

# ECOGRAPHY

## Research

### Cross-calibration of different radar systems for monitoring nocturnal bird migration across Europe and the Near East

Felix Liechti, Janine Aschwanden, Jan Blew, Mathieu Boos, Robin Brabant, Adriaan M. Dokter, Vladislav Kosarev, Maryna Lukach, Mercedes Maruri, Maarten Reyniers, Inbal Schekler, Heiko Schmaljohann, Baptiste Schmid, Nadja Weisshaupt and Nir Sapir

F. Liechti (<http://orcid.org/0000-0001-9473-0837>) ([felix.liechti@vogelwarte.ch](mailto:felix.liechti@vogelwarte.ch)), J. Aschwanden and B. Schmid (<http://orcid.org/0000-0002-7736-7527>), Swiss Ornithological Inst., Sempach, Switzerland. – J. Blew and V. Kosarev, BioConsult SH GmbH & Co.KG., Husum, Germany. – M. Boos, Cabinet d'Expertise et de recherche en Ecologie Appliquée, France. – R. Brabant, Royal Belgian Inst. of Natural Sciences (RBINS), Belgium. – A. M. Dokter (<http://orcid.org/0000-0001-6573-066X>), Cornell Lab of Ornithology, Cornell Univ., USA. – M. Lukach, National Centre for Atmospheric Science, Univ. of Leeds, UK. – M. Maruri, Univ. of the Basque Country, UPV/EHU School of Engineering, Applied Mathematics 2-Basque Meteorology Agency, Basque Country, Spain, and Meteorology Area, Energy and Environment Division, Tecnalia R&I, Basque Country, Spain. – M. Reyniers and ML, Royal Meteorological Inst. of Belgium, Belgium. – I. Schekler and N. Sapir (<http://orcid.org/0000-0002-2477-0515>), Dept of Evolutionary and Environmental Biology, Univ. of Haifa, Haifa, Israel. – H. Schmaljohann (<http://orcid.org/0000-0002-0886-4319>), Inst. for Biology and Environmental Science, Carl von Ossietzky Univ. Oldenburg, Oldenburg, Germany, and Inst. of Avian Research 'Vogelwarte Helgoland', An der Vogelwarte, Wilhelmshaven, Germany. – N. Weisshaupt, Univ. of the Basque Country, Bilbao, Spain.

## Ecography

42: 1–12, 2018

doi: 10.1111/ecog.04041

Subject Editor: Cecilia Nilsson  
Editor-in-Chief: Miguel Araújo  
Accepted 16 October 2018



Large parts of the continents are continuously scanned by terrestrial weather radars to monitor precipitation and wind conditions. These systems also monitor the mass movements of bird, bat, and insect migration, but it is still unknown how many of these systems perform with regard to detection and quantification of migration intensities of the different groups. In this study that was undertaken within five regions across Europe and the Middle East we examined to what extent bird migration intensities derived from different weather radars are comparable between each other and relate to intensities measured by local small-scaled radars, some of them specifically developed to monitor birds. Good correspondence was found for the relative day-to-day pattern in migration intensities among most radar systems that were compared. Absolute intensities varied between different systems and regions. The findings of this study can be used to infer about absolute bird migration intensities measured by different radar systems and consequently help resolving methodological issues regarding the estimation of migrant numbers in the Western-Paleartic region. It further depicts a scientific basis for the future monitoring of migratory bird populations across a large spatio-temporal scale, predicting their movements and studying its consequences on ecological systems and human lives.

Keywords: bird migration, radar monitoring, radar ornithology, cross-validation



[www.ecography.org](http://www.ecography.org)

© 2018 The Authors. This is an Online Open article  
This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

## Introduction

The lower atmosphere is the most relevant space for the exchange of biomass within and between continents (Chilson et al. 2017a, b). This airspace is continuously monitored by several sensors, mainly radar systems from the ground and from satellites (North 2015). A variety of such radar systems has been used to track animal movements across the airspace for more than 70 yr (Lack and Varley 1945, Suter 1957, Eastwood 1967, Able 1970, Bruderer and Steidinger 1972, Gauthreaux 1975, Alerstam 1976, Riley and Reynolds 1983, Buurma 1987, Chapman et al. 2004, Alerstam et al. 2011, Chilson et al. 2012, Drake and Reynolds 2012, Mirkovic et al. 2016). However, proper quantification of migratory intensities remained a challenge until today, and the statement made by Nisbet (1963) – ‘None of the quantitative results of this paper can be applied immediately to other radar stations used to study bird migration’ – still holds true. Among the variety of radar systems used for tracking birds, weather radars (WR) have become more and more a standard tool to monitor nocturnal broad front migration of birds (Able 1970, Gauthreaux and Belser 1998, Diehl et al. 2003, Chilson et al. 2011), and, to a much lesser extent, for quantifying nightly dispersal of bats (Horn and Kunz 2008, Frick et al. 2017) and insects (Leskinen et al. 2011, Rennie 2014).

In this study, we focus on the quantification of bird migration by radars. Within the last 20 yr the great potential of WR networks has been recognized and several explorations of these networks provided important insights regarding the migration biology of birds (Gauthreaux et al. 2003, Dokter et al. 2011, 2018, Kelly et al. 2012, van Doren and Horton 2018). These networks span across whole continents and are able to monitor nocturnal bird migration in almost real time. For such large-scale analyses, the comparability of migration intensities derived from a single type of radar system is essential. In the US, the NEXRAD network consists of a single radar type (WSR-88D) and all radar systems are operated with a very similar scanning mode (Kelly et al. 2012). In contrast, the European network OPERA covers only part of the continent and consists of many radar systems that are made by different manufacturers. Another drawback is that these systems operate in different scanning modes ruled by the national met-offices (Huuskonen et al. 2014). It is therefore not surprising that most published studies on bird migration using multiple WR systems are based on the US-WR network NEXRAD (Buler and Diehl 2009, Horton et al. 2016, La Sorte et al. 2017); but see Nilsson et al. (2019).

For a long time, extraction of bird movements from WRs was done more or less manually by visual inspection of the radar scans (PPIs) and migration intensities were consequently classified on a relative quantitative scale (Gauthreaux and Belser 1998, Diehl et al. 2005). An automated algorithm to extract height profiles of bird migration from European WR was developed in the Netherlands and its products

were cross-calibrated with those of dedicated bird radar (Dokter et al. 2011, van Gasteren et al. 2008). A recent study compared results from a WR and three other radars at a single specific site (Nilsson et al. 2018). The algorithm developed and improved through these campaigns is currently applied to a large number of European and US WRs.

In the present study we combine the results from five different field campaigns realized independently across Europe and the Near East. In these campaigns bird migration intensity was monitored with WR and at least one dedicated bird radar. The aim of this study is to gain insight into the comparability of bird migration intensities from different WRs in Europe and the Near East. Consequently, the two main questions that are addressed herein are: To what extent do migration intensities measured by different radar systems match on the relative and absolute scale? How does proximity between sites and height ranges covered by the various systems influence the correlations between the systems?

## Material and methods

There is an innumerable variety of radar systems which, at least theoretically could be used for tracking birds (Chilson et al. 2017a, b). In practice, there is a limited number of systems used for tracking bird targets (Drake and Bruderer 2017). Radar systems involved in this study include medium range WRs (tens of km) and short range (1–7 km) dedicated bird radars. Apart from various technical features, the extraction of bird intensity data differs considerably between WRs and the dedicated bird radars. In the WR the reflectivity of all birds within a single range is summed up, and Migration Traffic Rate (MTR) is calculated assuming a given average bird size. MTR is the number of birds crossing a virtual line of 1 km perpendicular to the main migratory direction within 1 h (Lowery 1951, Liechti et al. 1996). In short-range radar, tracks of single birds are summed up to calculate MTR.

In each of the five study regions nocturnal bird migration was monitored by one or two WRs in combination with one or two dedicated small-scale bird radars (Table 1, Fig. 1) or radar wind profiler. All WRs mentioned in this study are C-band Doppler radars. WRs are performing single 360° scans at several elevations, repeated every five minutes, up to every 15 min (varies between sites) continuously throughout the whole day. Values from all altitude bands within a range of 25 km were recalculated into an integrated value of MTR for each night. Heights covered by the different radars are given in Supplementary material Appendix 1 Fig. A1. Extraction of bird profiles followed the protocol implemented by Dokter et al. (2011), as available in the R-package bioRad (Dokter et al. 2019). To translate intensity of reflectivity into bird density we used a seasonal-average radar cross-section of 11 cm<sup>2</sup>. This value (11 cm<sup>2</sup>) was determined in a cross-calibration over a full spring and autumn season in western Europe (Dokter et al. 2011). The value corresponds

Table 1. Overview of the study regions and the radar systems compared within each region. WR=weather radar, FBR=fixed-beam bird radar (scans with a static beam at different elevations), VBR=vertical-beam bird radar (scans with nutating vertically looking beam), RBR=rotating-beam bird radar (scanning a vertical plan with a rotating T-bar antenna), RWP=vertical radar wind profiler (scans vertically with a static beam). The wave length of the radar system, nominal beam width (-3dB) of the radar antenna and operational range used for bird detection are given for each radar type.

Region	Radar systems	Frequency band	Beam width	Range [km]
Northern Germany	WR Hamburg	C (5.6 GHz)	~1°	5–25
	WR Rostock	C (5.6 GHz)	0.9°	5–25
	FBR Superfledermaus	X (9.4 GHz)	2.2°	0.2–7.5
Flanders (BE, FR)	WR Jabbeke	C (5.6 GHz)	1°	5–25
	VBR Herzele	X (9.4 GHz)	~25°	0.05–2
	RBR offshore	S (2.9–3.1 GHz)	2°/26.5°	0.05–4
Bay of Biscay (ES, FR)	WR Momuy	C (5.6 GHz)	1.1°	5–25
	WR Kapildui	C (5.6 GHz)	~1°	5–25
	RWP Bilbao	L (1.3 GHz)	6°	0.7–2
Northern Israel	WR Meron	C (5.6 GHz)	~1°	5–25
	WR Dalton	C (5.6 GHz)	~1°	5–25
	VBR Kisral	X (9.4 GHz)	~25°	0.05–2
North of the Alps (FR, DE, CH)	WR Montancy	C (5.6 GHz)	1.1°	5–25
	WR Memmningen	C (5.6 GHz)	0.9°	5–25
	FBR Peuchapatte	X (9.4 GHz)	2.2°	0.2–6
	FBR Provence	X (9.4 GHz)	2.2°	0.2–6
	FBR Bremelau	X (9.4 GHz)	2.2°	0.2–6

to an average size in between an European robin *Erithacus rubecula* and a song thrush *Turdus philomelos*. Data were extracted only for nocturnal migration, because quantification of diurnal migration is still a major and not yet solved

issue (Dokter et al. 2019). The night was defined as the period of time between evening and morning civil twilights, which represents the time when the sun position is at least six degrees below the horizon. All bird migration intensities are

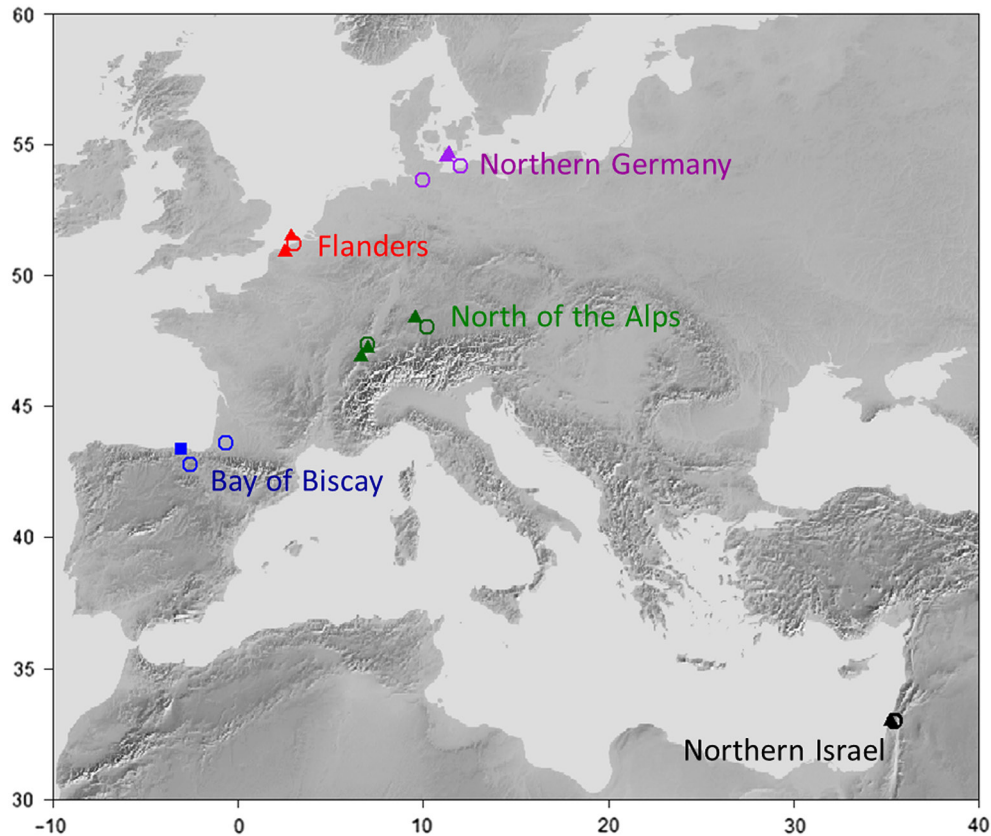


Figure 1. Geographical position of the radar sites included in this study. A specific color is assigned to each of the five regions, which is also used in Fig. 3 and 4. The open circles refer to weather radar sites, the filled triangles to bird radar sites, and the filled square to the wind profiler radar.

given as MTR. All WR systems, except the one from Spain and those from Israel are part of the European WR network (OPERA Huuskonen et al. 2014). Technical specifications of these radars are given on the official website of European meteorological services network (<[http://eumetnet.eu/wp-content/themes/aeron-child/observations-programme/current-activities/opera/database/OPERA\\_Database/index.html](http://eumetnet.eu/wp-content/themes/aeron-child/observations-programme/current-activities/opera/database/OPERA_Database/index.html)>).

## Northern Germany

Within an environmental impact assessment (EIA) (FEBI 2013) concerning the proposed traffic link from Puttgarden (Germany) to Rødbyhavn (Denmark), data on bird MTR were collected with the bird radar 'Superfledermaus', for technical details see (Bruderer 1997a), during the main migration periods in 2009 (20 Feb–29 May, 14 Aug–31 Oct) and 2010 (6 Mar–30 May, 15 Aug–5 Nov). In 2009 the bird radar 'Superfledermaus' was located on the Danish side of the Fehmarnbelt at Rødbyhavn (54.651°N, 11.359°E), 2 m a.s.l. In 2010 the same bird radar was located on the German side of the Fehmarnbelt, at Puttgarden (54.501°N, 11.232°E; 5 m a.s.l.). With the fixed beam measurement method, echoes are illuminated by the radar for a few seconds which allows differentiating between birds and other targets (mainly insects) based on the temporal pattern of echo intensity which reflects the target's wingbeat frequency (Bruderer and Steidinger 1972, Griffin 1973, Zaugg et al. 2008). MTR was calculated from the number of bird echoes crossing the fixed radar beam. A single quantitative measurement consisted of six fixed beam recordings lasting 4 min each, with the beam pointing towards two directions at four different elevation angles (2 towards the sea at an elevation of 3° and 6°, 4 over land at an elevation of 3°, 6°, 22.5° and 60°). Detection ranged from 0.2 to 7.5 km and the analysis included the height range of 25 to 4000 m above ground level (a.g.l.). These measurements were performed every hour throughout the night. Details on MTR calculation from these recordings are given in Schmaljohann et al. (2008). Within this study we refer to this as the fixed beam radar (FBR) measurement mode (Table 1). For the same seasonal periods raw data from WRs near Hamburg (53.622°N, 9.998°E; antenna height 30 m a.s.l.) and Rostock (54.176°N, 12.058°E; 36 m a.s.l.; Table 1) were used to extract information about bird MTR. The WRs were located to the east and the south-west of the FBR, about 150 km apart (Fig. 1, Supplementary material Appendix 1 Table A1).

## Flanders

Two dedicated bird radars were operated between 18 August 2016 and 13 October 2016 in the vicinity of the WR in Jabbeke (Belgium, 51.192°N, 3.064°E; 52 m a.s.l.). Bird volume data from the Jabbeke WR was extracted as described above. A BirdScan-MR1 (Swiss birdradar©) was installed in Herzele (50.888°N, 2.536°E; 12 m a.s.l.), near the Belgian–French border. One vertical marine radar (Merlin bird radar,

DeTect, FL, USA) is permanently installed on the offshore platform inside the C-Power wind farm on the Thorntonbank (51.494°N, 2.881°E; 38 m a.s.l.) in the Belgian part of the North Sea (Fig. 1, Table 1).

The BirdScan-MR1 is a vertical looking radar system based on a commercial marine radar (25 kW pulsed X-band radar, 9.4 GHz), further referred to as vertical beam radar (VBR). The detection range and range resolution depend on the pulse duration. We sequentially used 65 ns pulse duration (short-pulse, PRF 1800 Hz, range resolution 7.5 m, 300 m STC, –93 dB detection threshold) to register bird movements below 800 m, and 750 ns pulse duration (long-pulse, PRF 785 Hz, range resolution 110 m, 500 m STC, –102 dB detection threshold) to register bird movements above 800 m, up to 1400 m a.g.l. Targets crossing the beam are illuminated constantly and thus echo signature, which includes the temporal pattern of echo intensity, can be derived and used to distinguish birds from other targets (mainly insects). Based on the echo signatures, birds are classified into different groups (e.g. passerine-type, wader-type), and if possible wing-beat frequency is extracted. Target size is then empirically estimated from the echo signature (Schmid et al. 2019). MTR is calculated based on target size specific surveyed volume. For more details see (Nilsson et al. 2018).

The Merlin bird radar uses a solid state marine radar (170 W S-band antenna), vertically rotating at 20 rounds min<sup>-1</sup>. This radar is further being referred to as vertically rotating beam radar (RBR). The Merlin software links consecutive registrations of a target, and thus registers the flight path of a moving target (DeTect). The measurements cover altitudes from 0 to 3600 m a.g.l. The MTR is calculated as the sum of the number of bird tracks per hour, registered in two columns of 500 m wide selected from the entire measurement volume (250 to 750 m distance from the radar, both to the east and west; details in (Fijn et al. 2015)). The solid-state antenna simultaneously transmits a sequence of pulses of differing length, short (12 µs), medium (64 µs) and long (365 µs) pulse. The pulse repetition interval is respectively 1 µs, 5 µs, and 33 µs. No details are available on the relation between pulse length and detection range. Possibly, further discriminating inland from offshore MTR of the WR may give a better insight into the differences in correlations between the WR and both other respective radar systems.

## Bay of Biscay

Radar data for this study was retrieved from the 1290 MHz (23 cm wavelength) LAP 3000 boundary layer wind profiler with integrated Radio Acoustic Sounding System (RASS) owned by Euskalmet (Basque Meteorology Agency). The radar is located at the north-eastern side of the estuary of Bilbao, Spain (43.373°N, 3.063°W; 60 m a.s.l.), on a cliff top (Fig. 1, Table 1). Being based on a Doppler radar with a phased-array antenna, the system provides continuous, real-time vertical profiles of wind. Vertical bird profiles were extracted every 5 min from 133 m up to 2000 m a.g.l. Details on bird extraction procedure from this radar system and the



calculation of the MTRs adapted to the respective data collection mode are given in Weisshaupt et al. (2017). This radar is referred to as radar wind profiler (RWP).

WR data were obtained from Momuy, France (43.624°N, 0.609°W; 146 m a.s.l.) a radar integrated in the OPERA network, and from Kapildui, Spain (42.766°N, 2.538°W; 1169 m a.s.l.), a radar also owned by Euskalmet, which is not part of the OPERA network (Fig. 1). Nevertheless, the radar at Kapildui is very similar to the other WR (Table 1). Radar data were retrieved during the spring migration period from 5 Mar–1 Apr 2015.

## North of the Alps

In the context of two environmental impact assessments, bird MTR was recorded at three locations with a dedicated bird radar (BirdScanMT1, Swiss Ornithological Inst., Sempach, Switzerland). Two of these radars were situated in the northern part of the Swiss Jura mountains, one near Peuchapatte (47.225°N, 7.007°E; 1053 m a.s.l.) and the other near Provence (46.884°N, 6.635°E; 1261 m a.s.l.). A third radar was located near Bremelau (48.364°N, 9.549°E; 755 m a.s.l.) on the Swabian Alb, southern Germany (Fig. 1, Table 1). At all sites measurements were performed in a fixed beam mode, very similar to the measurements performed by the ‘Superfledermaus’ in northern Germany, see above for further information. Specific details of the radar system and the operation mode are given in Aschwanden et al. (2018). Maximum detection range was 6 km, somewhat shorter than with the ‘Superfledermaus’, but still covering all heights from 50 to 4000 m a.g.l. The measurements were performed continuously throughout the night. We refer to these measurements also as FBR mode (Fig. 1, Table 1).

Vertical bird profile data were extracted as described above from a WR near the Jura mountains (Montancy, France, 47.367°N, 7.019°E; 926 m a.s.l.) and a WR near the Swabian Alb (Memmingen, Germany, 48.042°N, 10.219°E; 779 m a.s.l.). The height range covered was 200 to 4000 m a.g.l. (Fig. 1, Table 1). Data were collected at all sites from 15 Aug–17 Nov 2015.

## Northern Israel

Data from three radars were collected during April 2016 (1–29 Apr for Meron and Kiswa, 1–13 Apr for Dalton). Kiswa BirdScan-MR1 radar (VBR) was positioned in the Western Galilee (32.980°N, 35.220°E; 386 m a.s.l.), about 14 km east of the Mediterranean Sea coast. The radar system is identical to the one used in Flanders (see above) and was operated as a part of an environmental impact survey. The Meron radar, a polarimetric WR, is positioned at the top of Mt Meron (32.977°N, 35.418°E; 1200 m a.s.l.), the highest peak of the Galilee mountain range. The radar is located about 19 km east north east of the position of the Kiswa radar and is operated continuously by the Israeli airforce for meteorological purposes. Since it is located on a mountain top with no higher peaks in its vicinity, this radar does not incur any

ground clutter. The Dalton radar, a dual-pol WR, is positioned at Mt Dalton (33.012°N, 35.492°E; 950 m a.s.l.) about 6.5 km north east of Meron radar. The radar is operated only around forecasted precipitation events by Mekorot – the national water company of Israel. Due to the serious ground clutter caused by the Meron mountain that is found in the vicinity of this radar (Supplementary material Appendix 1 Fig. A1), radar data are collected from an altitude of 250 m above ground, and thus Dalton and Meron radars collect data from an altitude of about 1200 m a.s.l. The WRs in Israel are not part of the OPERA network but they operate in a similar mode, wavelength (C-band) and range as the OPERA network WRs. The overlapping height band between the VBR and the WRs is about 500 m which is rather limited, a result of the differences in the location altitudes of the three radars (Fig. 1, Table 1).

## Data analysis

To calculate MTR, the WR transect was kept perpendicular to the extracted ground speed direction at all times (Dokter et al. 2019). For each study region we calculated mean MTR per night for all height ranges covered by an individual system, and additionally calculated a mean MTR for the overlapping height range of the different radar systems (Supplementary material Appendix 1 Table A1, Fig. A2). To compare the relative seasonal pattern, we calculated for each pairwise comparison the square of the Pearson’s correlation coefficient ( $r^2$ ) based on the log-transformed MTR for the total MTR and for the overlapping height band subsample. For the pairwise comparison of MTR between two radar systems, we additionally calculated the mean MTR for the shared time periods, and then divided the mean from the first sample by the sum of both samples. Thus, the resulting ratio was between 0 and 1. Accordingly, within a pairwise comparison, a ratio greater than 0.5 indicates higher MTR for the first sample, and a ratio lower than 0.5 indicates higher MTR for the second sample. All analyses were run with R (ver. 3.4.4.) using the R-package bioRad for inspecting profile data and calculating MTR from time series of vertical profiles.

## Results

Within each region we compared the parallel recordings of the seasonal course of MTR between the different radar systems. An example for one region is given in Fig. 2. The graphs for all regions are given in the supplemental material (Supplementary material Appendix 1 Fig. A3). Squared correlation coefficients ( $r^2$ ) given for all pairwise comparisons across all regions show a considerable variance (Fig. 3.). Within the two regions with only a few nights to be compared (northern Israel  $n=13$  and 29; Bay of Biscaya  $n=9$  and 18) correlations were relatively poor ( $r^2 < 0.25$ ). The best correlation ( $r^2=0.85$ ) was found between a WR and a bird radar (FBR) being at a distance of 16 km. High correlations

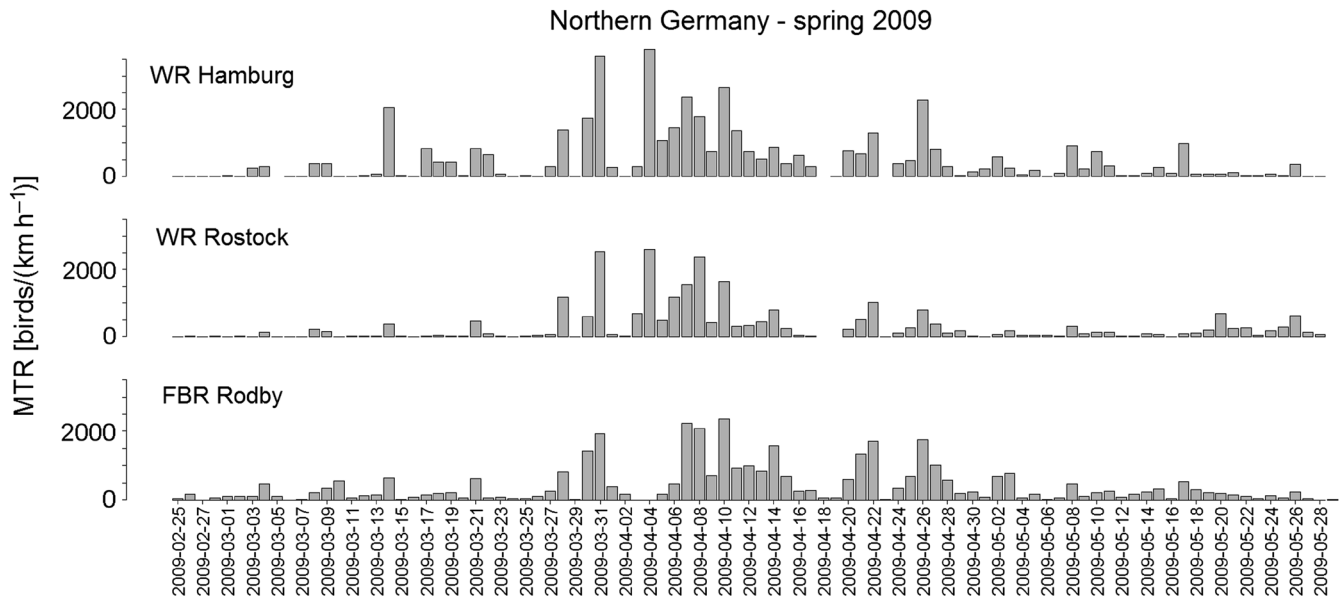


Figure 2. Example of a field campaign with three parallel measurements of the seasonal pattern of bird migration traffic rate (MTR) in northern Germany. Measurements performed in spring 2010 at two weather radar (WR) and one bird radar (fixed beam radar, FBR) site (Table 1).

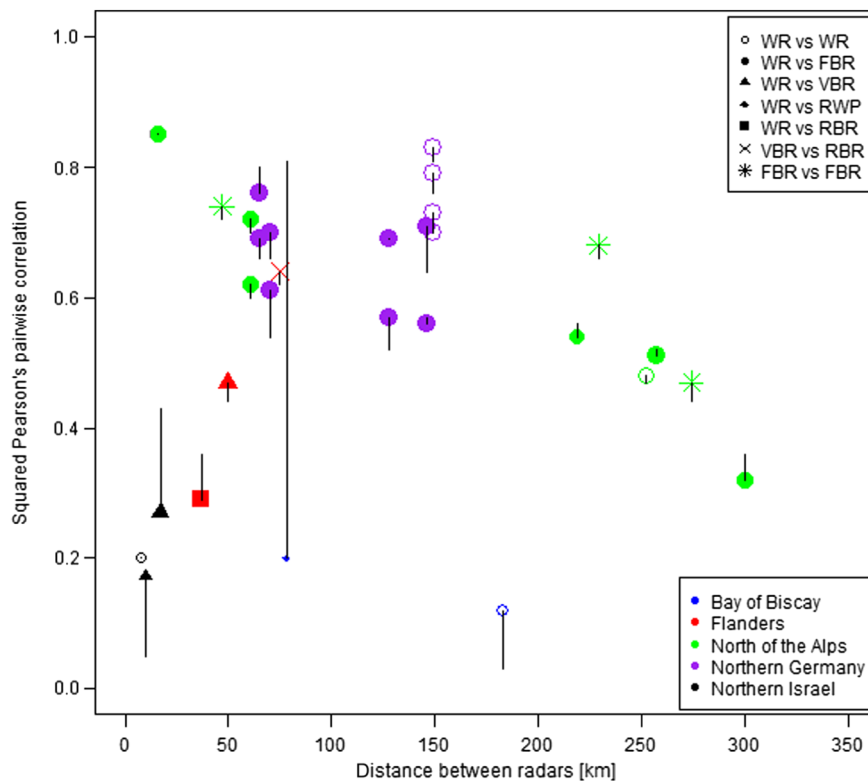


Figure 3. Correlation of parallel recordings of mean bird migration traffic rates between different radar systems in different regions, seasons, and years (Table 1) in relation to the distance between the systems. Given are the squared Pearson's correlation coefficients ( $r^2$ ) for each pair compared. Symbols represent the  $r^2$  including all height intervals available from a specific radar. The vertical lines indicate the change in  $r^2$  if only overlapping height intervals were included (Fig. 1). Colors indicate regions, filled symbols refer to comparisons between weather radar (WR) and any other radar, open symbols mark comparisons between two WRs, and 'line' symbols (crosses, etc.) represent comparisons between two bird radars. The size of the symbol is related to sample size. For abbreviations see Table 1.

were seen in comparisons within ‘northern Germany’ and the region ‘north of the Alps’. Correlations decreased significantly with increasing distance, irrespective of the systems compared ( $F=21.8$ ,  $p < 0.001$ ). A very strong relationship was found for the comparison of WR with FBR only ( $F=34.0$ ,  $p < 0.001$ ; filled circles in Fig. 3). For pairwise comparisons with a low overlap of observed heights (northern Israel, Bay of Biscay; Supplementary material Appendix 1 Fig. A1), there was a distinct increase in the squared correlation coefficient when only overlapping height intervals were considered (Fig. 3, vertical lines indicate change in  $r^2$ ). For example, in northern Israel,  $r^2$  increased from 0.21 to 0.43. At the Bay of Biscay the correlation between WR and RWP with only overlapping height intervals resulted in a similar high value as observed at other sites. Only at one site in northern Israel the low value of the coefficient dropped further (WR vs VBR). There was no considerable increase (or decrease) in correlations between pairs of sites where only a minor fraction the height bands did not match.

Figure 4 shows the pairwise comparison of absolute mean MTR by giving the proportion of the first sample in relation to the sum from both samples (see Material and methods). MTR measured by the different systems within the same region varied considerably, but were not related to the distance between two systems. WR measurements resulted

mostly in higher estimates for MTR than FBR (filled circles) and the RBR (filled square). The comparisons between WRs (open circles) provided similar MTR, and this was also the case for comparisons between WR and VBR, with the exception of northern Israel. In contrast, the WR estimates at the Bay of Biscay were much lower than the RWP estimates. Including only the overlapping height intervals did not result in a generally better consensus.

## Discussion

This broad overview confirms that in most cases bird MTR extracted from WR, when following the protocol implemented by Dokter et al. (2011), provide reliable results with respect to the relative pattern of day-to-day variation. However, MTR showed considerable differences even between sites in close vicinity to each other. Differences up to a factor four (ratios of 0.2 and 0.8 in Fig. 4) did occur between several sites. Considering only the overlapping height intervals decreased the differences only for few comparisons. WR generally showed higher MTR than most small-scale bird radar systems. Yet, one has to keep in mind that bird profiles retrieved from WR measurements do not measure single birds, but provides the total reflectivity of all birds within the

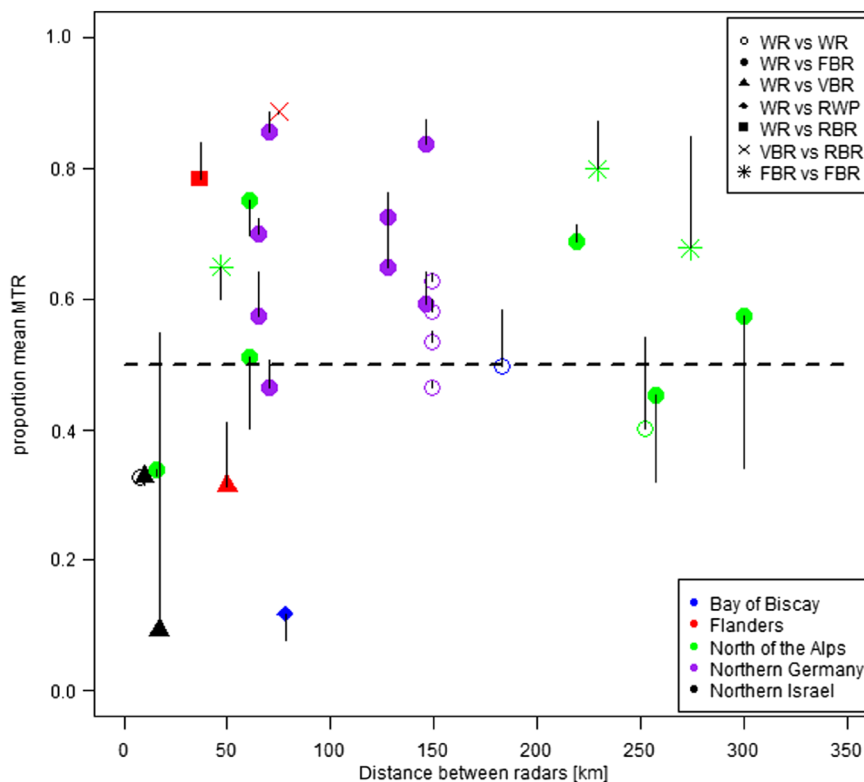


Figure 4. Pairwise comparison of seasonal mean migration traffic rate (MTR) between neighboring radar sites. The y-axis gives the proportion of the first sample in relation to the sum of both samples. The order of radar types (abbreviations are explained in Table 1) given in the legend refers to the first and second sample. The dashed horizontal line represents the case of equal MTR (0.5). Colors indicate regions, filled symbols refer to comparisons between weather radar and any other radar, open symbols mark comparisons between two weather radars, and ‘line’ symbols (crosses, etc.) represent comparisons between two bird radars, Table 1.

surveyed volume of airspace (Dokter et al. 2011). To convert reflectivity into MTR, an average bird size (radar cross section, RCS) was assumed for all sites (see Material and methods). This assumption is probably violated when comparing different sites and particularly when comparing different migration seasons and times. Underestimating the average size of birds leads to an overestimation of the number of birds involved in migration. In contrast, small scale bird radars may underestimate the number of individuals, because tight flocks are generally detected as a single target. Nevertheless, analyses of wing beat patterns of nocturnal radar targets indicate that except for dawn and dusk, most targets include only single birds (Bruderer 1997b, Larkin and Szafoni 2008). Although bird numbers were derived from the radar data by filtering non-biological scatter (e.g. precipitation) automatically, manual inspection for remaining non-bird echoes was necessary for all systems. This procedure eliminates obvious outliers, but cannot guarantee full comparability between the different datasets. Apart from these potential errors, the different sampling area sizes might also affect the comparisons between WR and the other systems. With a radius of 25 km, WR systems integrate the migratory movements within a range that is usually at least ten times larger than the one covered by the small-scaled bird radars (and RWP). Consequently, local MTR, as measured by these latter radars, are more influenced by topographical features like shorelines or mountain areas, and also by habitat types and landscape configuration in general. These potential effects are discussed in detailed for each study region.

### Northern Germany

While migration phenology was well correlated among all radar systems, seasons and years, there was a distinct difference between MTR in autumn between the two WRs and the bird radar located at the Fehmarn Belt. The comparable estimates of spring migration by all three radar systems at Fehmarnbelt, Hamburg, and Rostock may reflect the large-scale homogeneity of spring migration movements over northern Germany and the western Baltic Sea. Based on visual observations on diurnal migration, a concentration across the Fehmarn Belt was expected for the autumn season (FEBI 2013). On the contrary, migration was only about one fourth of what could be measured to the east (Rostock) and south-west (Hamburg). The fact that MTR corresponded well between all three radar sites in spring gives good supportive evidence that this discrepancy is not an artefact resulting from the different radar platforms. While migration monitored by the bird radar at the Fehmarn Belt consists exclusively of birds crossing the Baltic sea (coming from Scandinavia), the WR with their much larger surveyed range include a significant part of landbound migration coming from the northeast. This interpretation is in line with the results presented by Nilsson et al. (2019), showing that the influx of migrants from the northeast makes up the major part of nocturnal migrants tracked across northern Germany.

### Flanders

Correlations of the MTR between the radars deployed in the Belgian–French coastal area were significant, but rather low during the study period, with no improvement when only considering the overlapping height intervals. The specific habitats where these radars were set up may partially explain this observed weak correlation. The BirdScan-MR1 (VBR) was installed in a rural area at approximately 20 km from the coast. The Merlin radar (RBR) is installed on an offshore platform, and as such it only detects migrating birds at sea. The measurement volume of the WR in Jabbeke is partly inland and partly offshore. Although large numbers of birds are known to cross the North Sea (Buurma 1987, Alerstam 1990, Lensink et al. 2002, van Gasteren et al. 2002), these numbers are presumably smaller than at the coast and inland. Nevertheless, the seasonal pattern as detected by the three radars matches well, with a clear peak in MTR in early October. A storm front covering Germany and Poland at that time, resulting in (north-)easterly winds, pushed large numbers of birds to our study area (see also Nilsson et al. 2019).

We note that the difference between the WR and the VBR in absolute numbers was mainly due to intense movements at low altitudes (< 200 m a.g.l.), which was not included in the WR data (Fig. 4). There are several reasons why the absolute numbers detected by the RBR are lower compared to the WR and VBR. 1) The RBR antenna has a wavelength in the S-band spectrum (7.5–15 cm), which is less suited to register smaller birds and thus, presumably, the number of small songbirds detected by this radar is underestimated. 2) The Merlin tracking software (DeTect) of the RBR is not always able to differentiate between single birds and small groups of birds. As shown by Fijn et al. (2015), this might result in an underestimation of the MTR by up to 10%. 3) The orientation of the vertically rotating RBR antenna is along the E–W axis, which was logistically the only possibility. A radar positioning perpendicular to the main migratory routes ensures the highest detection probability for birds flying through the area (Fijn et al. 2015). Therefore, in this case MTR may have been slightly underestimated. Because no confirmed flight direction data is available in this study region, no corrections could be made for this potential bias in MTR calculations. 4) We considered RBR data up to an altitude of 3600 m a.s.l., and did not correct for a potential loss in detection probability with distance. There is no information available on target specific detection range for this type of solid state radar antenna. Thus, some small high-flying migrants might have been missed by the system. Nevertheless, based on the known radar specifications and our expert knowledge we assume that all birds, including small passerines, should have been detected up to at least a distance of 800 m. Due to the recorded height distributions by the WR and the VBR, it is unlikely that this detection loss is responsible for the low number of birds recorded by the RBR.



## Bay of Biscay

This study area comprises a highly complex topography with different climatic areas which can spatially affect or divert the migration flux. There was a poor coincidence in the temporal pattern of bird migration among all three sites compared. Nevertheless, the overall mean MTR between the two WRs was similar, but the MTR estimated by the RWP were about eight times higher. The WR at Kapildui is within a mountainous area positioned on the top of a mountain. Despite the inclusion of the negative measurement elevation ( $-0.5^\circ$ ), it cannot be ruled out that a certain proportion of birds flying below, within the valleys, would not be detected. The other WR is situated at Momuy in the lowlands, north of the Pyrenees. The RWP was located just on the coast of northern Spain. Precipitation was frequent during the study period and varied considerably between the three sites. This also had a negative impact on sample size. We assume that the low temporal consensus between the WRs results mainly from topographical and regional meteorological factors that potentially splits or deviates the migration flow. This became particularly obvious in the second half of March, which was indeed a rainy period, negatively affecting data quality by short term rain events within a night at both sites, Momuy and Kapildui. There was a huge difference in MTR along the coast monitored by the RWP compared to both WR sites inland. The RWP monitored movements just above the coastline. Local concentration of nocturnal migration along the coastline has been observed by radar and thermal imaging at several sites (Bruderer and Liechti 1998, Fortin et al. 1999, Weisshaupt et al. 2016) and therefore coastal versus inland radar positions may result in discrepancies related to such coastal concentrations of migrants. Another source of discrepancies could be differences in the radar measurements. Empirical comparisons have shown that the detection angle of a starring radar beam can be 2.5 times larger than the nominal beam width ( $-3$  dB) given by the manufacturer (Liechti et al. 1995). Thus, underestimating the surveyed volume would lead to an overestimation of MTR. However, according to the long wavelength used by the RWP (23 cm) compared to that used by the WRs (5 cm), we would expect lesser insect contamination than recorded by WR. Additional discrepancies might arise from the data level in the analysis (moments in WR vs time series in RWP). Finally, we conclude that the high intensity of migration at the RWP site is a mixture of a local concentration of birds, and the differences in the settings and features of the different radar systems.

## North of the Alps

This study region spanned a relatively large distance of about 300 km along the northern foreland of the Alps. Squared correlation coefficients between the different sites and systems were among the highest, and similar to those observed in northern Germany (Fig. 3). Most likely, squared correlation coefficients decreasing with distance are based on real differences in the migration phenology. Interestingly,

the correlation coefficients between identical radar systems (WR vs WR; FBR vs FBR) were within the range of correlations between the different systems. The good accordance of the two WR from two different countries, and thus met-offices (France and Germany) is promising for any further analyses of bird migration studies across western Europe (cf. Nilsson et al. 2019). At the two sites in Germany the temporal pattern between the WR (Memmingen) and the FBR (Bremelau) was similar ( $r^2=0.72$ ), but the mean absolute MTR differed by a factor of 3. In the Jura mountains the temporal pattern as well as the mean MTR measured by WR (Montancy) and FBR (Peuchapatte) were close to each other (Supplementary material Appendix 1 Table A1). The comparison of the two FBR sites (Peuchapatte and Provence) situated within 50 km distance, provides a valid example of how complex topography can influence the MTR of locally detected bird migration. All together these results give good evidence that differences in migration observed within this study region are predominately caused by the behaviour of the birds and not due to different radar recording systems.

## Northern Israel

Prior knowledge regarding migration intensities and other key migration features such as the direction of movement and migration altitude profile is completely lacking from this hilly and forested area that is found just east of the Mediterranean Sea. However, quantitative data regarding bird migration characteristics were collected in 1991–1992 in southern Israel, a highly arid area that is found about 250 km south of the current study region (Bruderer and Liechti 1995, Liechti and Bruderer 1995). In southern Israel, migration was recorded in two sites located 40 km apart on a west-east axis, and migration characteristics were overall very similar between these two sites. Within the hillier northern Israel, we predicted that the close proximity of the three radar sites that are located within a distance of 25 km would result in similar MTR, and consequently high correlations between the radar systems. Yet, our findings suggest a more complicated situation. Firstly, the VBR at Kiswa was positioned more than 800 m lower than the WR at Mt Meron and consequently the overlapping height intervals between the two radars was relatively small. When considering the overall MTR in both localities, the fit between these two sites was poor ( $r^2=0.21$ ), but this value doubled when data from the shared altitude range was considered ( $r^2=0.43$ , Supplementary material Appendix 1 Fig. A3). Nevertheless, these two radar systems seemed to record a similar migration phenology over this region (Supplementary material Appendix 1 Fig. A2). Moreover, MTR that were recorded by these two systems differed by about an order of magnitude and, as can be seen from the mean height distribution (Supplementary material Appendix 1 Fig. A4), this is because nocturnal bird migration was intense at low altitudes and substantially decreased with increasing altitude. Bruderer et al. (2018) found that spring migration intensities did not decrease with height for the lower 2000 m above ground in southern Israel, while our

data suggests a strong decrease with height above ground from Kisra VBR data such that about 90% of the birds flew below 800 m a.g.l., i.e. 1200 m a.s.l., resulting in a MTR in Meron WR that is only about 10% of the MTR recorded by the VBR in Kisra (Supplementary material Appendix 1 Fig. A4). This suggests that migration is not spatially homogenous, but rather strongly influenced by local topography. Hence, spring migration above northern Israel decreases sharply with increasing altitude a.s.l. with few birds passing over the high Galilee mountains, and birds rather concentrating in lower altitudes while traveling over this region. Locating WRs at high altitudes is a common phenomenon as a result of the WR need to detect mainly particles at high altitudes. This result demonstrates the limits researchers need to consider when analyzing data from WRs at high altitudes.

Data collected by the second WR at Dalton was poor in terms of the MTR values (Supplementary material Appendix 1 Fig. A3) and poorly matched to both Meron WR, that is only 6.5 km away from it, and to Kisra VBR, that was 25 km way from it. Moreover, when the shared height was compared between Dalton WR and Kisra VBR, no correlation could be detected between the data obtained by these two systems. The explanation for the large differences between data collected by the different WR radars, despite the short distance between them, relates to the different properties of the systems and their spatial position. We specifically suggest that bird detection and consequently MTR calculations from data obtained by Dalton WR, a dual-pol system, is flawed. Dalton WR suffers from serious problems of ground clutter in addition to coverage problem due to a large topographic blocking in several parts of its detection area. Also, some electronic transmission sources north of the radar within Lebanon may disrupt its detection quality (pers. comm. with radar operators). From the comparison of the MTR between Dalton WR to Meron WR and the VBR it is obvious that Dalton WR did not provide reasonable bird data. We hope that further data from this radar will allow us to better assess the reasons for the low quality of the bird data that is produced by this radar in order to try resolving this problem. This will hopefully make this WR suitable for the detection of biological scatter and consequently to reliably estimate the movement properties of flying animals in the future.

### Technical aspects

Wave-lengths used by the different radar systems ranged from 3 cm (FBR, VBR) to 23 cm (RWP). With an increasing wave-length the detection probability for small targets, like small passerines and insects, decreases. Thus, insect contamination is more likely in the radar systems FBR, VBR, and WR, whereas small passerines are more likely to be missed in RBR and RWP. However, power emitted, beam shape, receiver sensitivity and operational mode (starring or scanning) can compensate for this effect or further intensify it. In addition, insects were excluded from the FBR and VBR by the pattern of the echo signature, cf. Schmid et al. (2019). Thus, observed differences in MTR between radar systems were

not in line with potential biases related to wave-length differences. In measurements with direction specific differences in the surveyed range, like the fixed beam (FBR) and the vertical rotating beam (RBR), the resulting MTR is influenced by the flight directions. The chance to detect a bird when birds fly perpendicular or parallel to the orientation of the beam has an important impact on the resulting MTR (Fijn et al. 2015). However, as long as migratory directions are more or less constant and the orientation of the beam is approximately perpendicular to the main migratory directions, differences to directionally unbiased measurements (WR, VBR) are small. As both is true for FBR and RBR recordings, we conclude that this can explain the mismatch in absolute numbers only to a minor extent. A major source for differences in migration intensities may be the different detection ranges of the various systems. For the WR, detection probability can be regarded as constant within the range analysed (5 to 25 km, Dokter et al. 2011). The FBR and VBR system classify bird targets based on the wing flapping pattern into size-classes and applies a specific detection range to the different classes based on empirical results (Schmaljohann et al. 2008, Schmid et al. 2019), and thus corrects for a decreasing surveyed volume with distance. As mentioned above, the RBR system reconstructs tracks from consecutive scans and does not correct for decreasing detection probability with distance. Therefore, a reason for the much lower MTR might be due to a reduced detection probability for small passerines with distance, reinforced by the relatively long wave-length. For the RWP a first inventory of features and echo strengths has been provided for various targets (Weisshaupt 2015, Weisshaupt et al. 2017, 2018). However, echoes included in the MTR calculations had to be close to the beam center to be recognized as birds (Weisshaupt et al. 2017). Therefore it is unlikely that the high MTRs recorded by the RWP compared to the WRs are due a technical issue.

### Conclusion

This collection of cross-calibration analyses gives good evidence that within some limitations of accuracy the WR network can be used reliably to monitor nocturnal bird migration across Europe and the Near East. However, absolute intensities only matched in some cases and differences of up to two-fold must be accepted for the time being. More importantly, we could show that data collected from different countries by different met-offices can provide highly correlating bird profiles. Our analysis also shows that before a specific WR can be used as a grid point for modeling the spatial movement pattern of nocturnal migrants, its specific topographic position (e.g. mountain top) and ground clutter condition must be taken in to account. We note that positioning of WR on mountain tops may substantially reduce ground clutter problems, but could lead to serious underestimation of MTR of possibly an order of magnitude in the area, because migrants may circumvent a mountain range and fly along the valleys below the position of the radar. We recommend meteorologist to include scans at negative elevations for high-altitude

radars to improve the capabilities of retrieving low-altitude echoes of birds and insects. The comparison with the small-scale radar systems showed that although local conditions are strongly related to the large-scale pattern, absolute numbers of migrants can deviate locally considerably from the general average. Thus, we found good evidence that from a technical view WR data are comparable across countries on a relative and absolute scale, but the local geographical attributes must be considered carefully for each site.

The findings of this study are important for estimating absolute bird migration intensities measured by different radar systems over vast geographic areas in Europe and the Near East. Consequently, it may enable the estimation of migrant numbers in large parts of the Western-Palearctic region for long-term ecological monitoring of bird populations. This monitoring is essential for assessing population trends (Dokter et al. 2018) and for directing conservation measures to help mitigating risks for the resilience of migratory species.

*Acknowledgements* – We thank, Klaus Stephan ('Deutscher Wetterdienst' DWD), Cédric Legal (Météo France) and Günther Haase (BALTRAD, SMHI) for supporting the access to the WR data. We acknowledge the European Operational Program for Exchange of Weather Radar Information (EUMETNET/OPERA) for providing access to European radar data, facilitated through a research-only license agreement between EUMETNET/OPERA members and ENRAM. We thank Femern A/S for allowing us to publish data from the EIA (northern Germany). We thank Asaf Mayrose for facilitating radar data processing and analysis from northern Israel. We thank two reviewers for their helpful comments. *Funding* – The study was financially support by COST – European Cooperation in Science and Technology – through the Action ES1305 'European Network for the Radar Surveillance of Animal Movement' (ENRAM) for facilitating international collaboration. The Belgian case-study was part of the project RAVEN, which was funded by the Belgian Federal Science Policy office (BELSPO) under the BRAIN-be programme.

## References

- Able, K. P. 1970. A radar study of the altitude of nocturnal passerine migration. – *Bird Banding* 41: 282–290.
- Alerstam, T. 1976. Nocturnal migration of thrushes (*Turdus spec.*) in southern Sweden. – *Oikos* 27: 457–475.
- Alerstam, T. 1990. Bird migration. – Cambridge Univ. Press.
- Alerstam, T. et al. 2011. Convergent patterns of long-distance nocturnal migration in noctuid moths and passerine birds. – *Proc. R. Soc. B* 278: 3074–3080.
- Aschwanden, J. et al. 2018. Bird collisions at wind turbines in a mountainous area related to bird movement intensities measured by radar. – *Biol. Conserv.* 220: 228–236.
- Bruderer, B. 1997a. The study of bird migration by radar. Part 1: the technical basis. – *Naturwissenschaften* 84: 1–8.
- Bruderer, B. 1997b. The study of bird migration by radar. Part 2: major achievements. – *Naturwissenschaften* 84: 45–54.
- Bruderer, B. and Steidinger, P. 1972. Methods of quantitative and qualitative analysis of bird migration with a tracking radar. – In: Galler, S. et al. (eds), *Animal orientation and navigation*. NASA, pp. 151–167.
- Bruderer, B. and Liechti, F. 1995. Variation in density and height distribution of nocturnal migration in the south of Israel. – *Isr. J. Zool.* 41: 477–487.
- Bruderer, B. and Liechti, F. 1998. Flight behaviour of nocturnally migrating birds in coastal areas – crossing or coasting. – *J. Avian Biol.* 29: 499–507.
- Bruderer, B. et al. 2018. Vertical distribution of bird migration between the Baltic Sea and the Sahara. – *J. Ornithol.* 41: 282.
- Buler, J. J. and Diehl, R. H. 2009. Quantifying bird density during migratory stopover using weather surveillance radar. – *Geosci. Remote Sens. IEEE Trans.* 47: 2741–2751.
- Buurma, L. S. 1987. Patronen van hoge vogeltrek boven het Noordzegebied in oktober. – *Limosa* 60: 63–74.
- Chapman, J. W. et al. 2004. Migratory and foraging movements in beneficial insects: a review of radar monitoring and tracking methods. – *Int. J. Pest Manage.* 50: 225–232.
- Chilson, P. B. et al. 2011. Partly cloudy with a chance of migration: weather, radars, and aeroecology. – *Bull. Am. Meteorol. Soc.* 93: 669–686.
- Chilson, P. B. et al. 2012. Radar aeroecology: exploring the movements of aerial fauna through radio-wave remote sensing. – *Biol. Lett.* 8: 698–701.
- Chilson, P. B. et al. (eds) 2017a. *Aeroecology*. – Springer.
- Chilson, P. B. et al. 2017b. Radar aeroecology. – In: Chilson, P. B. et al. (eds), *Aeroecology*. Springer, pp. 277–310.
- Diehl, R. H. et al. 2003. Radar observations of bird migration over the Great Lakes. – *Auk* 120: 278–290.
- Diehl, R. H. et al. 2005. Introduction to the WSR-88D (Nexrad) for ornithological research. – In: Ralph, C. J. and Rich, T. D. (eds), *Bird conservation implementation and integration in the Americas. Proceedings of the Third International Partners in Flight Conference 2002*, pp. 876–888.
- Dokter, A. et al. 2011. Bird migration flight altitudes studied by a network of operational weather radars. – *J. R. Soc. Interface* 8: 30–43.
- Dokter, A. M. et al. 2018. Seasonal abundance and survival of North America's migratory avifauna determined by weather radar. – *Nat. Ecol. Evol.* 2: 1603–1609.
- Dokter, A. M. et al. 2019. bioRad: biological analysis and visualization of weather radar data. – *Ecography* 42: xxx–xxx.
- Drake, V. A. and Reynolds, D. R. 2012. Radar entomology. Observing insect flight and migration. – CABI.
- Drake, V. A. and Bruderer, B. 2017. Aeroecological observation methods. – In: Chilson, P. B. et al. (eds), *Aeroecology*. Springer, pp. 201–238.
- Eastwood, E. 1967. *Radar ornithology*. – Methuen.
- FEBI 2013. Fehmarnbelt fixed link EIA. Bird investigations in Fehmarnbelt – baseline. – Volume III, Bird migration, Report no. E3TR0011, <<http://vwm.femern.de/27.%20E3TR0011%20Vol%20III8fd1.pdf?filename=files/BR/27.%20E3TR0011%20Vol%20III.pdf>>.
- Fijn, R. C. et al. 2015. Bird movements at rotor heights measured continuously with vertical radar at a Dutch offshore wind farm. – *Ibis* 157: 558–566.
- Fortin, D. et al. 1999. Variation in the nocturnal flight behaviour of migratory birds along the northwest coast of the Mediterranean Sea. – *Ibis* 141: 480–488.
- Frick, W. F. et al. 2017. The lofty lives of aerial consumers: linking population ecology and aeroecology. – In: Chilson, P. B. et al. (eds), *Aeroecology*. Springer, pp. 379–399.



- Gauthreaux, S. A. 1975. Radar ornithology: bird echoes on weather and airport surveillance radars. – NASA STI/Recon Technical Report 75: 30397.
- Gauthreaux, S. A. and Belser, C. G. 1998. Displays of bird movements on the WSR-88D: patterns and quantification. – *Weather Forecasting* 13: 453–464.
- Gauthreaux, S. A. et al. 2003. Using a network of WSR-88D weather surveillance radars to define patterns of bird migration at large spatial scales. – In: Berthold, P. et al. (eds), *Avian migration*. Springer, pp. 335–346.
- Griffin, D. R. 1973. Oriented bird migration in or between opaque cloud layers. – *Proc. Am. Phil. Soc.* 117: 117–141.
- Horn, J. W. and Kunz, T. H. 2008. Analyzing NEXRAD doppler radar images to assess nightly dispersal patterns and population trends in Brazilian free-tailed bats (*Tadarida brasiliensis*). – *Integr. Comp. Biol.* 48: 24–39.
- Horton, K. G. et al. 2016. An assessment of spatio-temporal relationships between nocturnal bird migration traffic rates and diurnal bird stopover density. – *Mov. Ecol.* 4: 1–10.
- Huuskonen, A. et al. 2014. The operational weather radar network in Europe. – *Bull. Am. Meteorol. Soc.* 95: 897–907.
- Kelly, J. F. et al. 2012. Quantifying animal phenology in the aerosphere at a continental scale using NEXRAD weather radars. – *Ecosphere* 3: art16.
- La Sorte, F. A. et al. 2017. Seasonal associations with urban light pollution for nocturnally migrating bird populations. – *Global Change Biol.* 23: 4609–4619.
- Lack, D. and Varley, G. C. 1945. Detection of birds by radar. – *Nature* 156: 446.
- Larkin, R. P. and Szafoni, R. E. 2008. Evidence for widely dispersed birds migrating together at night. – *Integr. Comp. Biol.* 48: 40–49.
- Lensink, R. et al. (eds) 2002. *Vogeltrek over Nederland*. – Schuyt and Co.
- Leskinen, M. et al. 2011. Pest insect immigration warning by an atmospheric dispersion model, weather radars and traps. – *J. Appl. Entomol.* 135: 55–67.
- Liechti, F. and Bruderer, B. 1995. Direction, speed and composition of nocturnal bird migration in the south of Israel. – *Isr. J. Zool.* 41: 501–515.
- Liechti, F. et al. 1995. Quantification of nocturnal bird migration by moonwatching: comparison with radar and infrared observations. – *J. Field Ornithol.* 66: 457–468.
- Liechti, F. et al. 1996. Herbstlicher Vogelzug im Alpenraum nach Mondbeobachtungen – Topographie und Wind beeinflussen den Zugverlauf. – *Ornithol. Beobacht.* 93: 131–152.
- Lowery, G. H. 1951. A quantitative study of the nocturnal migration of birds. – *Univ. Kansas Publ. Mus. Nat. Hist.* 3: 361–472.
- Mirkovic, D. et al. 2016. Electromagnetic model reliably predicts radar scattering characteristics of airborne organisms. – *Sci. Rep.* 6: 35637.
- Nilsson, C. et al. 2018. Field validation of radar systems for monitoring bird migration. – *J. Appl. Ecol.* 278: 3074.
- Nilsson, C. et al. 2019. Revealing patterns of nocturnal migration using the European weather radar network. – *Ecography* 42: xxx–xxx.
- Nisbet, I. C. T. 1963. Quantitative study of migration with 23-centimetre radar. – *Ibis* 105: 435–460.
- North, G. R. (ed.) 2015. *Encyclopedia of atmospheric sciences*. – Academic Press.
- Rennie, S. J. 2014. Common orientation and layering of migrating insects in southeastern Australia observed with a Doppler weather radar. – *Meteorol. Appl.* 21: 218–229.
- Riley, J. R. and Reynolds, D. R. 1983. A long-range migration of grasshoppers observed in the Sahelian zone of Mali by two radars. – *J. Anim. Ecol.* 52: 167–183.
- Schmaljohann, H. et al. 2008. Quantification of bird migration by radar – a detection probability problem. – *Ibis* 150: 342–355.
- Schmid, B. et al. 2019. Size matters in quantitative radar monitoring of animal migration: estimating monitored volume from wingbeat frequency. – *Ecography* 42: xxx–xxx.
- Suter, E. 1957. Radar Beobachtungen über den Verlauf des nächtlichen Vogelzuges. – *Rev. Suisse Zool.* 64: 294–303.
- van Doren, B. M. and Horton, K. G. 2018. A continental system for forecasting bird migration. – *Science* 361: 1115–1118.
- van Gasteren, H. et al. 2002. Kwantificering van vogelbewegingen langs de kust bij Umuiden: een radarstudie. – Ministerie van Verkeer en Waterstaat, Directie Noordzee.
- van Gasteren, H. et al. 2008. Extracting bird migration information from C-band Doppler weather radars. – *Ibis* 150: 674–686.
- Weisshaupt, N. 2015. Analysis of wind profiler data in the context of bird migration. – STSM report, Cost Action ES1305-European Network for the Radar surveillance of Animal Movement (ENRAM), <[www.enram.eu/stsm/](http://www.enram.eu/stsm/)>.
- Weisshaupt, N. et al. 2016. Nocturnal bird migration in the Bay of Biscay as observed by a thermal-imaging camera. – *Bird Study* 63: 533–542.
- Weisshaupt, N. et al. 2017. Radar wind profilers and avian migration. A qualitative and quantitative assessment verified by thermal imaging and moon watching. – *Methods Ecol. Evol.* 8: 1133–1145.
- Weisshaupt, N. et al. 2018. Time-series based approach to identify and process biological targets in radar wind profiler data for cross disciplinary purposes. – *Proceedings of the European Conference on Radar in Meteorology and Hydrology (ERAD)*, Ede-Wageningen, Holland.
- Zaugg, S. et al. 2008. Automatic identification of bird targets with radar via patterns produced by wing flapping. – *J. R. Soc. Interface* 5: 1041–1053.

Supplementary material (Appendix ECOG-04041 at <[www.ecography.org/appendix/ecog-04041](http://www.ecography.org/appendix/ecog-04041)>). Appendix 1.