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Key-words:	Bird migration, Radar monitoring, Ground speed, Migration traffic rate, Nocturnal migration, Flight Behavior, Weather radar, Environmental assessment studies

Field validation of radar systems for monitoring bird migration

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Abstract

1. Advances in information technology are increasing the use of radars as a tool to investigate and monitor bird migration movements. We set up a field campaign to compare and validate outputs from different radar systems.
2. We compare the pattern of nocturnal bird migration movements recorded by four different radar systems at a site in southern Sweden. Within the range of the weather radar (WR) Ängelholm, we operated a "BirdScan" (BS) dedicated bird radar, a standard marine radar (MR), and a tracking radar (TR).
3. The measures of nightly migration intensities, provided by three of the radars (WR, BS, MR), corresponded well with respect to the relative seasonal course of migration, while absolute migration intensity agreed reasonably only between WR and BS. Flight directions derived from WR, BS and TR corresponded very well, despite very different sample sizes. Estimated mean ground speeds differed among all four systems. The correspondence among systems was highest under clear sky conditions and at high altitudes.
4. *Synthesis and applications:* All of the systems provide useful information on nocturnal bird migration, but have distinctly different strengths and weaknesses. WR continuously detects avian biomass flows across a wide altitude band, making it a useful tool for monitoring and predictive applications at regional to continental scales that do not rely on resolving individuals. BS and MR's strengths are in local and low altitude applications, such as collision risks with man-made structures and airport safety, although MR should not be trusted for absolute intensities of movement. In quantifying flight behavior of individuals, TR is the most informative.

Keywords:

Bird migration, Radar monitoring, Ground speed, Migration traffic rate, Nocturnal migration, Flight Behavior, Weather radar, Environmental assessment studies.

Introduction

Radar is a powerful tool to observe and track animals. It requires no tags or handling and can be used to remotely observe the movements of free-flying animals (birds, bats and insects). Radar is particularly suitable for monitoring migratory movements, as these typically take place at high altitudes and during the night, which are ideal conditions for radar monitoring but make other types of observations difficult.

Technological advances have made both radars and radar data more accessible, leading to an increased use of marine radars, dedicated bird radars and weather radar networks to monitor animal movements and migration passage, especially in environmental assessment studies. Common applications include monitoring of bird movements in relation to collision risks with man-made structures, in particular wind farms (Plonczkier & Simms 2012; Fijn *et al.* 2015); bird strike prevention, with radars being used at airports to avoid collisions during take-off and landing (Gerringer, Lima & Devault 2016); and identifying hotspots of animal movement to inform airport management, as well as measuring high-altitude migration intensities for subsequent issuing of flight restrictions for military training flights (Van Belle *et al.* 2007).

The most recent development in radar ornithology has been an increased focus on using weather radar for bird movement studies (Shamoun-Baranes *et al.* 2014; Bauer *et al.* 2017) . Consequently, weather radar data are increasingly utilized by biologists, supplying a completely new spatial and temporal coverage of bird migration movements, and offering new possibilities for monitoring applications (Dokter *et al.* 2011; Horton, Shriver & Buler 2014; Bauer *et al.* 2017). These new applications include monitoring of flyways for dispersal of pests and disease (Bauer *et al.* 2017), large scale attraction of migrants to artificial light (Van Doren *et al.* 2017), identifying stopover sites for informing conservation (Buler & Dawson 2014) and using weather radar as a monitoring tool for assessing long-term population changes (Bauer *et al.* 2017).

Despite the recent popularization of radar monitoring, extensive cross-validation of animal movement data obtained by different radar systems have been sparse (Dokter *et al.* 2011, 2013). Several studies have compared small-scale radars with visual observations and infrared detection (eg. Gauthreaux et al. 2006; Schmidt et al. 2017). We present the first large-scale, co-located calibration campaign with several radars dedicated to tracking biological targets at a single site. We evaluate the strengths and weaknesses of four different radar systems and provide recommendations for using radar systems to monitor bird movements, with particular focus on nocturnal migration.

Methods

During September–October 2015 we deployed three small radar systems dedicated to extracting bird signals at a site approximately 22 km from the weather radar Ängelholm (fig. 1, table 1). The site (56˚16'51 N, 12˚31'38 E) is part of the Kullaberg nature reserve located on the southern slope of the Kullaberg ridge, in southern Sweden.

Due to ground clutter interference, we limited most of the analyses to data from two altitude intervals where there was good coverage from all systems: 200-800 meters above sea-level (asl) and 800-1400 m asl ('low' and 'high', respectively). This will exclude some low and high-flying migrants. We also limited the analysis to nighttime, where nights were defined as starting at 17:00 and ending at 08:00, local time (CEST). Sunset/sunrise occurred at 19:48/06:30 at the start and 17:31/08:16 at the end of the sampling period (9 September to 31 October 2015). Throughout this study we use Migration Traffic Rate (MTR) to compare migration intensity among the different systems. MTR represents the number of birds passing over a virtual transect, perpendicular to the migration direction, of 1 km within an hour (Lowery 1951; Bruderer 1971). We chose MTR as the main way of describing migration intensity as it was reliably available from all radar systems (except the tracking radar, which was not used for intensity comparisons). MTR is a flux measure combing both bird density (birds per volume) and bird speed, reflecting the number of birds passing through a given area.

Weather radar (WR)

The dual-polarization weather radar Ängelholm (56° 22' 3" N, 12° 51' 6" E, fig. 1, table 1) is part of the Swedish weather radar network. It operates at C-band (5.35 cm wavelength) and the antenna is 209 m asl. The radar operates in 5 minute cycles, in which the atmosphere is scanned at 10 different elevation angles ranging from 0.5 to 40 degrees. Radial velocities of objects detected by the radar are collected as well as radar reflectivities.

Bird profile extraction

Vertical profiles of birds (VPBs) were calculated following Dokter et al. 2011, and only briefly described here. Reflectivity factors (dBZ) were converted to reflectivity η (cm^2/km^3), and averaged into 200 m altitude bins from resolution volumes identified as containing biological scattering only, including ranges up to 25 km. Lowest altitude bin includes samples from 244 to 400m asl, with 244 meter being the lowest surveyed altitude at 5 km range. Bird speed and direction were calculated using a volume velocity processing (VVP) technique (Waldteufel & Corbin 1978; Holleman 2005). Bird density was obtained by dividing the averaged η value by a radar cross section of 11 cm^2, which was the average cross section of nocturnal migrants determined during a validation campaign spanning a full autumn and spring in western Europe (Dokter et al. 2011). As opposed to the other radar systems used in this study, scattering due to rain (as well as insects) is removed automatically, using criteria based on reflectivity and radial velocity texture for target identification. One additional post-processing step was applied to minimize the risk of rain contaminations. When 80% of the profile in the 0-2 km range measured a reflectivity factor of > 7 dBZ (a conventional lower threshold used by meteorologists for precipitation) we assumed it was raining and no bird data were calculated.

For each vertical bird profile, MTR (individuals/km/h) in each altitude bin was calculated by multiplying bird density (individuals/km^3), flight speed (km/h) and the height of the bin (0.2 km). The MTR of altitude bins in each altitude interval (low and high) were summed to obtain the total migration traffic rates in these two larger altitude bands of interest. Finally, we averaged these band-specific MTRs into nightly averages.

For calculating the mean ground speed and mean flight direction per night and altitude interval (low and high) only nights with 5 or more altitude bins containing a bird density higher than 5 birds per km^3, were included. This excluded 16 out of 55 nights in the low altitude interval and 31 out of 55 nights in the high altitude interval.

BirdScan (BS)

A BirdScan-MR1 ornithological radar (BS) from the Swiss Ornithological Institute was operated during the entire campaign, from the 1 September–5 November, 24h per day. BirdScan-MR1 is a newly developed vertical-looking radar system designed to monitor bird movements in real-time (Swiss-BirdRadar.com). BirdScan-MR1 is a 25kW pulsed X-band radar (9.4 GHz) based on a commercial marine radar (table 1). The radar was operated in short pulse (65 ns, range resolution 7.5m, PRF 1800 Hz) and long pulse (750 ns, range resolution 110m, PRF 785 Hz) modes. With a nutation of 2°, the rotating antenna tracks objects within the radar-beam and retrieves information on flight direction and ground speed. BirdScan-MR1 uses characteristics of the echo signature to classify tracks as bird or non-bird, and further classifies birds based on the wing-beat pattern as 'passerine-type' and 'wader-type' (Zaugg et al. 2008). We computed migration traffic rates, accounting for distance (height) dependent detection probabilities for the different sized classes (Schmaljohann et al. 2008).

In this study, the BirdScan-MR1 radar detected echoes using four operation modes of 15 minutes each: static short-pulse, rotating short-pulse, static long-pulse, and rotating long-pulse. We restricted the computation of MTR to echoes detected using short-pulse at 200 - 800 m asl because the maximal detection range of small birds under short-pulse does not exceed 800 m. At 800 - 1400 m asl, we used echoes detected using long-pulse only. We computed no MTR if the effective monitoring time fell below 5 min per 30 min protocol period (short- or long-pulse) because of rain or technical shut-down. Data on flight behavior are only retrieved under rotating mode. Means per night were used in this study if at least 10 bird tracks were available. See supplement for additional technical details of the BirdScan-MR1 system.

Vertical scanning marine bird radar (MR)

The marine radar system operated from 5–17 October 2015, 24h per day. The radar (manufacturer: GEM, Italy) is a 25 kW X-band radar (9.1 GHz), with a 2.17m T-bar antenna (nominal beam width of 22° in elevation and 1° in azimuth) rotating with 34 revolutions per minute (RPM) (table 1). The antenna was oriented vertically (horizontal rotation with an additional antenna was not possible due to ground clutter), with the rotation plan along North-South (the expected main flight direction) in order to detect longer trajectories of the birds. With only vertical rotation it is not possible to determine the direction of a bird flying across the radar beam, which sets limitations on the use of some of the produced information (in particular the track length and speed). During data collection, the radar operated in long pulse mode (200 ns and PRF 1000 Hz).

It is not possible to access the raw data from the marine radar, as the acquisition software ExtraSea (from the radar manufacturing company GEM) automatically pre-processes the raw data, directly returning the visual result of this processing (green moving echoes on the screen) (see supplement for details). The visual output of the acquisition software was recorded continuously by using a screen capture software (NCH). We processed the recorded video using the R-package RadR (Taylor et al. 2010) (R Core Team 2017) to reconstruct bird tracks from the subsequently recorded echoes potentially originating from the same individual bird trajectories. To exclude insects, we ignored tracks shorter than 200 meters and with less than four consecutive echoes. In addition, we also excluded tracks within 300 m from the radar and tracks characterized by a ground-speed lower than 30 km/h and higher than 100 km/h (Bruderer & Boldt 2001; Schmaljohann et al. 2008).

The number of tracks processed by RadR (not the number of echoes) theoretically corresponds to the number of detected objects. However, with increasing track duration, RadR tends to split tracks of single objects into more than one track. This trend is intensified with an increasing number of simultaneous echoes. Thus, an overestimation of the number of tracks can occur, leading to a greater increase in the numbers of tracks as the number of actual targets increases.

To calculate MTR, we assumed that all birds crossed the beam parallel to the rotation axis of the radar (N-S). We used the estimated beam width at 100 m altitude layers to weight the number of echoes and compute MTR. To calculate the ground speed, we also assumed that the birds flew parallel to the rotation axis of the radar. We thus underestimate the track length, and thereby ground speed, for birds with flight direction that deviate from the N-S axis.

Tracking radar (TR)

A manually-operated tracking radar was operated during 8 nights (7, 9, 28, 30 September and 3, 7, 11, 14 October). The tracking radar tracks individual birds, following one target at a time; it is a mobile 200 kW X-band radar (0.25 µs pulse duration, PRF 504 Hz, 1.5˚ beam width). Targets are located manually by an operator scanning the sky and then automatically tracked from 1-10 minutes. During tracking the exact position of the target is recorded every second, giving precise measurements of flight altitude, ground speed and track direction. Targets are classified as non-bird, bird, passerine or flock by the operator based on the characteristics of the echo signature (e.g., temporal variation in the echo intensity) representing, in case of a single bird, the wing-beat pattern. Methods closely resembled those in Karlsson et al. (2012) and Bäckman & Alerstam (2003).

All birds, passerines and flocks are included in this comparison. Only nights with more than 10 birds tracked were included in the nightly means. The tracking radar was used in the comparisons of track directions and ground speed. The manual selection of object to track and duration of tracking, may introduce biases in the numbers of targets tracked. Therefore, the tracking radar data were not used to estimate migration intensity or for comparisons of altitude distributions.

Falsterbo ringing (FBO)

Falsterbo (55° 22' 27" N, 12° 48' 29" E, fig. 1) bird observatory has a long-standing ringing regime, with standardized mist net captures since 1980 (Karlsson 2009). Mainly actively migratory birds are caught as the immediate area is not suitable for stopover and has few resident birds (Zehnder & Karlsson 2001). As an approximate estimate of migration intensity, the total number of birds ringed in the lighthouse garden during the morning immediately following the night in question was used (e.g., for the night between 5 and 6 September, ringing on the morning of 6 September was used). Ringing starts half an hour before sunrise and continues for at least 6 hours (Karlsson 2009). All species are included in the total sum of birds.

Weather stations and rain filtering

We retrieved hourly rain measurements from two SMHI weather stations in the nearby area (http://opendata-catalog.smhi.se/explore, fig. 1): Hallands Väderö (56° 26' 58" N, 12° 32' 49" E, 18 km North from the field site), and Helsingborg A (56° 1' 49" N, 12° 45' 55" E, 30 km South-East from the field site). We used data from the station with the largest amount of rain recorded per night in the comparisons, and a night was counted as a "rain night" if any precipitation was measured at either station during the night. This was to make sure that also nights with very light rain would be included, as light rain could pose a challenge to the bird detection algorithms.

There are principal differences in how the weather radar bird algorithm, BirdScan and marine radar filters out precipitation (table 1). For the weather radar, the algorithm extracting bird echoes filters out events with precipitation automatically. Cases with light precipitation are most challenging to filter out, especially when reflectivity values are similar to those observed in bird migration. Precipitation may therefore be classified as birds on some rare occasions. BirdScan works with a threshold of occupied cells, above which track detection is stopped. However, before the threshold is reached, false tracks are recorded and sometimes wrongly classified as birds. Therefore, the raw track time series is checked manually to exclude events with notable false echoes. For the marine radar data, events with precipitation were manually excluded from the analysis by visual inspection. The tracking radar did not operate during rain events.

Statistics

To investigate under which circumstances the relative patterns of MTR among systems was most robust, we used model II major axis regressions in R package lmodel2 (Legendre 2018). We compared the match among systems on nights with and without rain and, for all nights, at low and high altitudes.

Differences in absolute MTRs among systems were tested with Wilcoxon signed rank tests using R version 3.4.1 (R Core Team 2017).

To investigate flight speeds we tested the measured mean ground speed per night among the different radar systems in pairwise t-tests (R Core Team 2017). Correlations of flight directions over the season were tested with circular correlations using the R package "circular" (Agostinelli & Lund 2013). The nightly mean directions were tested against each other with Moors paired test for circular data in Oriana 4.0 (Kovach Computing services, Anglesey, UK).

Results

Migration intensity

We compared the measured intensity of migration among three of the radar systems (WR, BS, MR) based on the mean migration traffic rate (MTR) per night (fig. 2 and table 2). The tracking radar was not included in the comparison of intensities. The relative intensity of migration and detection of peak nights corresponded well among the three radar systems from which intensity measures were available (WR, BS, MR), fig. 2 and table 2. Absolute MTRs differed significantly among all three systems at low altitude (Wilcoxon signed rank tests; WR-BS: $v=268$, $p < 0.001$, WR-MR; $v=78$, $p < 0.001$, MR-BS; $v=78$, $p < 0.001$). Absolute MTRs corresponded well between BirdScan and weather radar at high altitudes, but the marine radar differed significantly from both (fig. 2; Wilcoxon signed rank tests; WR-BS: $v=548$, p=N.S., WR-MR; $v=78$, $p < 0.001$, MR-BS; $v=78$, $p < 0.001$). The marine radar provided generally much higher MTRs than the other systems (note the secondary y-axis in fig. 2). Correlations were stronger for the high altitude interval (table 2, above the diagonal). The mean MTRs also matched reasonably well with the total number of ringed birds at Falsterbo bird observatory (fig. 2, table 2). It is important to note that there are many reasons to expect significant differences between birds sampled in the air during active migration and birds caught on the ground at a site further south, and we don't expect them to match perfectly. However, a high correlation has been found between number of birds ringed and birds aloft at this site (Zehnder & Karlsson 2001). On nights with no rain, the measured migration intensities from all the systems, including ringing at Falsterbo, clearly matched better than on the nights with rain present (supplement, table S1 and table S2).

Altitude distribution

We compared the distribution of migration intensity (MTR) across altitude to see whether the vertical profiles differed among systems (fig. 3). We compared the weather radar and BirdScan over the entire season, and the weather radar, BirdScan and marine radar during the period of the marine radar deployment (5-16 October). The relative mean MTRs at different heights were highly correlated among all systems (model II major axis regressions, entire season: WR & BS r^2= 0.91, time of MR deployment: WS & BS r^2= 0.92, WR & MR r^2= 0.97, BS & MR r^2= 0.85). The BirdScan showed a higher proportion of MTRs at the lowest altitude bin (200-400 m asl) (fig. 3). The difference in mean MTR between the BirdScan and the marine and weather radar was also much greater in the lowest altitude bin. The difference between weather radar and BirdScan is more prominent during clear nights than during nights with rain (supplement, fig. S1).

Ground speed

Mean ground speed per night varied considerably among all the systems (fig. 4). Speeds derived from the BirdScan were significantly higher than those from the weather radar at low ([all tests pairwise t-tests] $t_{(df=23)}$ = -10.35, p < 0.000) and high altitudes ($t_{(df=13)}$ =-5.93, p < 0.05). Tracking radar mean speed differed from weather radar data at low ($t_{(df=4)}$ = -4.50, p = < 0.05) and high altitudes ($t_{(df=3)}$ = -4.15, p < 0.05). Results from the tracking radar did not differ from the BirdScan estimates at low altitude ($t_{(df=3)}$ = 1.21, p = 0.31), and there were not enough nights to test at high altitude. The marine radar speeds did not differ significantly from the weather radar at low ($t_{(df=9)}$ =1.55, p = 0.11) or high altitudes ($t_{(df=4)}$ =2.02, p = 0.16). There were not enough nights to test the marine radar with the other systems.

The overall mean groundspeed was, at low altitude, WR: 8.6 ±2.2 m/s, BS: 12.8 ±3.4 m/s, MR: 8.7 ±1.2 m/s, TR: 14.4 ±3.0 m/s and at high altitude WR: 11.9 ±2.8 m/s, BS: 15.5 ±2.6 m/s, MR: 8.8 ±0.2 m/s and TR: 12.8 ±3.6 m/s. The weather radar gives only the average speed of the entire scan volume at a specific height interval, while the other radars measure speeds of individuals (directly or indirectly). Weather radar thus measures the average ground speed of many individuals, which is lower than the ground speed of individuals when individuals fly in varying directions within the scan volume. To estimate the size of this effect we used the system with likely the most reliable speed measurements (TR) and calculated mean speeds per night by averaging the Cartesian speed components of the individuals per night, as well as the individual speeds. The average difference between these two methods was 0.96 m/s per night (8 nights, sd=0.66), which only partially accounts for the low speeds on the weather radar (mean absolute differences at low altitude: WR and BS: 4.38 m/s (24 nights), WR and TR 4.68 m/s (5 nights), WR and MR: 0.56 m/s (10 nights); high altitude: WR and BS: 4.00 m/s (14 nights), WR and TR 3.01 m/s (4 nights), WR and BS: 2.58 m/s (5 nights)).

Flight direction

Mean track directions per night were well correlated among the three systems (WR, BS, TR) at both altitudes (fig. 5, supplementary table S3) with R^2 values ranging from 0.67 to 0.84. Overall mean directions and circular standard deviations at low altitude were WR: 204˚ (n=25, sd=37˚), BS: 195˚ (n=24, sd=26˚) and TR: 199˚ (n=5, sd=26˚) and high altitude: WR: 194˚ (n=15, sd=23˚), BS: 196˚ (n=14, sd=20˚) and TR: 190˚ (n=4, sd=11˚). Paired tests showed that the weather radar and BirdScan were significantly different (supplementary table S3), however they were still highly correlated with very similar mean directions during most nights (fig. 5, supplementary table S3). The overall mean directions fit well with the expected migration direction in the area (Sjöberg & Nilsson 2015). There is more variation in directions at low altitude compared to high altitude, both between nights and within nights (fig. 5). The weather radar shows less variation within nights (smaller sd) than the BirdScan and the tracking radar. This is expected as the weather radar bird profile only gives an average direction for each scan volume, while the tracking radar and BirdScan are based on individual directions.

Discussion

Migration intensity

The monitoring of the intensity of bird movements requires an unbiased method that can account for distance-dependent detection probabilities (Schmaljohann *et al.* 2008). In this study, we show that weather radar, BirdScan and marine radar provide reliable measures of relative MTR over the season, and weather radar and BirdScan provide reliable measures of absolute MTR.

Overall the weather radar and BirdScan matched well, but there were some discrepancies at low altitude. We should keep in mind that the air volume scanned by the weather radar is very much larger than the volume scanned by the other systems. For instance, the range of the weather radar (radius of 25 km) extended out over sea, whereas the BirdScan (radius 500m) detected only birds that flew over land. The overall good agreement of absolute migration intensity retrieved from the weather radar and the BirdScan confirm previous results comparing two similar radar systems (Dokter et al. 2011).

In the weather radar measurements, stationary components, such as residual clutter contributions to the signal of resolution volumes (e.g. due to imperfect Doppler filtering), as well as non-migratory bioscatter (e.g. bats foraging around a roost), have an average radial velocity near zero, which will bias speeds downward, but also bias densities upward by the same proportion. The product of speed and density, the migration traffic rate, is therefore expected to be largely free from stationary components, and thus we recommend using MTR to report migration intensity.

The most serious outlier in terms of absolute MTR values was the marine radar, and two issues contribute to the exaggerated MTR values. Firstly, the MTR calculation is sensitive the alignment of the vertical rotation axis and the main flight direction of birds. The marine radar was oriented N-S, while the mean flight direction during this period was SSW-SW (fig. 2). The radar thus surveyed a narrower air column relative to the birds tracks than if the beam would have been aligned perpendicular to the mean flight direction (supplement, fig. S2). Quantitative measurements with vertically rotating marine radar are more reliable when the axis of rotation is adjusted perpendicular to the expected main flight direction, because the theoretical length of the transect varies in relation to the sine of the angular difference between flight direction and rotational axis. The same deviation therefore causes much less variation in the transect length at 90° than around 0°. Whenever possible, nightly mean flight directions should be considered for calculating migration intensities with marine radar data. Secondly, the processing software used, RadR, tends to split long tracks into several tracks, causing an overestimation of the number of tracks, also inflating the MTR. This is more likely to happen with high migration intensity, because the automatic algorithm for a proper allocation of blips of consecutive scans to individual tracks seems to be overstrained. This accords well with the serious overestimates during peak migration nights (fig. 2).

Precipitation had a negative impact on the correlations among the systems, which we believe is mainly due to differences in the exclusion of these events among the systems. The decreased match on nights with rain could be due to either rain contamination of the actual measurements, or that the lower migration intensity on rain nights in itself decreases the match among the systems. At low migration intensities there might also be more spatial structure in the migration, leading to variation between small-scale (BS and MR) and large-scale systems (WR). Heavy rain situations are usually well filtered out, and as migration seldom occurs during heavy rain situations (eg Erni et al. 2002), there is little risk of excluding significant migration. Light rain can pose more of a problem, as it can produce weak and varying targets that may sometimes be mistaken for co-occurring migration (however, manual checking of the data easily identifies cases like this). Mainly for non-polarimetric weather radars, variable rain patterns within the volumes are in some cases hard to automatically distinguish from light migration. This distinction is greatly simplified in the new generation polarimetric radars (in this study no polarimetric products were used). However, with respect to the impact of weather on extracted migration intensities, we encourage manual plausibility checking of processed data by trained researchers for all three types of radar systems. The correlation with Falsterbo ringing data also decreases on nights when rain is present. This could be due to rain contamination in the data, but it could also be that ringing in Falsterbo and the passage of migrants over the Kullaberg area are less well correlated on nights with unfavorable conditions for migration and lower overall migration activity.

Altitude

Relative altitudinal distributions matched quite well among the three systems compared (fig. 3). Only at the lowest height bin investigated (200-400m asl) did BirdScan show higher intensities than the weather radar, especially on nights without rain (fig. S1).

The weather radar could potentially have reduced coverage in the lowest scans because masks used to remove ground clutter could also mask low flying migratory movements. The topography can locally influence the height distribution of migratory birds and the surveyed area of the WR includes important variation in topography and a prominent part over sea. Hence, the height distribution observed by the BirdScan may not be representative of the entire area covered by the weather radar.

Even though not obvious from this study, the upper detection limit of marine radars could make them miss some high altitude migration, see Dokter *et al.* 2013. Although the marine radar sampled the same area as the BirdScan, the marine radar showed proportionally lower movement intensity at the lower altitude bin than the BirdScan. Ground clutter and low sensitivity settings generally used to mask ground clutter could also reduce the detection probability of small nocturnal passerines migration in the marine radar. The relative migration intensity of the weather radar and marine radar matched well, also in the lowest altitude bin.

Accurate information of migration intensity at low altitude (below 200 m above ground) is crucial for impact assessment studies aiming to estimate collision rates with human-made structures. In that perspective, the vertical-looking antenna of the BirdScan provides a clear advantage to monitor low-flying migration movements, as it minimizes the effect of ground clutter.

Ground Speed

Ground speed showed variation among all systems (WR, BS, MR and TR), and should be interpreted with caution at the moment. Since the tracking radar measures speeds of individuals directly, we are confident that the speeds registered by the tracking radar reflect "true" ground speeds. However, the tracking radar samples only a small proportion of the total migration and may not be fully representative of all migration movements. For instance, it is possible that larger targets are slightly overrepresented, leading to an upwards bias in the speeds measured by the tracking radar.

In general, the weather radar showed lower ground speeds than the tracking radar. The underestimation of ground speed from the weather radar is not surprising, as the calculation of ground speed is based on the radial velocities of all birds included in a measurement volume. Only if all birds flew in exactly the same direction, would true mean ground speed be measured. This issue is similar for both the weather radar and the marine radar in vertical mode, and they also show quite similar speeds. We estimated this effect by calculating mean ground speed in a similar way with the tracking radar data, but found that there was still a difference even with this effect taken into account. The lower speed on weather radar would also increase with larger scatter in flight directions, as typically observed at lower altitude compared to high altitude, and when bird movements are influenced by topography. At low altitudes, it is also possible that a limited amount of clutter mixed in with the relatively weak bird signals (collected at close ranges from the radar) can explain some of the lower speeds detected by weather radar. We conclude that mean ground speeds derived from weather radar are reliable when directional scatter is small.

Ground speeds provided by the BirdScan matched tracking radar data at low altitude, but were overestimated at high altitudes. The overestimated ground speeds somewhat exceeds previously observed values from former studies in this area (eg Nilsson, Bäckman & Alerstam 2014). The estimated speed depends on the measured transit-time of the bird within the beam (duration of echo), as well as the estimated beam width at the flight altitude. At low altitudes, the beam width is well defined; in contrast, towards the edge of the detection range small differences in the echo size can provide important differences in the estimated beam width. Without going into further details, the overestimated speeds indicate that the true beam width at high altitude should be somewhat smaller than applied in our calculations. However, the beam width not only varies with altitude, it also depends on the birds' detection probability (which varies with size, shape and behavior), leading to uncertainty in the calculated ground speeds. Until further improvements have been made to estimate the true echo size and the beam width, BirdScan estimates of ground speeds for high-flying birds should be interpreted cautiously.

Flight directions

All systems where directions were available (WR, BS, TR) showed consistent, well-correlated mean directions. The tracking radar and BirdScan both showed larger scatter of flight direction at low altitudes than at high-altitude, corroborating earlier reports in the study area (Sjöberg & Nilsson 2015).

This means that weather radar, BirdScan and tracking radar would all be appropriate for investigating flight directions, and marine radars operating in a horizontal mode can also measure direction, see table 3.

Target identification

In general, species identification of targets is not possible with any of the systems used in this study, except when combined with visual observations or under special circumstances (Dokter et al. 2013; Panuccio et al. 2016). Combining with visual observations is possible at a very local scale with the tracking radar, BirdScan and marine radar, but is difficult with the weather radar as it covers large areas. Broad species group classification based on wingbeat patterns is available in the BirdScan and tracking radar.

Depending on site and timing, insect contamination should be carefully taken into account, especially for the marine radar and the weather radar. The BirdScan separates insects from birds based on echo characteristics and the tracking radar does not track objects as small as insects. We do not expect that insects had a significant effect on our comparison, as mass southward migrations of insects in north-west Europe typically occur in August and early September (Chapman et al. 2010; Hu et al. 2016) before the large peaks of bird migration observed in this study, and previous studies (Alerstam *et al.* 2011; Chapman *et al.* 2015, 2016).

Availability

The different systems differ in accessibility for applied use (see table 1). Access to weather radar data differs depending on the meteorological institute involved and their data policy, though open data policies are becoming more common (c.f. the United States and the Netherlands). Weather radar data are of course also limited to the geographical area surrounding the weather radar stations, limiting coverage for example offshore. The use of weather radars to monitor animal movements have so far mainly been explored in continental US and Europe, but it has the potential to be used in other countries with extensive weather radar networks, like Russia, China and India. In the US the entire data archive of all 143 continental NEXRAD weather radar stations are publicly available (Ansari *et al.* 2018) and in Europe the European Network for the Radar Surveillance of Animal Movement (ENRAM) together with the Operational Program for the Exchange of Weather Radar Information (OPERA) is in the process of making bird profiles from European weather radars available (Shamoun-Baranes *et al.* 2014).

BirdScan (Swiss-BirdRadar.com) and marine radars, as well as other similar types of scanning radars [such as MERLIN Avian Radar Systems (DeTect, Inc, USA) and ROBIN (ROBIN Radar Systems, the Netherlands)], are commercially available products. They have the advantage of being able to be placed at almost any site, also offshore.

Tracking radars, like the one used here, have extremely limited availability and are not commercially available. However, some dedicated bird radars, and marine radars operated in horizontal mode, also have tracking functions.

Recommendations

In this study, we show a high degree of agreement among the different radar systems in describing the relative bird migration intensity and flight directions, and to a reasonable extent the absolute migration intensity and flight speed. The differences observed in absolute migration intensity and flight behaviors highlight the strengths and weaknesses of the different radar systems for different applications (see tables 1 and 3). The choice of the most appropriate radar will depend on the spatial, temporal, and taxonomic scale of the study (table 3).

Of the three radars providing reliable migration intensity measures, the weather radar is best suited to investigate large-scale flows of migration, such as mapping flyways to identify important stopover sites or predicting spread of pests and disease (see table 3). The extensive coverage, and the possibility of obtaining long time series makes the weather radar data well suited for planning and evaluating effects of large constructions and developments, such as major infrastructure projects. The possibility of obtaining historical data (for example the US NEXRAD originating in 1991) also makes weather radar data particularly valuable for planning, conservation and monitoring of long-term changes. As the weather radar data does not contain species information, it is most appropriate for investigating effects at the assemblage level, for example the effect of artificial light structures on all passing nocturnal migrants (Van Doren *et al.* 2017; McLaren *et al.* 2018) or identifying which stopover areas are used in large numbers (Buler & Dawson 2014). If species composition is deemed important, the weather radar data can be complemented by other methods such as connecting to bird counts (Sullivan *et al.* 2014) or acoustic monitoring of flight calls (Farnsworth 2005).

The highly mobile small scale radar system such as BirdScan, marine radar and tracking radar can temporally monitor site-specific animal movements aloft. A BirdScan type radar is more appropriate for investigating intensity of movements on a local scale, such as the risk of airstrikes in the immediate area surrounding an airport or the local impact of a wind farm. Marine radars also operate on the local scale, but are, depending on software used, appropriate for investigating relative patterns, rather than absolute migration intensity. Ground clutter and the placement of the radar generally determines at how low altitude a radar can give reliable data. A vertical pointing radar, such as the BirdScan, and to some extent marine radars, will be less affected by ground clutter and are therefore appropriate for applications that require low-altitude information, such as most collision risks with human-made structures. A BirdScan type radar also has the advantage of recording wingbeat patterns, which makes it possible to assign targets to species groups (Bruderer *et al.* 2010).

For detailed investigations of flight behavior the weather radar is best suited to investigate over larger areas, while BirdScan type radars, marine radar and tracking radars all can give reliable information on flight directions (as well as amount of variation and changes in flight direction) at a single site. Only a radar with tracking capabilities can however provide a detailed view of individual bird's reactions and flight paths.

In conclusion, all radar systems we investigated have the potential for being useful to investigate and monitor bird movements and migration, however careful attention should be given to which questions can be answered by which system.

Acknowledgements

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Data will be made available on Dryad.

Author contributions

FL, JWC, CN and JB planned and organized the study. CN and JB collected and processed the tracking radar data, MS and GDO collected and processed the marine radar data, AMD, LV, GH and HL extracted and processed the weather radar data, BS and FL collected and processed the BirdScan data. CN did the analysis and wrote the paper with substantial input from all authors.

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Table 1. Main characteristics of the settings and data recording of the four radars compared in this study. Details for each radar are given in the method section. Photo credits: WR: smhi.se, BS: swiss-birdradar.com, MR: Ornis italica, TR: Johan Bäckman.

	WEATHER RADAR (WR) 	**BIRDSCAN (BS)** 	**MARINE BIRD RADAR (MR)** 	**TRACKING RADAR (TR)** 
RECORDING METHOD	Horizontal scanning (360°)	Vertical pointing	Vertical scanning (180°)	Tracking single targets
FREQUENCY	C-band	X-band	X-band	X-band
OPERATION RANGE FOR BIRDS	5 to 25km	0.05 - 2km	0.1 – 3km	0.3 - 10 km (size dependent)
BIRD DATA OUTPUT	Vertical profiles of biomass density and ground speed	Multiple continuous individual tracks	Multiple individual tracks built from repeated scans	Continuous single individual tracks
OPERATION MODE	Automatic	Automatic	Automatic	Manual
RAIN FILTER OF BIRD DATA	Automatic	Automatic, manual check	Manual	Not applicable
BIRD ECHO CLASSIFICATION	Radial velocity pattern and echo strength	Wing-beat pattern specific size classes	Distance, speed	Wing-beat pattern
ASSUMPTIONS FOR BIRD MIGRATION QUANTIFICATION	Standard bird size (RCS), bird movements mainly well directed	Distance dependent detection probability for each size class	Constant detection probability	Representative sample of speed and direction
AVAILABLITY OF EQUIPMENT/DATA	High/low depending on country and meteorological institute	High	High	Low

Table 2. R2 values and number of nights of major axis regressions of mean MTR per night from the different systems and total nr of caught birds in Falsterbo. Upper diagonal = high altitude lower diagonal = low altitude

	WR	BS	MR	FBO	
WR		0.87 n=55	0.92 n=12	0.38 n=60	High altitude
BS	0.44 n=55		0.92 n=12	0.44 n=59	
MR	0.67 n=12	0.92 n=12		0.11 n=12	
FBO	0.14 n=60	0.40 n=59	0.19 n=12		
	Low altitude				

Table 3. A summary of the result of this study; which systems we recommend for obtaining different types of data.

TYPE OF DATA	WR	BS	MR	TR
Relative Migration Intensity over Time	✓	✓	✓	-
Absolute Migration Numbers	✓	✓	-	-
Large Spatial Coverage	✓	-	-	-
Detailed Site Information	-	✓	✓	✓
Long Time Series	✓	✓	-	-
Data in (near) Real Time	-	✓	-	-
Overall Direction of Migration	✓	✓	✓[1]	✓
Relative flight speeds over time (GS)	✓	✓	✓	✓
Absolute Flight Speeds (GS)	Conditional	Conditional	Conditional	✓
Flight Speed of Individuals	-	Conditional	-	✓
Tracks of Individuals	-	-	-	✓
Relative Height Distribution	✓	✓	✓	-
Low Altitude Migration	-	✓	✓[1]	-
Species Identification	-	✓[2]	✓[2]	✓[2]
Wing beat pattern	-	✓	-	✓
Insect Movements	Conditional	✓	-	-

[1]DEPENDING ON OPERATION MODE
[2]IF COMBINED WITH VISUAL OBSERVATIONS

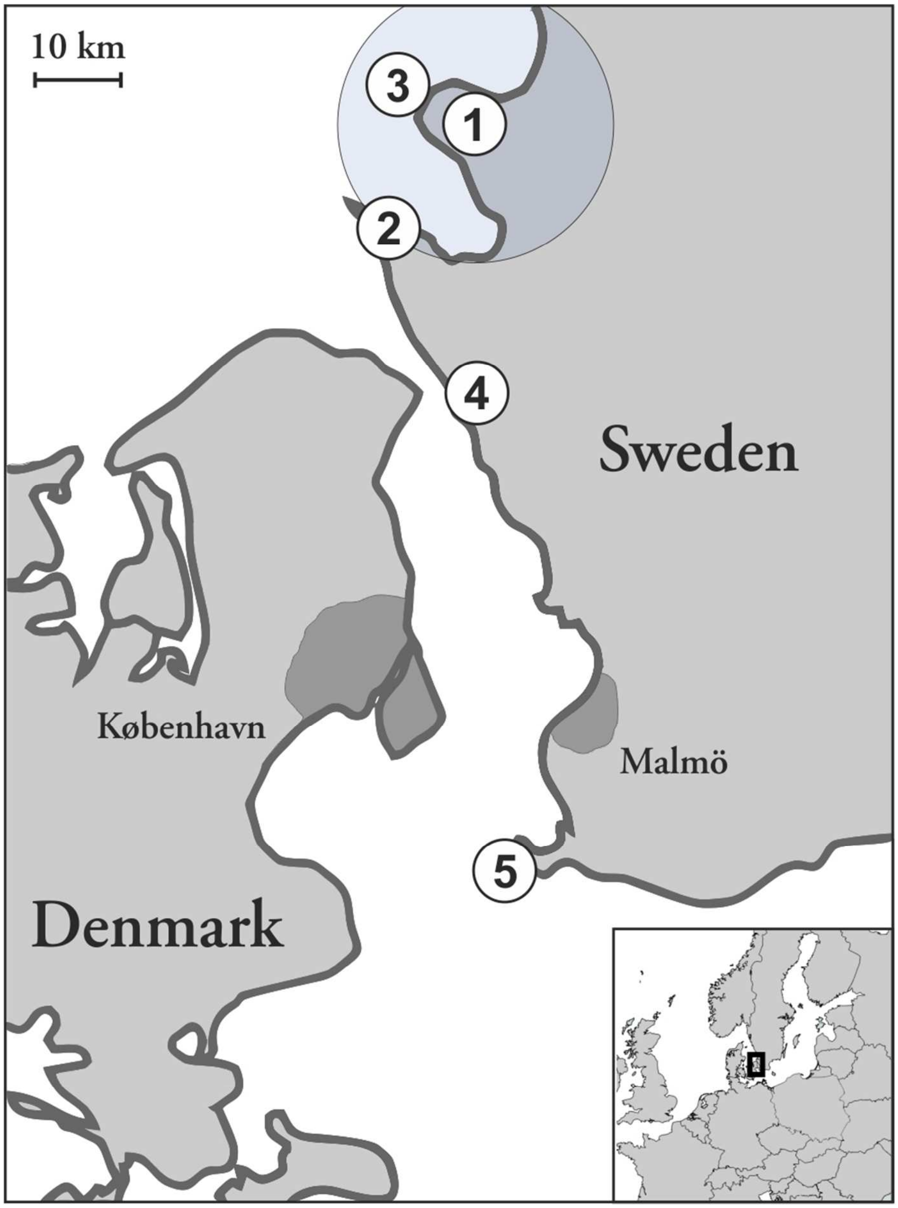


Figure 1. Map of southwestern Sweden and Öresund. 1. Weather radar Ängelholm with the 25 km detection range for birds. 2. Kullaberg field site. 3 and 4: Weather stations. 5. Falsterbo bird observatory.

83x112mm (300 x 300 DPI)

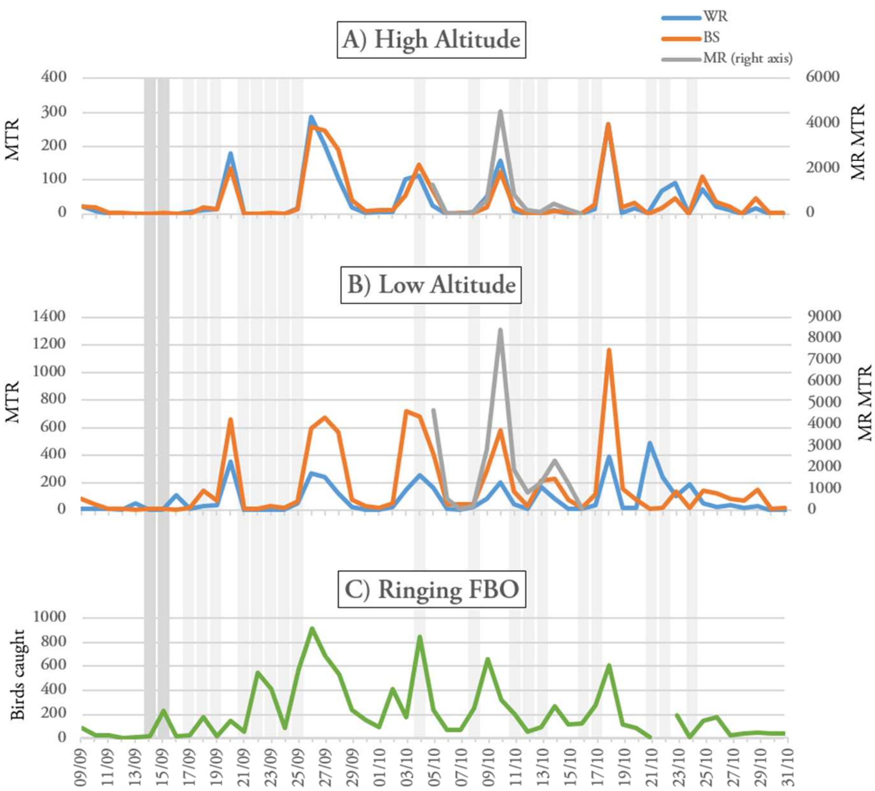


Figure 2. A) Mean MTR per night (start date) in the high altitude interval; 800-1400m. Weather radar (WR) and BirdScan (BS) on left axis, marine radar (MR) on secondary, right axis. B) Mean MTR per night in the low altitude interval; 200-800m. WR and BS on left axis, MR on secondary, right axis. C) Total sum of ringed birds, all species, at Falsterbo ringing station on the morning directly following the night of the indicated start date. Nights with light rain (<5mm per night) indicated in light gray, nights with more than 5 mm rain indicated in dark grey.

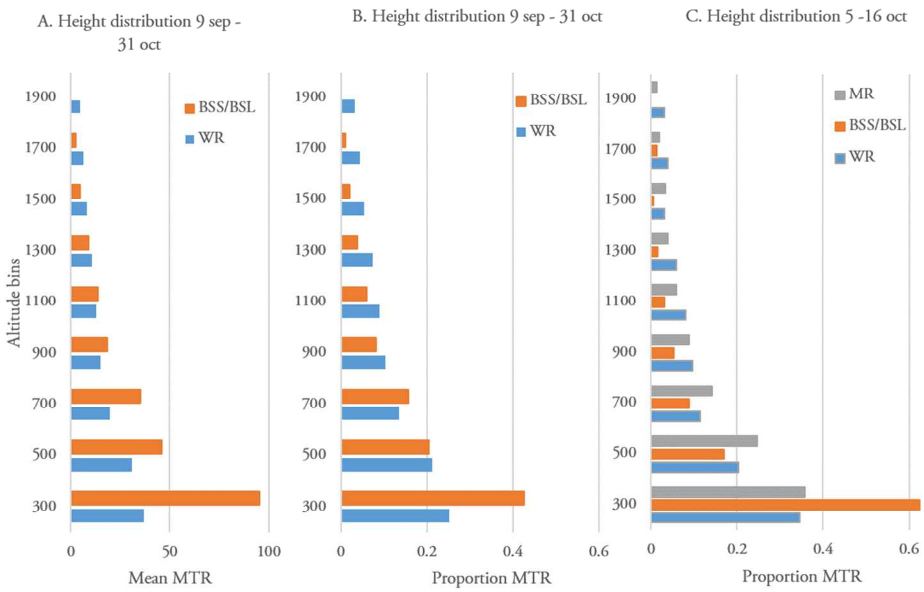


Figure 3. A) Mean MTR per height bin during the entire season (9 sep - 31 oct) for weather radar and BirdScan. B) Proportion of mean MTRs in different height bins for the weather radar and BirdScan during the entire season (9 sep - 31 oct). C) Proportion of mean MTR in the different height bins during the period the Marine radar was deployed (5 -16 oct). Y axis is labeled with the middle of each height bin (for example bin 1100 contains data from 1000 to 1200 m), altitude in meters above sea level. For BirdScan short pulse (BSS) is used for 300-700 m asl bins and long pulse (BSL) for 900 m bins and up.

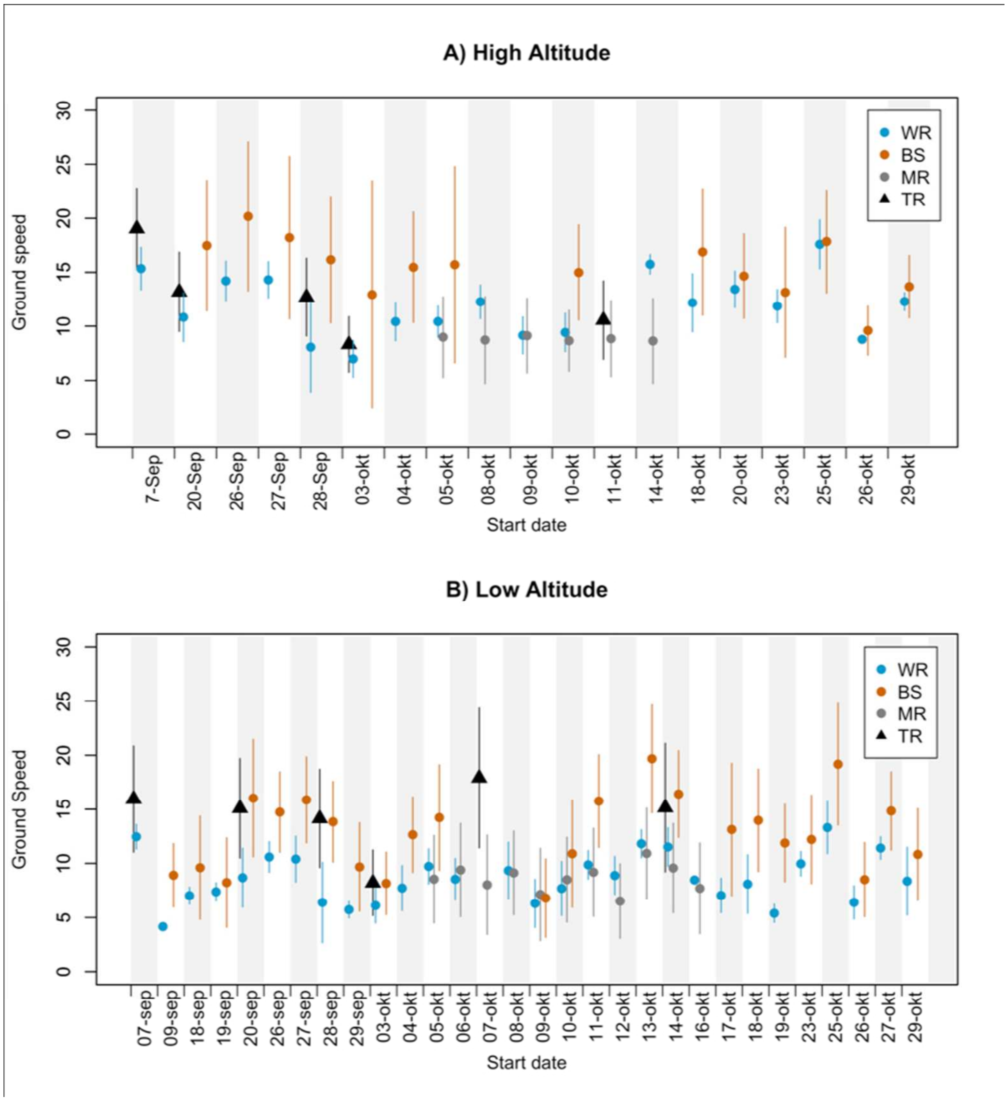


Figure 4. A) Mean ground speed per night for weather radar (WR), BirdScan (BS) and tracking radar (TR) in the higher altitude interval, 800-1400m. B) Mean ground speed per night in low altitude interval, 200-800 m asl.

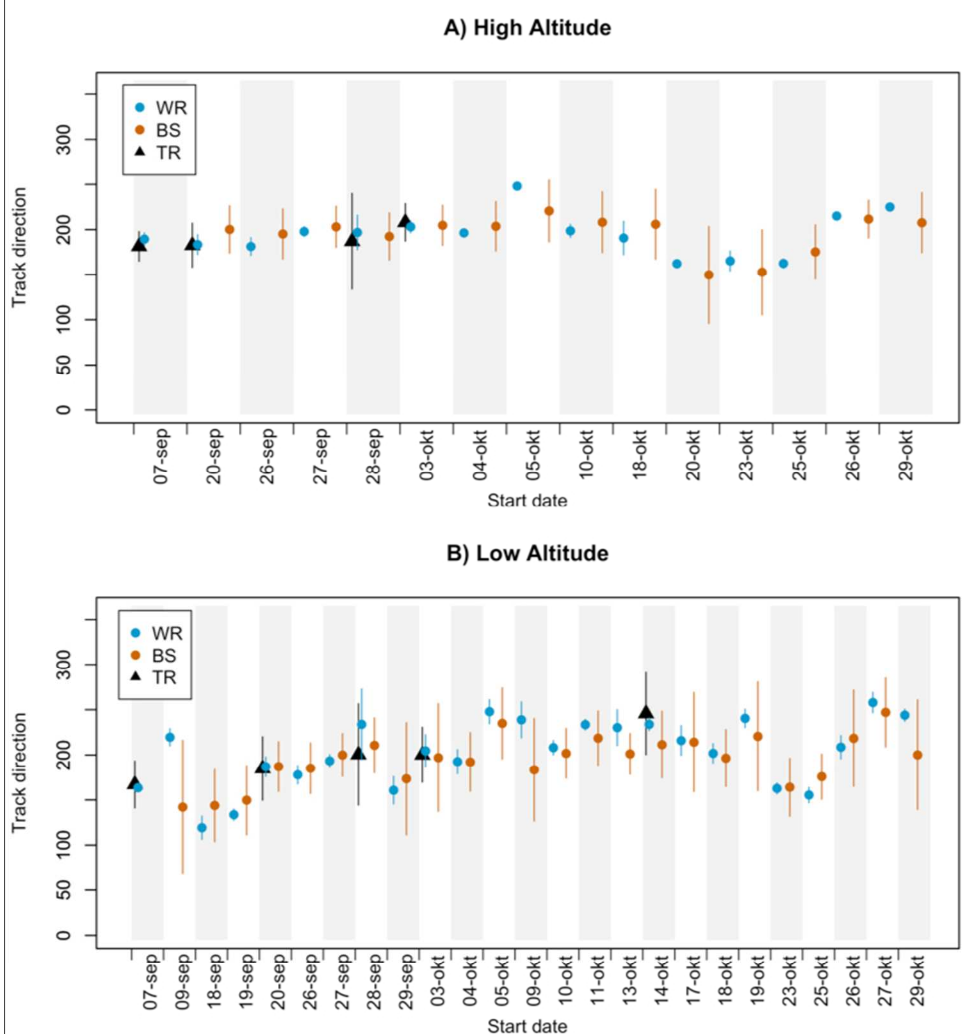


Figure 5. A) Mean track direction per night as measured by the different systems: weather radar (WR), BirdScan (BS) and tracking radar (TR) in the higher altitude interval, 800-1400m. B) Mean track direction per night in the low altitude interval, 200-800 m asl.

Supplement

Additional technical details

BirdScan (BS)

Maximum detection range depends on pulse length and the size of the target. Estimated from the antenna diagram of the BirdScan, theoretical maximum detection ranges for a bird of the size of a chaffinch are 750 m in short-pulse, and 1010 m in long-pulse mode, and for a bird of the size of a godwit maximum ranges are 1900 m and 2600 m, respectively. The Horn antenna of the BirdScan radar has a nominal beam width of approx. 20°. We only included echoes with 180° ± 60° angle between the bird entry and exit of the beam in relation to beam center. Thus, birds only flying along the edge of the beam were excluded. Customized hard- and software was applied to extract echo information from the raw video signal (manufacturer: swiss-birdradar.com).

Vertical scanning marine bird radar (MR)

The raw data from the marine radar are not directly accessible, since the acquisition software ExtraSea (from the radar manufacturing company GEM) automatically pre-processes the raw data, directly returning the visual result of this processing (green moving echoes on the screen). During the collection of data, the acquisition software was set at 2 km range and the radar position was off-centered (lowered with respect to the center of the screen) in order to extend the range detection up to the height of approximately 3 km. Moreover, the detection area of the radar was limited to a 180° sector extending from the azimuth towards the sky, while the remaining sector (below the ground surface) was blanked to reduce clutter disturbance.

The visual output of the acquisition software was recorded continuously by using a screen capture software (NCH) and stored in separate 3-hours video clips (in .avi format). The videos were then processed using RadR (Taylor et al. 2010), a plugin of the statistical software R (R Core Team 2014).

With RadR we could reconstruct bird tracks from the recorded echoes according to a variety of different settings, such as: minimum and maximum blip area (a graphical measurement of the number of pixels occupied by the echo, not directly related to the impulse intensity), minimum and maximum speed, maximum angle and maximum time interval between subsequent points, and minimum number of consecutive echoes to build a track.

Table S1. R^2 values and number of nights of major axis regressions of mean MTR per night at high altitude (800-1400 m). Also tested against total nr of caught birds in Falsterbo. Upper diagonal = no rain, lower diagonal = some rain during night.

	WR	BSL	MR	FBO	
WR		0.88 n=33	0.93 n=7	0.53 n=36	No rain
BSL	0.70 n=22		0.91 n=7	0.57 n=37	
MR	0.65 n=5	0.93 n=5		0.07 N=7	
FBO	0.30 n=24	0.49 n=22	0.10 n=5		
		Rain			

Table S2. R2 values and number of nights of major axis regressions of mean MTR per night at low altitude (200-800 m). Also tested against total nr of caught birds in Falsterbo. Upper diagonal = no rain, lower diagonal = some rain during night.

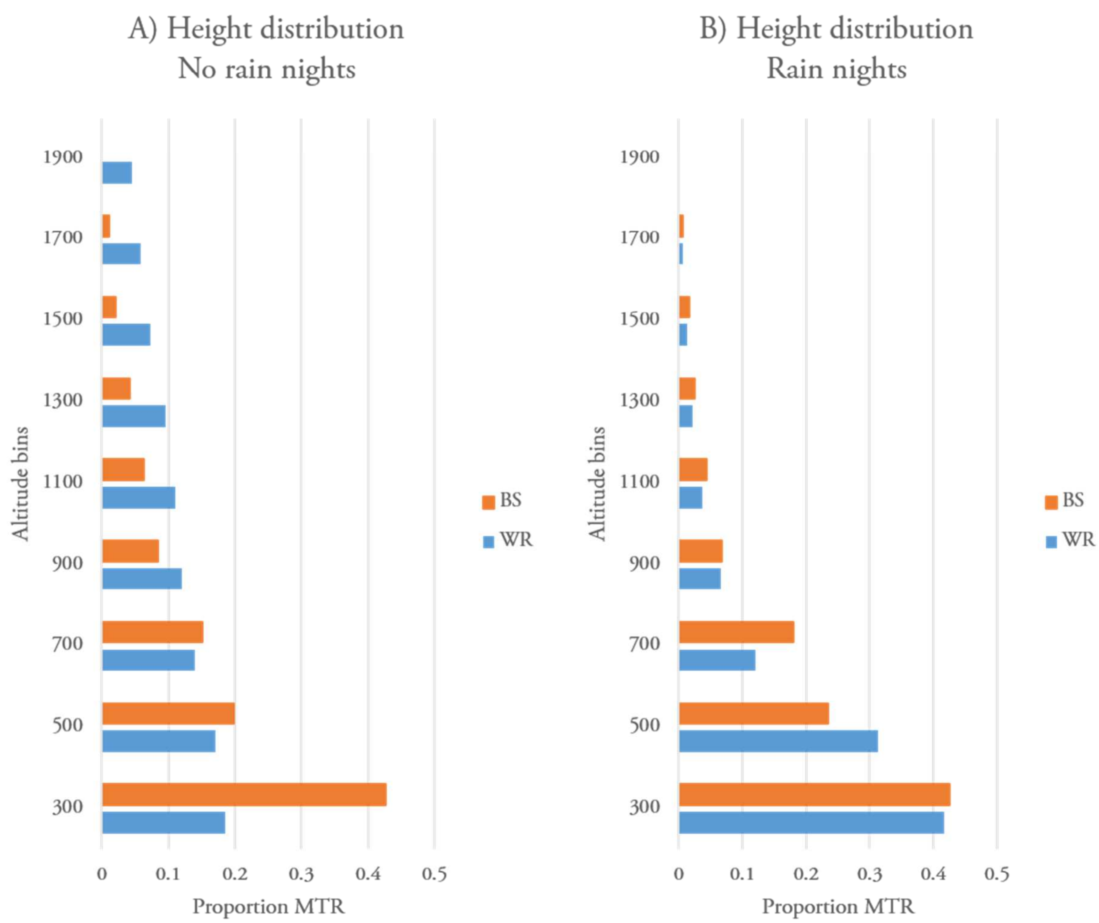
	WR	BSS	MR	FBO	
WR		0.86 n=33	0.93 n=7	0.36 n=36	No rain
BSS	0.082 n=22		0.96 n=7	0.47 n=37	
MR	0.21 n=5	0.55 n=5		0.17 n=7	
FBO	0.002 n=24	0.43 n=22	0.007 n=5		
		Rain			

Table S3. Circular correlations and Moors paired test for circular data. Correlations of flight directions over the season were tested using the R package "circular" (Agostinelli & Lund 2013) and Moors paired test for circular data were tested in Oriana 4.0 (Kovach Computing services, Anglesey, UK).

Low altitude						
		Circular correlation			Moors paired test	
	N	Correlation coef.	Test stat.	P value	R'	P value
WR - TR	5	0.84	1.57	NS	0.36	NS
WR - BSS	24	0.76	2.81	0.005	1.38	< 0.005
TR - BSS	4	0.73	1.33	NS	0.30	NS

High altitude						
		Circular correlation			Moors paired test	
	N	Correlation coef.	Test stat.	P value	R'	P value
WR - TR	4	0.85	1.38	NS	0.41	NS
WR - BSL	14	0.84	2.24	<0.05	0.37	NS
TR - BSL	3	0.67	1.94	NS	0.78	NS

36



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38 **Figure S1.** Proportion of MTRs in different height bins for the different systems during the entire

39 season (9 sep – 31 oct) **A)** on nights with rain present (n=21) and **B)** on nights with no rain (n=31). Y

40 axis is labeled with the middle of each height bin. For BirdScan short pulse is used for 200-700 m bins

41 and long pulse for 900 m bins and up.

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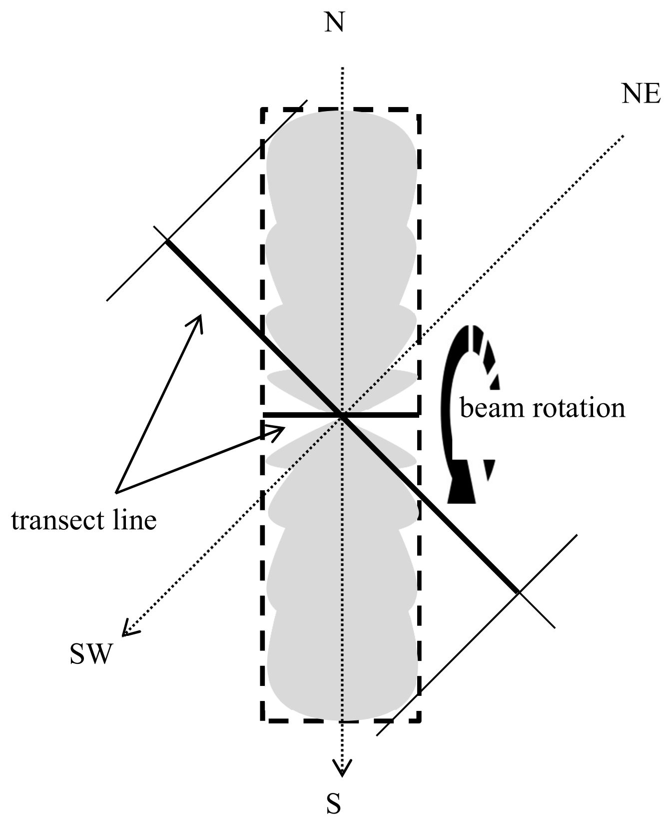

Figure S2. Calculation of MTR from a vertically rotating marine radar. The number of birds counted in the radar is related to a reference length of a transect line (bold lines) perpendicular to the main flight direction. The length of the transect line varies considerably with respect to flight direction and detection range. Be aware that surveyed volume is a circular sector and thus, the length of the transect line additionally decreases with altitude in relation to the flight direction.