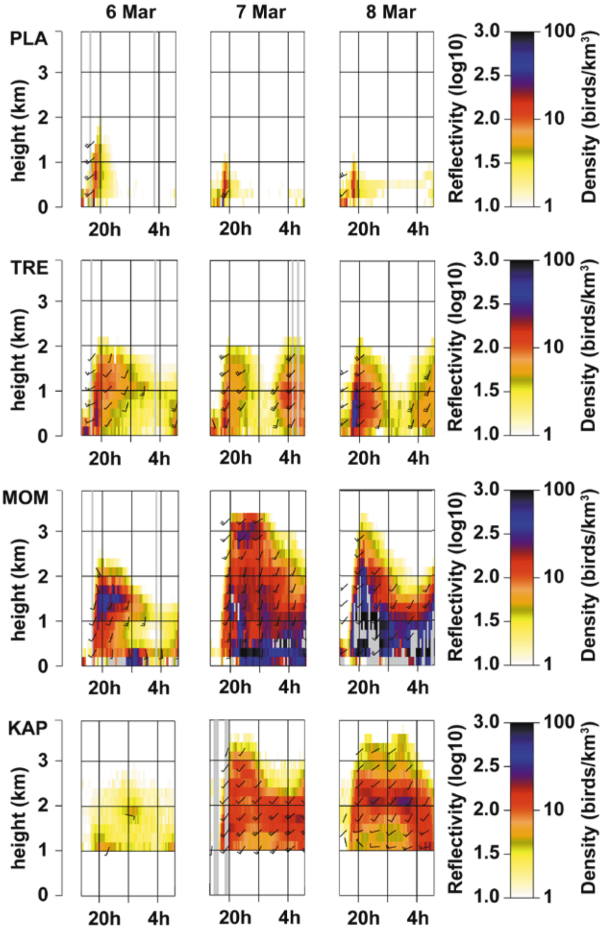

FIG. 3 *Examples of weather radar data from 6-8 Mar 2015: strong continuous patterns at Kapildui (KAP) and Momuy (MOM); bimodal pattern at Tréillères at 40 km (TRE); and evening peaks (20:00 h) at Plabennec (PLA). Bordeaux was out of service.*

Homogeneity between the mean directions at each radar site was tested by a Watson-Wiliams 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 (i.e. uniform vs. concentrated). Only directions with bird densities of >5 birds/km^3 were included to avoid biases arising from low densities.

Further methodological issues are presented and discussed in the supplement from a more technical perspective.

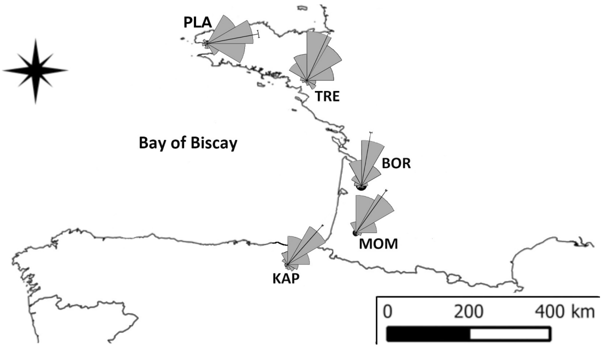

FIG. 4 *The nocturnal migration directions and mean resultant direction (±SE) per site (Kapildui: KAP; Momuy: MOM; Bordeaux: BOR; Tréillères: TRE; Plabennec: PLA).*

TABLE 1. *Rank of the model with lowest AIC and the null model (MTR~ 1) to identify the variables determining the intensity of nocturnal bird migration at five radar sites in spring 2015. Tailwind refers to values at 775m at 00:00 h. Other candidate models were ranked within a position of >2 AICc values from the model one.*

Models	AICc	⊿AICc	AICc weight	No. parameters
1. Site × Tailwind 775	166.22	0.0	0.99	11
3. Null	214.95	48.73	0.00	1

TABLE 2. *B-parameter estimates obtained from model averaging of the models 1 of Table 1 for the seven radar sites: Kapildui (KAP), Momuy (MOM), Bordeaux (BOR), Tréillères (TRE) and Plabennec (PLA).*

Parameters	*B*	*se (B)*	*P*
(Intercept)	2.47	0.21	<0.001
KAP[a]	- 0.08	0.24	0.752
MOM[a]	- 0.11	0.25	0.676
PLA[a]	- 0.97	0.23	<0.001
TRE[a]	- 0.31	0.29	0.195
TW_925	0.08	0.03	0.015
KAP × Tailwind 775	- 0.07	0.04	0.118
MOM × Tailwind 775	- 0.06	0.05	0.256
PLA × Tailwind 775	- 0.04	0.04	0.252
TRE × Tailwind 775	- 0.04	0.04	0.351

[a] *Reference values (B = 0): Site: Bordeaux.*

TABLE 3. *Mean directions (±SE) and Rayleigh test results (p-value) per site.*

	Kapildui	Momuy	Bordeaux	Tréillères	Plabennec
Mean direction	41.78° (±0.37°)	35.70° (±0.43°)	9.92° (±0.73°)	24.63° (±95°)	79.47° (±2.02°)
Rayleigh Test P	<0.001	<0.001	<0.001	<0.001	<0.001

RESULTS

MIGRATION TRAFFIC RATES

Mean nocturnal MTRs were highest in the Kapildui data and gradually decreased northwards, with the lowest MTRs at Plabennec (Fig. 2). There were significant variations in MTR between the sites Bordeaux-Tréillères (t=16.09, df=15, p<0.001) and Tréillères-Plabennec (t=3.67, df=26, p<0.05).

The general pattern of bird echoes was an increase at sunset and a decrease at sunrise (Fig. 1). In the southern radars Kapildui, Momuy and Bordeaux a more uniform and continuous nocturnal pattern was observed (Fig. 3). Interestingly, Tréillères showed a pronounced peak each at the beginning and towards the end of the night (Fig. 3). There was a significant difference between the low MTRs of the middle decade and the peaks of both the first evening (t=2.40, df=16, p<0.05) and last morning decade (t=2.16, df=16, p<0.05). Plabennec showed very low MTRs overall, with minor peaks at sunset, if any (Fig. 3).

In the wind analysis only one model was in the range of AICc<2 (Table 1 and 2). This model included the radar sites and tailwind at 775m above ground level. There was a significant negative relationship between MTRs and the northernmost site (Plabennec) and a slightly positive relationship between MTRs and tailwinds at 775 m.

FLIGHT DIRECTIONS

Flight directions indicated a general NE direction (range: 11.56-79.47°, Table 3) with a significantly different mean migratory direction at each site (Table 3, all p < 0.001). The southern radars Kapildui and Momuy had a more pronounced NE direction than Bordeaux, which pointed almost north. Tréillères directions were again directed more towards NE, while Plabennec pointed eastwards (Fig. 4).

FLIGHT ALTITUDES

In the three southern radars, i.e. Kapildui, Momuy and Bordeaux, migration extended up to an altitude of about 3-4 km (Fig. 3). In the Tréillères radar, the radius of 40 km allowed identifying a migration altitude of 2 km (Fig. 3). Plabennec showed lower migration altitudes of up to 1.5 km (Fig. 3).

DISCUSSION

MIGRATION TRAFFIC RATES

The decrease from Kapildui towards Momuy and Bordeaux, and further up, suggests that the three southern sites are situated in the same migratory flow evolving over land, while the two northern radars receive far lower numbers. In the event of uniform broad-front migration across the open sea, more similar MTRs would be expected at the two northern sites, in particular also higher MTRs at Plabennec. Findings from nocturnal autumn migration (Weisshaupt et al. 2016) suggest a more southward flight direction about 100 km south of Kapildui compared to the coast. Together with the present MTR patterns, this could suggest a funnelling effect between the sea and the Pyrenees, i.e. birds cluster in the lower foothills to avoid both the open sea and the high mountain ridges further east. A similar scenario was found for example in the Alps (e.g. Bruderer and Jenni 1990, Liechti et al. 1996). However, more (south-) eastern data from the mountain region and western coastal data would be necessary to confirm this pattern.

Overall, there were three different nocturnal activity patterns: The two southernmost radars (Kapildui and Momuy) showed rather uniform nocturnal activity. Bordeaux showed a similar tendency, though also some more bimodal patterns in some nights, which could indicate an increase based on an influx from sea. This bimodal pattern was even more pronounced in the Tréillères radar (Fig. 3). It can be assumed that the evening peaks represent take-off of resting birds and the morning peaks originate from birds crossing the sea, with low or no arrivals in between, similar to patterns known from Mediterranean islands (e.g. Speich 1999).

The overall low numbers at Plabennec could be linked to the long distance of about 500 km over water which sea crossing from the Spanish coast would involve. Similar avoidance of long flight distances over sea is known from the Mediterranean (Bruderer and Liechti 1999), which in the end leads to the high concentrations at Gibraltar and the Bosporus. The weak peaks at the beginning of the night, but no movements in the rest of the night, suggests that there is no further nocturnal influx from the sea. The evening patterns could stem from birds that could have accumulated during the day over land and potentially head towards northwestern Europe. So even though a flight of 500 km from the Spanish coast should be feasible for a passerine in one night (Bruderer and Bolt 2001), results indicate that birds do avoid the long distance to Plabennec over sea, and venture only shorter distances, i.e. up to Tréillères. Alternatively it is possible, that the northern corner of the bay would only receive migrants departing in more western areas on the Iberian Pensinsula, while the southeastern corner receives confluent migration from central and northern Iberia and possibly from Africa, gathering in much higher quantities. However, in case of nocturnal sea crossing a peak in the morning rather than in the evening would be anticipated. To clarify this aspect, it would be necessary to access data from more southwestern sites at the bay.

As to wind assistance, the significance of tailwind at 775m shows that birds make use of favourable wind conditions, even though the positive effect is only low. This minor positive effect could be due to the fact that there was an unusual predominance of weak E or SE winds, if any, until end of March at the presumed departure coastal region in Northern Spain. This period included two peak migration events (6-8 Mar, 16-17

Mar). In late March winds changed to SW/W coinciding with a new increase in migration activity. So birds seem to travel also in suboptimal conditions as found e.g. by Karlsson et al. (2011). Otherwise a higher tailwind effect would have been expected. Additionally, the high migration intensities coincided with cease of rain. For example in the second half of March, there were 9 consecutive days of precipitation. So birds apparently also wait for precipitation-free weather as shown previously in other studies (Alerstam 1990).

FLIGHT DIRECTIONS

Flight directions, together with the MTRs, show that the broad front NE migration generally assumed for spring (Zink 1970, Hilgerloh 1989, Trösch et al. 2005) exhibits actually major spatial structuring with areas of higher and lower densities of migrants.

The similarity between the directions of Kapildui, Momuy and Bordeaux could potentially represent the same bird flow. In contrast, the stronger NE direction at Tréillères compared to Bordeaux, paired with the bimodal nocturnal MTR patterns suggest the arrival of birds from the sea. The pattern is very pronounced and there is a significant drop in activity during the middle of the night (Fig. 3). So the main migration evolves near the eastern coast of the bay with some birds crossing the sea, as indicated by the directional and quantitative patterns at the Tréillères and Kapildui radar, and some continuing over land, similar to findings from Diehl et al. (2003) and Gagnon et al. (2010). The eastern mean directions at Plabennec remain unclear, in particular based on the almost inexistent nocturnal patterns. They could stem from a minor proportion of birds heading north towards Britain and following the coastline at Plabennec. Previous studies have shown that birds readily make use of coastlines as landmarks for orientation at night (Alerstam 1990, Åkesson 1993).

FLIGHT ALTITUDES

Flight altitudes were overall in a similar range as observed in other parts of Europe (Alerstam 1990, Dokter et al. 2010, Weisshaupt et al. 2014). Interestingly, the flight altitudes decreased from south to north, i.e. from migration up to 3-4 km in the Kapildui, Momuy and Bordeaux radars, to about 2 km at Tréillères and <1.5 km at Plabennec. High flight altitudes have been previously associated with the proximity to ecological barriers (Bruderer and Liechti 1998, Nilsson et al. 2014). Bruderer and Liechti (1998) measured higher flight altitudes over land than over the sea in the Mediterranean. These findings would nicely fit with the observed pattern of higher flight altitudes in the southern region, where birds fly over land and where the Pyrenees might have a certain influence as well, and lower altitudes in connection with birds arriving from the sea in the more northern parts.

CONCLUSIONS

Analysing data from the five weather radars along the eastern side of the Bay of Biscay allowed identifying preferred migratory directions as well as a novel data on a quantitative and altitudinal N-S gradient along the eastern coastline. The uniform continuous patterns in the two southern radars confirm strong migration over land, with an apparent shift from uniform to bimodal nocturnal patterns from Bordeaux to Tréillères being strongly indicative of sea crossing at these latitudes. The number of birds crossing the sea diminished with increasing distance over water resulting in a limited spread of the migration flow over the sea. The observed pattern probably describes a compromise between flying extensive distances over sea or alternatively over high mountains further east. A slightly positive effect of tailwind was observed at a level of 775m, while migration ceased during precipitation periods. The higher migration intensity in the southeastern region supports the importance of the respective areas as passage zones for nocturnal migrants.

However, it remains to be studied what proportion of migrants actually undertakes sea crossing and to what extent the concentration in the southeastern corner is predetermined by large-scale dynamics over western Iberia, either by different origins and routes of migrants or additional barriers such as the Pyrenees. The more southward directions found by Weisshaupt et al. (2016) would support the funnelling hypotheses, though appropriate remote-sensing data would be needed to further explore the evolvement and distribution of the migratory flow on a larger scale on the Iberian Peninsula. The study undermines the importance of large-scale studies in migration research to understand migration dynamics and potential barrier effects from a broader bird's eye view.

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SUPPLEMENT

DATA ACQUISITION

Radar data was obtained from different entities, which provided varying levels of support and information at different (or no) costs. Depending on the manufacturers and operators and/or the predetermined technical specifications, data of the various radars were also quite heterogeneous in regard to format, filtering and data availability. For example, in the Kapildui data, reflectivity and radial velocity data were stored in separate files which required first merging the data into one file before running the algorithm. The Kapildui radar provided six hourly measurements vs. four hourly measurements in the French and in the AEMET radars. This did not have any negative effect, though. Then the application of a special non-precipitative filter in the AEMET data removed any kind of biological signals and thus the respective radars were not suitable for the analysis (Suppl. Fig. 1A). Two radars (Jata and Bordeaux) were out of service in two out of five weeks in the selected study period.

Therefore, when requesting data, it is essential to specify exactly the required data type and format, period, elevations and site(s) and to check data quality beforehand. Ideally a sample file is provided which will allow the user to verify the quality and format of the data before engaging in any major data petition (and

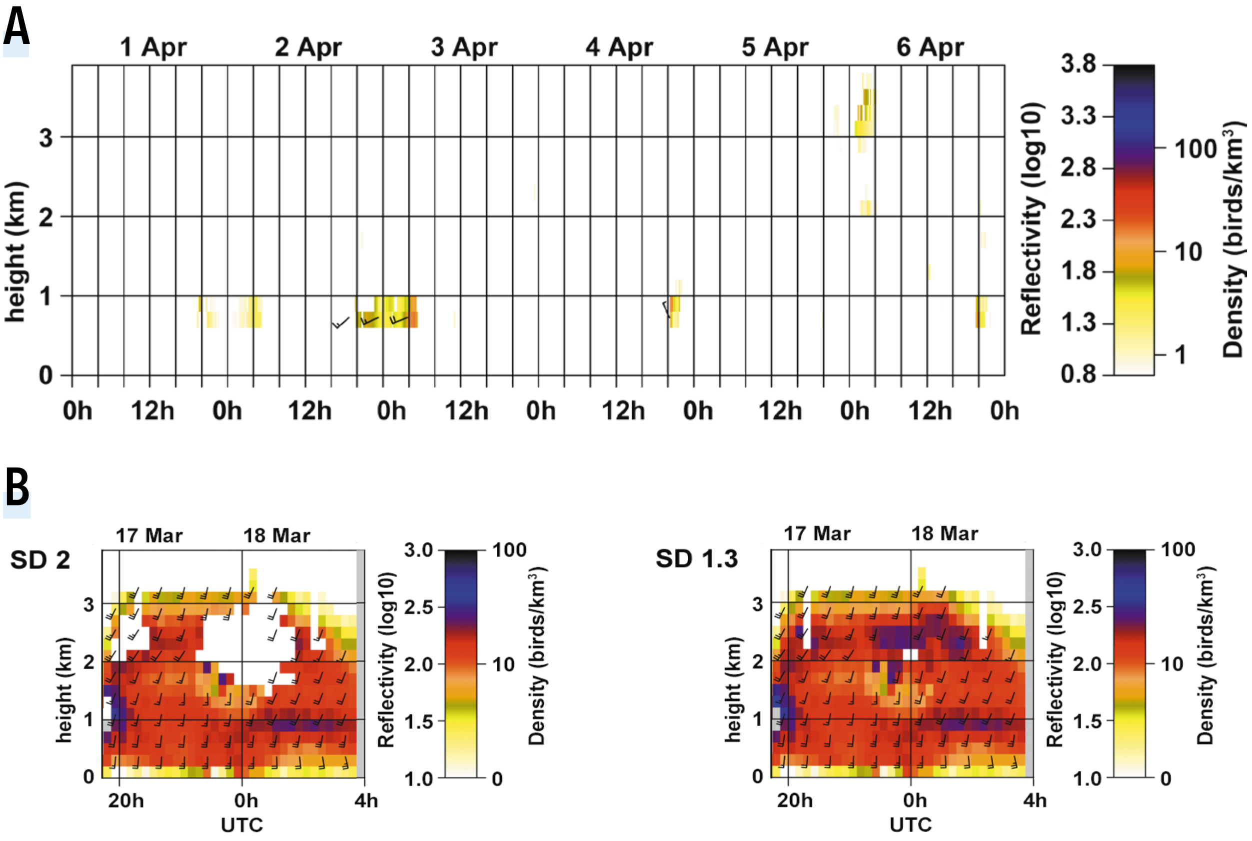

FIG. 1 *Examples of weather radar data: (A) data from the Jata radar filtered by special non-precipitative echo removal algorithm; (B) Gaps created by high bird densities with corresponding MTR curve before (SD=2) and after (SD=1.3) adaptation of standard deviation during the precipitation free night of 17 Mar in the Bordeaux radar.*

consequently costs) which might not fulfil the requirements of the bird algorithm, i.e. format, degree of filtering, data availability or other. The variable extent of data availability might be particularly important in case of planned large-scale comparisons involving multiple radar sites.

BIRD IDENTIFICATION BY WEATHER RADARS

The bird algorithm makes use of the different echo characteristics of birds vs. atmospheric or other biological targets. First, radial velocity of birds, i.e. the movement relative to the radar, is spatially more diverse as a result of the birds' individually varying flight speeds and directions (Koistinen 2000). Generally, birds travel at higher speeds than insects, which are mainly carried passively by the wind (Chapman et al. 2003), and can fly both in tailwinds and headwinds (Alerstam 1990, Larkin 1991). Therefore, radial velocities of birds deviate from velocities of surrounding non-bird echoes (Dokter et al. 2010). Depending on meteorological conditions and densities of targets, standard deviations of radial velocity measures between birds, insects and atmospheric signals may overlap. As the algorithm uses standard deviations to distinguish between these different targets, challenges may also arise from data quality.

DATA PROCESSING BY THE BIRD ALGORITHM

A key issue during processing the French data by the algorithm was the relatively low quality of radial velocity data. There were many dealiasing errors, and certain regions showed folded velocities (perceived as abrupt change in the colour scale of the velocity field), probably because of the French triple-PRT scanning scheme. This aspect was especially problematic as it affects the extraction of bird echoes because the algorithm uses the amount of variability in radial velocity data (standard deviation) as an indicator of bird migration.

A second issue encountered were challenging meteorological situations, such as some few highly convective weather situations to which no good linear radial velocity model could be fitted.

POST-ALGORITHM PROCESSING

There were consequently some issues related to the separation of birds vs. other targets which required manual post-processing. As stated previously, birds are identified by SD values of ≥2ms-1, while lower values are assigned to precipitation. However, weather radars can perceive spatially extensive high bird densities as one large object with low radial velocity SD <2ms-1 which are consequently removed by the algorithm as non-birds. As a consequence of the removal, the algorithm creates gaps in the altitudinal profiles (Suppl. Fig. 1B). Besides this cosmetic aspect, MTR values are affected and the evolvement of nocturnal migration intensity is erroneous, i.e. it can create a bimodal nocturnal MTR pattern even though migration would evolve rather uniformly, and may lead to inappropriate conclusions. In order to prevent any bias, it is necessary to lower the threshold for radial velocity, e.g. from 2 to 1.7ms-1 or lower for the affected sites and/or nights, until the gaps are filled and MTRs corrected. Importantly, if precipitation days have not been excluded from the analysis, this adjustment will also allow for more precipitation in the data. So at the present stage it is advisable to completely exclude precipitation days.

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