

Temporal Patterns in Offshore Bird Abundance During the Breeding Season at the Dutch North Sea Coast

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Abstract

The expanding development of offshore wind farms brings a growing concern about the human impact on seabirds. To assess this impact a better understanding of offshore bird abundance is needed. The aim of this study was to investigate offshore bird abundance in the breeding season and model the effect of predictable environmental factors. We used a bird radar, situated at the edge of a wind farm (52.427827°N, 4.185345°E), to record hourly aerial bird abundance at the North Sea near the Dutch coast between May 1st and July 15th in 2019 and 2020. The effect of sun position, week in the breeding season, and astronomic tide on hourly bird abundance was evaluated using generalized additive modelling. Sun position and week in the breeding season had a modest and statistically significant ($p < 0.001$) effect on bird abundance, while astronomic tide did not. Predicted abundance was higher during the day than during the night, with highest abundance in the morning. Abundance increased throughout the breeding season until the end of June, but decreased again in July. In total the model explained 18.5% of deviance in bird abundance, indicating offshore bird abundance is partially dependent on predictable external factors. The high variability in bird abundance at scales ranging from hours up to weeks emphasizes the need for long term and continuous data which radar technology can provide. The findings of this study can help improve offshore bird density estimations and provide context on the temporal fluctuations in bird abundance for marine policy making.

Introduction

The Dutch Continental Shelf (DCS) of the North Sea is home to ecologically diverse avian species that fluctuate in number and composition year-round (Camphuysen and Leopold 1994; Fijn et al. 2018) and utilize the intertidal, coastal and pelagic areas of the DCS to roost and forage. The DCS is also heavily exploited through human activities including fisheries, shipping, gas extraction, and increasingly wind farm development (Rijksoverheid 2015). As wind farm development is expanding on the North Sea, especially in coastal waters, the concern for its effect on birds utilizing the area has grown, as is seen in the growing field of research (Desholm and Kahlert 2005; Hüppop et al. 2006; Garthe et al. 2017; Thaxter et al. 2018; Vanermen et al. 2019). In spring and summer, central place foraging colonial seabirds, such as gulls and terns, commute regularly between breeding sites onshore and foraging grounds at sea (Wetterer 1989; Fryxell and Lundberg 1998). Due to this foraging strategy, coastal seabirds may have recurrent encounters with offshore wind farms by which they may be impacted (Drewitt and Langston 2006; Lindeboom et al. 2011). Additionally, a meta-analysis by Dierschke et al. (2016) on interactions between seabirds and wind farms on the North Sea identified species that appear to be generally attracted towards wind farms, including the lesser black-backed gull (*Larus fuscus*) and the European herring gull (*Larus argentatus*), which are among the most abundant species on the DCS around this time of year (Camphuysen and Leopold 1994), further increasing concern for these species.

While it is clear birds are impacted by offshore wind farm development, the scope of this impact is difficult to assess as information on temporal fluctuations of offshore bird abundance is lacking due to inherent limitations of various monitoring techniques. On the North Sea, visual observations through ship surveys (Camphuysen and Leopold 1994), airplane surveys (Fijn et al. 2018), and stations along the coast (Camphuysen and Dijk 1983) have been used to determine bird species distribution and abundance year round. This provides information on a broad range of species active during daylight hours and this information has been combined into global species distribution maps (Halpin et al. 2009). However, due to the often high logistic costs of ship and aerial surveys, and the obvious geographical constraints of coastal bird monitoring, large temporal and/or spatial gaps exist that can make accurate offshore distribution estimations difficult. Radar is a remote sensing technology which has been applied to monitor avian abundance and flight characteristics at sea (Lack 1959; Hüppop et al. 2006; Plonczkier and Simms 2012; Fijn et al. 2015). Although limited in range, bird radar can monitor bird abundance and flight characteristics within an observation area at a high spatio-temporal resolution for extended periods of time, enabling research on factors that influence both short- and long-term temporal patterns in offshore abundance. In particular, the effect of highly predictable external factors on bird

abundance is of interest, as their predictable nature can structurally affect bird behaviour and can be taken into account when assessing bird-wind farm interactions.

Three external variables that are highly predictable and have been noted to affect the behaviour of coastal seabirds are daylight availability, the time of year, and the tide. Daylight availability is important for visual foragers and the daily rhythm of animals, including central place foragers such as seabirds (Fryxell and Lundberg 1998; Shealer 2002). The time of year affects the breeding stage of animals. During the different breeding stages these species may adjust their foraging effort and behaviour. For example, lesser black-backed gulls from coastal breeding colonies in the Netherlands (Camphuysen et al. 2015) and the UK (Thaxter et al. 2015) have been found to increase the proportion of time spent at sea during chick rearing, and some herring gulls on Texel switch to marine diets during chick rearing (van Donk et al. 2017). Lastly, the tide impacts the sea currents and can create foraging opportunities at sea through upwelling. For example, the common tern (*Sterna hirundo*) and roseate tern (*Sterna dougallii*) use upwelling caused by tidal currents to access prey (Urmy and Warren, 2018).

The aim of this study is to investigate hourly fluctuations in non-migratory aerial bird abundance (henceforth: bird abundance) near an offshore wind farm and analyse the effect of the aforementioned external variables with predictable temporal variation on this abundance (daylight availability, time of year, and tide). Particularly, we are interested in local movements of birds at sea during the breeding season, when colonial seabirds forage and commute between their colonies and the feeding areas at sea. We use a bird radar system positioned at the edge of Luchterduinen offshore wind farm to measure hourly bird abundance and model the effect of sun position, week in the breeding season, and astronomic tide. We have the following expectations, based on the existing literature (see previous references): i) offshore bird abundance will be higher during daylight hours than during night, ii) abundance will be higher in the later stages of breeding than at the start of breeding, and iii) abundance will be higher between low and high tide, when the tidal current is strongest and might create foraging opportunities through increased upwelling. The external variables are all highly regular, and could be used to better predict offshore bird abundance on the North Sea during the breeding season if found to have a significant impact on bird abundance.

Methods

Radar measurements

Bird flight was monitored by a bird radar system (RobinRadar 3D-fix) consisting of a vertically rotating X-band antenna and horizontally rotating S-band antenna (Furuno Marine) both rotating at $0.75 \text{ rotations s}^{-1}$. The system was mounted on the service platform of turbine 42 (52.427827°N, 4.185345°E) situated at the edge of Luchterduinen, 25 km from the coast near IJmuiden (Fig. 1). The X-band antenna had a power of 25Kw an approximate maximum range of 3 km for small birds (200 g), whereas the S-band antenna had a power of 60Kw and approximate maximum range of 3.5 km for small birds.

Figure 1 Overview of the sample area and Luchterduinen offshore wind farm (box) and the position of the radar in relation to the coast of the Netherlands (map). Map: tidal water height was measured at Hoorn platform (blue dot, 52.92064°N, 4.09822°E), blue plusses indicate the resolution grid of ERA5 data (0.25° Lon-Lat grid), and ESAS5.0 species observation data was sampled between 51.8°N-53°N and 3.7°E-4.7°E (dashed black square). Box: black dots show the individual turbines, the red dot shows the turbine that has the radar-system installed (52.42783°N, 4.18535°E). The 1km² area of interest is shown in red with black lining; it is delimited by the 1000 and 2000m ranges and the 22.5° and 60.7° azimuth angles from the radar. The dotted grey square shows the grid cell from which ERA5 reanalysis data were sampled

The measurements of the radar system were automatically processed to create tracks of birds using proprietary software developed by RobinRadar. The resulting tracks were stored in a centralized spatial database. The radar software had clutter filters to reduce the probability of non-avian scatters being erroneously tracked as birds. These filters were applied dynamically in each radar image to remove unwanted reflections caused by landscape features, waves or rain, and information on filtering was stored per image. Furthermore, each track was classified by the software based on its properties: tracks with a maximum airspeed of 36.1 m s^{-1} and a signal-to-noise ratio typical for birds (between -10 and 65) are categorised as birds. Airspeed was calculated by the proprietary software using wind speed and direction measured at the radar (AIRMAR 150WX WeatherStation).

Radar data was collected in the years 2019 and 2020. The relevant period within these years was chosen to match the breeding period(s) of the most abundant species. Based on species observation data taken from the European Seabird at Sea database (ESAS 5.0, accessed 16-02-2021, Camphuysen et al., 2004; Reid and Camphuysen, 1998) near the wind farm (51.8°N-53°N, 3.7°E-4.7°E, Fig. 1) in the months of May, June and July, the lesser black-backed gull was found to be the most prevalent species by far in this part of the North Sea (56.8% of observations, see Online Resource 1). This was also confirmed by species observation reports made at the nearby OWEZ wind farm (Krijgsveld et al. 2011) and before construction of Luchterduinen (Gyimesi et al. 2019) during spring and summer. The lesser black-backed gull was therefore designated as the key species for deciding our period of interest. Based on field observations of egg laying and fledging at colonies along the North Sea coast (Camphuysen and Gronert 2010; Cottaar et al. 2018, 2020) we selected the period of May 1st to July 15th as the breeding season.

The bird detection probability of the radar is not equal over the whole radar observation window. The reflective size of a bird and thus its detection probability changes with range to the radar and position within the radar beam (Schmid et al. 2019). To account for this, data was selected from an area in which detection probability would be more or less homogeneous based on the properties of the radar and the position of the radar system relative to the wind farm. To account for detection loss occurring because of a decrease in radar beam power with range, the maximum range from the radar was set at 2000 m. Beyond this range the detection probability for small birds (< 62.5 g) drops below 80% at certain scanning altitudes (Online Resource 2). On the other hand, the high power of the radar beam at close range can produce false positive bird tracks caused by other features reflecting the radar beam. Therefore, the minimum range for track inclusion was set at 1000 m. Detection rate at different azimuth angles (scanning angle of the horizontal radar) differed because of turbine placement of the wind farm. As the radar itself was installed on the service platform of a wind turbine, the radar beam was blocked by the turbine between 275° to 346° degrees. Additionally, the other turbines in the wind farm were situated roughly between 80° to 260°, creating a zone in which bird detection is impaired around each turbine. To avoid detection bias in these regions, data was sampled from an azimuth angle between 22.5° and 60.7° from 1000–2000 m from the radar, resulting in a 1 km^2 area of open sea in the North-East section of the radar range (Fig. 1). Only tracks which occurred (partially or entirely) within this area were analysed in this study. The radar system only measures birds in flight, leaving birds floating on the water unseen.

Environmental data

Astronomic tide was retrieved from the nearest observation station at Hoorn Platform (52.92064°N, 4.09822°E, approximately 55km North-West of the study site, Fig. 1) from the Rijkswaterstaat public database (Rijkswaterstaat 2020, accessed 19 October 2020), which contains astronomic tide acquired through harmonic analysis as water height in centimetres above Mean Sea Level (cm - MSL). Tidal information was retrieved at the half-hour mark each hour (xx30 hr) to best reflect average tidal height for each hour (xx00-xx59 hr).

For data filtering purposes, we extracted wind data to independently calculate air speed of the radar tracks (see radar data processing). Hourly wind data was acquired from the ECMWF (European Centre for Medium-Range Weather Forecasts) ERA5 reanalysis data (Hersbach et al. 2018; Hersbach et al. 2020, accessed 15 September 2020). Wind

conditions are described by u- and v-components (both in m s^{-1}), where the u-component is the zonal wind (wind from the west is positive) and the v-component is the meridional wind (wind from south is positive). The u- and v-components have a temporal resolution of 1 hour and spatial resolution of 0.25° latitude & longitude, but were interpolated to a 0.04° latitude & longitude zone around the study area ($52.42^\circ\text{N} - 52.46^\circ\text{N}$ & $4.18^\circ\text{E} - 4.22^\circ\text{E}$, Fig. 1) through bilinear interpolation (conducted within the data query by the ECMWF data platform). Wind components were selected from the lowest atmospheric layer, 10 m above the sea surface, to match both the properties of the radar observations and known flight heights of the relevant bird species. The radar observes birds reliably only in the lower layer (up to an altitude of 300m, see Online Resource 2) and we expected flight altitudes of most species to be close to the sea surface during local movements (Johnston et al. 2014; Corman and Garthe 2014; Ross-Smith et al. 2016; Borkenhagen et al. 2017).

Radar data processing

Each track created by the radar software included at least five track points and several track properties: geolocation plus timestamp (UTC) per track point and track direction based on a vector drawn from the starting point to the end point of the track (radians). Per track, straight line displacement (m) was calculated as the great circle distance between the first and last track point, and the track length (m) was calculated as the sum of the great circle distance between consecutive track points. Ground speed per track was calculated as track length divided by track duration (m s^{-1}). Airspeed per track was calculated using ground speed, track direction and hourly u- and v-wind components nearest to the first timestamp of the track according to Shamoun-Baranes et al. (2007). Track straightness was calculated by dividing the straight line displacement by the track length. Tracks with an airspeed lower than 5 m s^{-1} were removed as nearly all seabird species fly at higher airspeeds (Spear and Ainley 1997; Alerstam et al. 2007; Shamoun-Baranes et al. 2016). Furthermore, tracks with a track duration longer than 60 min were removed, as manual data exploration indicated that these tracks represented reflections from the sea surface, vessels or structures and it was highly unlikely these tracks belonged to bird targets.

To analyse bird abundance throughout the breeding season, we calculated the total number of tracks occurring in the area of interest per hour (from here on reported as birds h^{-1}). All tracks with a start time between xx00 – xx59 hr were included in hour xx. Sun position (azimuth angle, extracted using the `suncalc` package v0.5.0; Thieurmél and Elmarhraoui 2019) and astronomic tide (cm - MSL) were collected at the half-hour mark (xx30 hr) to reflect the average conditions within that hour. During the study period the radar was occasionally not operational and hours in which the radar was (partially) offline were not included in the analysis. Furthermore, during exploratory analysis it became clear that birds were no longer detected by the radar when the clutter filter of the radar was highly active. Therefore, to reduce the chance of analysing artificial lows in bird abundance caused by high filter activity, we removed all hours with an average filter activity above a set threshold of 0.240 (elaboration available in Online Resource 3).

Though we designated a sampling period (May 1st to July 15th) in which we expected to observe predominantly local movements of species that breed in the region, migration might still occur, strongly impacting measured hourly abundance. To remove these occurrences, we identified moments of migration in our dataset by looking at the hourly average flight characteristics. We first calculated the mean hourly track direction (radians), the hourly mean of track straightness (0–1), and the circular uniformity of hourly track direction (0–1). This last characteristic was calculated by treating the flight direction of each observation as a unit vector, calculating the resultant vector of all vectors in the hour combined, and dividing the resultant vector by the number of observations using the `circular` package (v0.4-93; Lund and Agostinelli 2017). We identified migration events as hours of relatively high bird abundance and with relatively high directional uniformity compared to the total data sample, and with straight flight paths on average. The following criteria were used to identify migration hours: hourly abundance > mean of data (112 birds h^{-1}), uniformity of hourly flight direction > 90th percentile of data (0.61), and mean track straightness > median of data (0.78). Within these migration

hours, tracks with straightness > 0.78 and a track direction within a 45° window around the hourly mean track direction were removed from these hours.

After applying the aforementioned selection criteria, 1879 hourly values of bird abundance remained (based on 208.504 tracks). This data formed the basis for further analysis. For a summary of data retained after each selection step and the total number of tracks per season see Table 1.

Table 1

Overview of bird tracks measured by radar during the study period in 2019 and 2020, the amount of tracks removed per processing step, and the remaining tracks, including an overview of the number of measurement hours per season, the hours the radar was offline or the filter threshold was exceeded, and the final number of hours from which were analysed further. Processing steps are listed in order of processing. Percentages are based on number of raw tracks or total hours per year

	2019		2020	
	# of tracks	% of total	# of tracks	% of total
Total tracks	109641	100	119766	100
Non-bird tracks (air speed < 5m s ⁻¹ , track duration > 3600s)	- 4293	3.9	- 2787	2.3
Tracks during offline hours	- 2813	2.6	- 46	< 0.1
Tracks during hours of high filter activity	- 4371	4.0	- 3992	3.3
Migration tracks	- 839	0.8	- 1762	1.5
Remaining tracks	97325	88.8	111179	92.8
Total hours	1824	100	1824	100
Radar offline	- 227	12.4	- 340	18.6
Filter activity above threshold	- 598	32.9	- 604	33.1
Remaining hours	999	54.8	880	48.3

Data analysis

To model the effects of the external variables on bird abundance and test for significance of these effects, generalized additive models were fitted to the data using the mgcv package (v1.8-32; Wood 2020), with predictors sun azimuth (using a cyclic P-spline smoother), week in the breeding season (using a thin plate regression spline smoother) and tidal water height (using a thin plate regression spline smoother), and year as a fixed random effect to account for yearly variability. We assumed a quasi-Poisson distribution for the model error, which was verified with the model residuals after fitting the model and did not require any adjustment. We checked whether each predictor contributed to the models by creating sub-models with one predictor removed and comparing for lowest AIC-scores. If a sub-model scored better, we would use this model instead of the complete model and tested whether further model-reduction would be warranted by repeating the process. The best scoring model was explored further for the individual predictor effects and treated as the main result of the research. The effects of the individual predictors within this best model were approximated by subtracting the explained deviance from the sub-model without the predictor from the deviance explained by the complete model. All analyses were performed in R version 4.0.0 (R Core Team 2020).

Results

Hourly bird abundance

Hourly bird abundance varied between 0 and 1401 birds h^{-1} in 2019 (Fig. 2) and 0 and 820 birds h^{-1} in 2020 (Fig. 3). Mean hourly abundance in 2019 was 97 birds h^{-1} (95% confidence interval = 91–104 birds h^{-1}) and 126 birds h^{-1} (95% confidence interval = 177–135 birds h^{-1}) in 2020. Hourly abundance was available for 123 out of 152 observation days, with 29 days which were completely observed (24 observation hours d^{-1}). Over the breeding season of 1824 observation hours, 417 hours were not covered in either season (overview available in Online Resource 4), in particular week 2 (May 8th – 14th), week 3 (May 15th – 22nd), and week 9 (June 26th – July 2nd) missed more than a third of the observation hours (80, 60, and 96 observation hours out of 168 hours respectively).

Effect of external variables

The complete model, with all predictors included, scored the best (lowest AIC-score). Therefore, the full models and effects were selected as main results in this study and explored further below, with a focus on the individual predictor effects that were significant. Bird abundance was significantly related to sun position ($p < 0.001$) and week of the breeding season ($p < 0.001$), but not to astronomic tide ($p = 0.175$). The complete model explained 18.5% of data deviance ($R^2 = 0.17$). Of the three predictors, week of breeding season had the strongest estimated effect on bird abundance (8.5% of deviance), followed by sun position (5.6%), and tide (0.3%, non-significant). Year as a random effect was significant ($p = 0.002$), but accounted only for 0.5% of deviance. The significant effects are visualized in Fig. 4. The effect of sun position (Fig. 4A) highlighted the large difference between the mean predicted number of birds h^{-1} during the day (130 birds h^{-1}) versus that during the night (75 birds h^{-1}), which matched our expectations. Bird abundance appeared to peak approximately three hours after sunrise (at ~ 1000 hr UTC for June 1st), with lower numbers in the afternoon, and relatively constant low values during the night. The effect of week of the breeding season (Fig. 4B) showed a steady increase in mean predicted bird abundance from the last weeks of May with values around 80 birds h^{-1} to a peak of 175 birds h^{-1} in late June (week of June 19th), similar to our expectations. After this peak hourly abundance dropped to a mean predicted 139 birds h^{-1} in the last week of July.

Discussion

In this study we show that hourly bird abundance near an offshore wind farm can strongly fluctuate and is affected by daylight availability (operationalized by sun azimuth) and time of the year (operationalized by week in breeding season), but not by astronomic tide. The results support our expectation that observed patterns of offshore bird abundance reflect both diurnal and seasonal processes throughout the breeding season.

We expect the most abundant species near Luchterduinen are central place foragers (namely lesser black-backed gull, herring gull, and great cormorant (*Phalacrocorax carbo*), Online Resource 1) and our results support our expectation that these birds mainly undertake their foraging bouts after sunrise when daylight can aid them in their foraging. The drop in bird abundance throughout the day might indicate some birds return to their colony earlier than others. Indeed offshore foraging trip duration of several seabird species common in the breeding season varies greatly: lesser black-backed gull 8.0 ± 6.3 h (Garthe et al. 2016) and $8.3 \pm 10.2\text{h}/6.9 \pm 11.9\text{h}$ (long trips for males/females, Camphuysen et al. 2015), Sandwich tern 2.3 ± 1.1 h (Fijn et al. 2017). If most birds fly out from their colony around sunrise to undertake foraging bouts of several hours at sea, a steady decrease in their abundance throughout the day would be expected. The slight peak in abundance before sunset might be caused by an increase in the flux of birds returning to the coast from farther at sea, or more likely by birds also foraging in the evening which is supported by Schwemmer and Garthe (2005) who found a higher proportion of foraging lesser black-backed gull over the North Sea both in the morning and evening hours. Though we considered the breeding birds on the Dutch coast to be diurnal, with peaks in offshore activity during the day, there was activity recorded during the night as well. Several gull species such as the lesser black-backed gull and herring gull are known to be out at sea during the night (Camphuysen et al. 2015) and forage on fishery discards during the night

(Garthe and Hüppop 1996; Garthe et al. 2016). We note that these studies are species specific, whereas our results depict a general trend in bird abundance, reflecting a combined activity pattern for all species observed in the study area.

In some species breeding stage can affect foraging behaviour (e.g. Sandwich tern (Fijn et al. 2017), and lesser black-backed gulls (Thaxter et al. 2015)). However, whether these changes affect the overall distribution of birds offshore has not been confirmed by observations and remained unclear. Our results show that after a period of relatively low hourly abundance in May, offshore bird abundance increases from the end of May to the end of June (Fig. 4B). This aligns with our expectations that offshore bird abundance increases throughout the breeding season, based on the assumption that coastal seabirds breeding in the region shift to a more marine diet during the chick rearing period (Spaans 1971; Annett and Pierotti 1989), which for lesser black-backed gulls begins around the end of May (Camphuysen and Gronert 2010; Cottaar et al. 2018, 2020). We expected offshore bird abundance to increase further throughout July, yet we observed a decrease in abundance from the end of June (Fig. 4B). The decrease sets in before we would expect to see an effect from the first fledglings in nearby colonies, which starts in the second week of July (Camphuysen and Gronert 2010). It is possible there is a decrease in foraging effort within colonies as more breeding pairs experience breeding failure. In the lesser black-backed gull colony on Texel on average 70.3% of eggs hatch per season while only 23.7% of the hatchlings fledge (Camphuysen and Gronert, 2010, updated to 2020 (unpublished data, Online Resource 1)), and failed breeders might spend less time foraging due to a decrease in energy demands. An alternative explanation for the seasonal patterns observed in this study may be a seasonal fluctuation in offshore food availability. Herring gulls and lesser black backed gulls in the region forage on fishery discards during the breeding season (Camphuysen 1995; Tyson et al. 2015; van Donk et al. 2017) and temporal and spatial fluctuations in fishery activity may influence bird abundance at sea. In lesser black-backed gulls on a colony in Texel, foraging trips differ between the period of incubation of the eggs, and chick rearing (Camphuysen et al. 2015): foraging trip duration decreased during chick rearing compared to egg incubation, while the trip range increased as well as proportion of time spent at sea. The increase in abundance modelled in this study roughly aligns with the median hatching date of lesser black-backed gulls recorded on Texel (Camphuysen and Gronert 2010; Camphuysen et al. 2015) and might be caused by this shift in behaviour.

Opposed to our expectation, we found no effect on tide on offshore bird abundance. We expected bird abundance to be highest between low and high tide, when the tidal current might cause increased turbulent mixing in the wake of the wind park (Schultze et al. 2020) and provide temporary foraging opportunities. Our results indicate that if this effect is present, it did not affect foraging opportunities enough to significantly affect bird abundance, nor was there any other effect of tidal water height found.

The bird observations used in this study were captured by a radar system installed near the Dutch West coast. Compared to the size of the North Sea, the sampling area for the dataset was small (Fig. 1), and thus our findings may also be limited to a specific area on the North Sea. The foraging range of coastal seabirds can differ between (Thaxter et al. 2012) and within species (Redfern and Bevan 2014), and spatial preference can even differ per year within the same colony, as seen in Sandwich terns (Fijn et al. 2017). Therefore, temporal patterns in bird abundance offshore may differ spatially in relation to distance to nearby breeding colonies, the foraging strategies prevalent within those colonies, and per year. The difference in the average seasonal abundance between the years 2019 and 2020 was large (97 birds h^{-1} in 2019 and 126 birds h^{-1} in 2020), though the effect of year as a random effect (0.5%) in the model was small. Additionally, gaps in the data can cause increased uncertainty in the model if data is unavailable for one or both years. As the gaps occur randomly, additional years of data will decrease the influence of these gaps, since it is more likely the full range of environmental conditions of interest will be covered. To separate yearly variability from repeating seasonal patterns and cover the full study period despite the gapped data, multiple years of continuous monitoring are required to illuminate underlying patterns and mechanisms in bird distribution offshore. This shows long-term monitoring is vital to understanding the variability in bird abundance offshore, as has been noted before for tracking studies (Thaxter et al. 2015). Additionally, the question remains whether the findings in this study reflect patterns and processes in other parts

of the North Sea. The inclusion of abundance data from different regions of the North Sea might reveal spatial components affecting the temporal patterns of birds offshore and further reveal the underlying processes that lead to observed patterns. For example, central foragers have a foraging range around their colony (Camphuysen et al. 2015; Garthe et al. 2016), and we suspect the daily observed abundance will differ with distance to shore and/or distance to nearest seabird colonies. Ideally these data should cover long periods of time, and bird radars could fulfil a role here to acquire year-round abundance patterns in multiple locations. Finally, the integration of the measured abundance from bird radar with the intricate biological information which can be gained from bio-logging data would strengthen our capacity to understand the underlying processes influencing bird flight behaviour and distributions offshore (Bauer et al. 2019), also in relation to solving potential conflicts including wind energy and aviation safety (Shamoun-Baranes et al. 2018), and merits future exploration.

The radar used in this study dynamically applies a filter over its observed area to prevent clutter (caused by e.g. rainfall or high waves) from contaminating bird measurements, and therefore birds flying in range of the radar might be filtered out during periods of high filter activity. In our study period, 33% of all hours could not be studied because filtering activity was estimated to be too high to yield accurate results (Table 1, additional elaboration in Online Resource 3). In general these filters become increasingly active as sea state increases or precipitation occurs, thus our results do not reflect bird abundance when sea state is high and during precipitation. Even when filter activity is low, some birds could still be filtered out by the radar software and cause an underestimation of observed bird abundance. However, there was no indication this underestimation was influenced by the variables of the model or had an effect on the model outcome.

Understanding temporal variation in bird abundance at sea can have important implications for wildlife management and estimating the impact of anthropogenic development in an area such as wind farm development, and can improve species distribution estimations at sea. On the DCS the Dutch government plans to produce 11.5GW of offshore wind energy by the end of 2030 (Rijksoverheid 2019) and the cumulative effect of this development on offshore birdlife is difficult to predict. A commonly used method to analyse the impact of wind farms is to determine collision risk through modelling (Masden and Cook 2016). These models incorporate turbine measurements, weather conditions, bird morphometrics, flight speed and altitude, and bird abundance estimations to calculate collision risk for a specific wind farm. The specific methods these models employ can differ, but the majority assumes a linear relationship between bird abundance and collision risk. As we have shown, bird abundance can fluctuate greatly on both an hourly and seasonal scale, and this knowledge can improve the temporal accuracy of collision risk models to better inform policy makers. For example, predictions of collision risk can be used to initiate temporary shutdown of turbine during periods of high bird abundance and with better temporal bird abundance estimations wind farm uptime can be maximized without endangering large numbers of birds.

This study shows that two of the three predictable external factors evaluated in this study, daylight availability and time of the year, affect bird abundance on the North Sea during the breeding season. The third factor, astronomic tide, appears to have no effect. The diurnal pattern in bird abundance shows a distinctive peak in the morning another lower peak later in the afternoon before sunset while it is constantly low during night. The pattern over the breeding season shows an increasing trend until the end of June, after which bird abundance decreases. Due to its capability to monitor bird movements in an area for extended periods of time, bird radar monitoring allows us to discover general patterns in bird movement and, when accounting for its limits, bird radar can continue to play a role in improving our knowledge of the spatial and temporal distribution of birds offshore.

Declarations

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Author contributions

Study was conceived and designed by JAvE, JSB and EEvL. Data collection was performed by JAvE and CJC. Data preparation and processing was performed by JAvE. Statistical analysis was performed by JAvE and EEvL. The first draft of the manuscript was written by JAvE, and all authors contributed to subsequent versions of the manuscript. All authors read and approved the final manuscript.

Conflicts of interest

The authors declare that they have no conflict of interest.

Data availability

Bird radar tracks with the external variables that were used in the data analysis and support the findings of this study are available in the figshare repository <https://doi.org/10.21942/uva.14261609>. ESAS5.0 species distribution counts used in this study are available in the supplementary information (Online Resource 1).

Code availability

The code used in the data processing and analysis is available in the figshare repository <https://doi.org/10.21942/uva.14261609>

Ethical approval

Ethical approval was not applicable to this study as no animal test subjects were involved in this study.

Informed consent

Informed consent for participation was not applicable to this study as no human test subjects were involved.

References

1. Alerstam T, Rosén M, Bäckman J, Ericson PGP, Hellgren O (2007) Flight Speeds among Bird Species: Allometric and Phylogenetic Effects. *PLoS Biol* 5:e197. <https://doi.org/10.1371/journal.pbio.0050197>
2. Annett C, Pierotti R (1989) Chick Hatching as a Trigger for Dietary Switching in the Western Gull. *Colonial Waterbirds* 12:4–11. <https://doi.org/10.2307/1521306>
3. Bauer S, Shamoun-Baranes J, Nilsson C, Farnsworth A, Kelly JF, Reynolds DR, Dokter AM, Krauel JF, Petterson LB, Horton KG, Chapman JW (2019) The grand challenges of migration ecology that radar aeroecology can help answer. *Ecography* 42:861–875. <https://doi.org/10.1111/ecog.04083>
4. Borkenhagen K, Corman A-M, Garthe S (2017) Estimating flight heights of seabirds using optical rangefinders and GPS data loggers: a methodological comparison. *Mar Biol* 165:17. <https://doi.org/10.1007/s00227-017-3273-z>
5. Camphuysen C, Dijk J (1983) Zee- en kustvogels langs de Nederlandse kust, 1974-79. *Limosa* 56:81–230
6. Camphuysen CJ, Gronert A (2010) De broedbiologie van Zilver- en Kleine Mantelmeeuwen op Texel, 2006–2010. *Limosa* 83:145–159
7. Camphuysen CJ, Leopold MF (1994) Atlas of seabirds in the southern North Sea. Netherlands Institute for Sea Research, The Netherlands
8. Camphuysen CJ, Fox AD, Leopold MF, Petersen IK (2004) Towards Standardised Seabirds at Sea Census Techniques in Connection with Environmental Impact Assessments for Offshore Wind Farms in the UK. Report commissioned by CORWRIE. Texel. Royal Netherlands Institute for Sea Research, The Netherlands. <https://doi.org/10.13140/RG.2.1.2230.0244>
9. Camphuysen CJ (1995) Herring Gull *Larus argentatus* and Lesser Black-backed Gull *L. fuscus* feeding at fishing vessels in the breeding season: Competitive scavenging versus efficient flying. *Ardea* 83:365–380
10. Camphuysen CJ, Shamoun-Baranes J, van Loon EE, Bouten W (2015) Sexually distinct foraging strategies in an omnivorous seabird. *Mar Biol* 162:1417–1428. <https://doi.org/10.1007/s00227-015-2678-9>
11. Corman A-M, Garthe S (2014) What flight heights tell us about foraging and potential conflicts with wind farms: a case study in Lesser Black-backed Gulls (*Larus fuscus*). *J Ornithol* 155:1037–1043. <https://doi.org/10.1007/s10336-014-1094-0>
12. Cottaar F, Verbeek-Cottaar J, van Kleinwee M (2018) Onderzoek aan Kleine Mantelmeeuw, Zilvermeeuw en Scholekster op het Forteiland IJmuiden in 2018. Haarlem, The Netherlands. <https://vogeltrekstation.nl/sites/vt/files/Forteiland%2C%20IJmuiden%202018.pdf>. Accessed 18 August 2020
13. Cottaar F, Verbeek-Cottaar J, van Kleinwee M (2020) Onderzoek aan Kleine Mantelmeeuw, Zilvermeeuw en Scholekster op het Forteiland IJmuiden in 2019. Haarlem, The Netherlands. <https://kustfort.nl/wp-content/uploads/2020/02/forteiland-2019.pdf>. Accessed 18 August 2020
14. Desholm M, Kahlert J (2005) Avian collision risk at an offshore wind farm. *Biol Lett* 1:296–298. <https://doi.org/10.1098/rsbl.2005.0336>
15. Dierschke V, Furness RW, Garthe S (2016) Seabirds and offshore wind farms in European waters: Avoidance and attraction. *Biol Cons* 202:59–68. <https://doi.org/10.1016/j.biocon.2016.08.016>
16. Drewitt AL, Langston RHW (2006) Assessing the impacts of wind farms on birds. *Ibis* 148:29–42. <https://doi.org/10.1111/j.1474-919X.2006.00516.x>
17. Fijn RC, Krijgsveld KL, Poot MJM, Dirksen S (2015) Bird movements at rotor heights measured continuously with vertical radar at a Dutch offshore wind farm. *Ibis* 157:558–566. <https://doi.org/10.1111/ibi.12259>
18. Fijn RC, de Jong J, Courtens W, Verstraete H, Stienen EWM, Poot MJM (2017) GPS-tracking and colony observations reveal variation in offshore habitat use and foraging ecology of breeding Sandwich Terns. *J Sea Res* 127:203–211.

<https://doi.org/10.1016/j.seares.2016.11.005>

19. Fijn RC, Arts FA, de Jong JW, Beuker D, Bravo Rebolledo EL, Engels BWR, Hoekstein MSJ, Jonkvorst R-J, Lilipaly S, Sluijter M, van Straalen KD, Wolf PA (2018) Verspreiding en abundantie van zeevogels en zeezoogdieren op het Nederlands Continentaal Plat 2017–2018. Bureau Waardenburg & Delta Project Management, Culemborg. https://puc.overheid.nl/rijkswaterstaat/doc/PUC_154358_31/. Accessed 02 October 2020
20. Fryxell JM, Lundberg P (1998) Individual behavior and community dynamics. Chapman & Hall, London
21. Garthe S, Hüppop O (1996) Nocturnal Scavenging by Gulls in the Southern North Sea. *Colonial Waterbirds* 19:232–241. <https://doi.org/10.2307/1521861>
22. Garthe S, Schwemmer P, Paiva VH, Corman A-M, Fock HO, Voigt CC, Adler S (2016) Terrestrial and Marine Foraging Strategies of an Opportunistic Seabird Species Breeding in the Wadden Sea. *PLoS ONE* 11:e0159630. <https://doi.org/10.1371/journal.pone.0159630>
23. Garthe S, Markones N, Corman A-M (2017) Possible impacts of offshore wind farms on seabirds: a pilot study in Northern Gannets in the southern North Sea. *J Ornithol* 158:345–349. <https://doi.org/10.1007/s10336-016-1402-y>
24. Gyimesi A, Dorenbosch M, de Jong JW, Boonman M, Teunis M, Fijn RC (2019) Achtergronddocument ten behoeve van MER en PB windenergiegebied Hollandse Kust A (Zuid). Bureau Waardenburg, Culemborg. <https://commissiemer.nl/projectdocumenten/00004267.pdf> Accessed 19 October 2020
25. Halpin PN, Read AJ, Fujioka E, Best BD, Donnelly B, Hazen LJ, Kot C, Urian K, LaBrecque E, Dimatteo A, Cleary J, Good C, Crowder LB, Hyrenbach KD (2009) OBIS-SEAMAP: The World data center for marine mammal, sea bird, and sea turtle distributions. *Oceanography* 22:104–115. <https://doi.org/10.5670/oceanog.2009.42>
26. Hersbach H, Bell B, Berrisford P, Biavati G, Horányi A, Muñoz Sabater J, Nicolas J, Peubey C, Radu R, Rozum I, Schepers D, Simmons A, Soci C, Dee D, Thépaut J-N (2018) ERA5 hourly data on single levels from 1979 to present. Copernicus Climate Change Service (C3S) Climate Data Store (CDS). Accessed on 15 September 2020. <https://doi.org/10.24381/cds.adbb2d47>
27. Hersbach H, Bell B, Berrisford P, Hirahara S, Horányi A, Muñoz-Sabater J, Nicolas J, Peubey C, Radu R, Schepers D, Simmons A, Soci C, Abdalla S, Abellan X, Balsamo G, Bechtold P, Biavati G, Bidlot J, Bonavita M, Chiara G, Dahlgren P, Dee D, Diamantakis M, Dragani R, Flemming J, Forbes R, Fuentes M, Geer A, Haimberger L, Healy S, Hogan RJ, Hólm E, Janisková M, Keeley S, Laloyaux P, Lopez P, Lupu C, Radnoti G, Rosnay P, Rozum I, Vamborg F, Villaume S, Thépaut J (2020) The ERA5 global reanalysis. *QJR Meteorol Soc* 146:1999–2049. <https://doi.org/10.1002/qj.3803>
28. Hüppop O, Dierschke J, Exo K-M, Fredrich E, Hill R (2006) Bird migration studies and potential collision risk with offshore wind turbines. *Ibis* 148:90–109. <https://doi.org/10.1111/j.1474-919X.2006.00536.x>
29. Johnston A, Cook ASCP, Wright LJ, Humphreys EM, Burton NHK (2014) Modelling flight heights of marine birds to more accurately assess collision risk with offshore wind turbines. *J Appl Ecol* 51:31–41. <https://doi.org/10.1111/1365-2664.12191>
30. Krijgsveld KL, Fijn RC, Japink M, van Horssen PW, Heunks C, Collier MP, Poot MJM, Beuker D, Dirksen S (2011) Effect studies Offshore Wind Farm Egmond aan Zee. Bureau Waardenburg. <https://tethys.pnnl.gov/publications/effect-studies-offshore-wind-farm-egmond-aan-zee-final-report-fluxes-flight-altitudes>. Accessed 19 October 2020
31. Lack D (1959) MIGRATION ACROSS THE NORTH SEA STUDIED BY RADAR PART 1. SURVEY THROUGH THE YEAR. *Ibis* 101:209–234. <https://doi.org/10.1111/j.1474-919X.1959.tb02376.x>
32. Lindeboom HJ, Kouwenhoven HJ, Bergman MJN, Bouma S, Brasseur S, Daan R, Fijn RC, de Haan D, Dirksen S, van Hal R, Hille Ris Lambers R, ter Hofstede R, Krijgsveld KL, Leopold M, Scheidat M (2011) Short-term ecological effects of an offshore wind farm in the Dutch coastal zone; a compilation. *Environmental Research Letters* 6:035101. <https://doi.org/10.1088/1748-9326/6/3/035101>
33. Lund U, Agostinelli C (2017) circular: Circular Statistics. Version 0.4–93. <https://cran.r-project.org/web/packages/circular/index.html>

34. Masden EA, Cook ASCP (2016) Avian collision risk models for wind energy impact assessments. *Environ Impact Assess Rev* 56:43–49. <https://doi.org/10.1016/j.eiar.2015.09.001>
35. Plonczkier P, Simms IC (2012) Radar monitoring of migrating pink-footed geese: behavioural responses to offshore wind farm development. *J Appl Ecol* 49:1187–1194. <https://doi.org/10.1111/j.1365-2664.2012.02181.x>
36. R Core Team (2020) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna
37. Redfern CPF, Bevan RM (2014) A comparison of foraging behaviour in the North Sea by Black-legged Kittiwakes *Rissa tridactyla* from an inland and a maritime colony. *Bird Study* 61:17–28. <https://doi.org/10.1080/00063657.2013.874977>
38. Reid J, Camphuysen CJ (1998) The European Seabirds at Sea database. In: Spina S. & Grattarola A. (eds). *Proceedings of the 1st meeting of the European Orn Union Biol Cons Fauna* 102:291
39. Rijksoverheid (2015) Nationaal Waterplan 2016–2021. Dutch Ministry of Economic Affairs, The Hague. <https://www.rijksoverheid.nl/documenten/beleidsnota-s/2015/12/14/nationaal-waterplan-2016-2021>. Accessed 09 February 2021
40. Rijksoverheid (2019) Klimaatakkoord. Rijksoverheid, The Hague. <https://www.rijksoverheid.nl/onderwerpen/klimaatverandering/documenten/rapporten/2019/06/28/klimaatakkoord>. Accessed 01 October 2020
41. Rijkswaterstaat (2020) Rijkswaterstaat Waterinfo. In: Rijkswaterstaat Waterinfo. <https://waterinfo.rws.nl/#!/nav/expert/>. Accessed 19 Oct 2020
42. Ross-Smith VH, Thaxter CB, Masden EA, Shamoun-Baranes J, Burton NHK, Wright LJ, Rehfish MM, Johnston A (2016) Modelling flight heights of lesser black-backed gulls and great skuas from GPS: a Bayesian approach. *J Appl Ecol* 53:1676–1685. <https://doi.org/10.1111/1365-2664.12760>
43. Schmid B, Zaugg S, Votier SC, Chapman JW, Boos M, Liechti F (2019) Size matters in quantitative radar monitoring of animal migration: estimating monitored volume from wingbeat frequency. *Ecography* 42:931–941. <https://doi.org/10.1111/ecog.04025>
44. Schultze LKP, Merckelbach LM, Horstmann J, Raasch S, Carpenter JR (2020) Increased mixing and turbulence in the wake of offshore wind farm foundations. *Journal Geophysical Research: Oceans* 125:e2019JC015858. <https://doi.org/10.1029/2019JC015858>
45. Schwemmer P, Garthe S (2005) At-sea distribution and behaviour of a surface-feeding seabird, the lesser black-backed gull *Larus fuscus*, and its association with different prey. *Mar Ecol Prog Ser* 285:245–258. <https://doi.org/10.3354/meps285245>
46. Shamoun-Baranes J, van Loon EE, Liechti F, Bouten W (2007) Analyzing the effect of wind on flight: pitfalls and solutions. *J Exp Biol* 210:82–90. <https://doi.org/10.1242/jeb.02612>
47. Shamoun-Baranes J, Bouten W, van Loon EE, Meijer C, Camphuysen CJ (2016) Flap or soar? How a flight generalist responds to its aerial environment. *Philos Trans R Soc Lond B Biol Sci* 371:20150395. <https://doi.org/10.1098/rstb.2015.0395>
48. Shamoun-Baranes J, van Gasteren H, Ross-Smith V (2018) Sharing the Aerosphere: Conflicts and Potential Solutions. In: Chilson P, Frick W, Kelly J, Liechti F (eds) *Aeroecology*. Springer, Cham, pp 465–497
49. Shealer DA (2002) Foraging behavior and food of seabirds. In: Schreiber EA, Burger J (eds) *Biology of Marine Birds*. CRC Press, Boca Raton, pp 137–178
50. Spaans AL (1971) On the feeding ecology of the Herring Gull *Larus argentatus* Pont. in the northern part of the Netherlands. *Ardea* 55:73–188. <https://doi.org/10.5253/arde.v59.p73>

51. Spear LB, Ainley DG (1997) Flight speed of seabirds in relation to wind speed and direction. *Ibis* 139:234–251. <https://doi.org/10.1111/j.1474-919X.1997.tb04621.x>
52. Thaxter CB, Lascelles B, Sugar K, Cook ASCP, Roos S, Bolton M, Langston RHW, Burton NHK (2012) Seabird foraging ranges as a preliminary tool for identifying candidate Marine Protected Areas. *Biol Cons* 156:53–61. <https://doi.org/10.1016/j.biocon.2011.12.009>
53. Thaxter CB, Ross-Smith VH, Bouten W, Clark NA, Conway GJ, Rehfish MM, Burton NHK (2015) Seabird–wind farm interactions during the breeding season vary within and between years: A case study of lesser black-backed gull *Larus fuscus* in the UK. *Biol Cons* 186:347–358. <https://doi.org/10.1016/j.biocon.2015.03.027>
54. Thaxter CB, Ross-Smith VH, Bouten W, Masden EA, Clark NA, Conway GJ, Barber L, Clewley GD, Burton NHK (2018) Dodging the blades: new insights into three-dimensional space use of offshore wind farms by lesser black-backed gulls *Larus fuscus*. *Mar Ecol Prog Ser* 587:247–253. <https://doi.org/10.3354/meps12415>
55. Thieurmel B, Elmarhraoui A (2019) suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase. Version 0.5.0. <https://cran.r-project.org/web/packages/suncalc/index.html>
56. Tyson C, Shamoun-Baranes J, van Loon EE, Camphuysen CJ, Hintzen NT (2015) Individual specialization on fishery discards by lesser black-backed gulls (*Larus fuscus*). *ICES J Mar Sci* 72:1882–1891. <https://doi.org/10.1093/icesjms/fsv021>
57. Urmey S, Warren J (2018) Foraging hotspots of common and roseate terns: the influence of tidal currents, bathymetry, and prey density. *Mar Ecol Prog Ser* 590:227–245. <https://doi.org/10.3354/meps12451>
58. van Donk S, Camphuysen CJ, Shamoun-Baranes J, van der Meer J (2017) The most common diet results in low reproduction in a generalist seabird. *Ecol Evol* 7:4620–4629. <https://doi.org/10.1002/ece3.3018>
59. Vanermen N, Courtens W, Daelemans R, Lens L, Müller W, van de Walle M, Verstraete H, Stienen EWM (2019) Attracted to the outside: a meso-scale response pattern of lesser black-backed gulls at an offshore wind farm revealed by GPS telemetry. *ICES J Mar Sci* 77:701–710. <https://doi.org/10.1093/icesjms/fsz199>
60. Wetterer JK (1989) Central place foraging theory: When load size affects travel time. *Theor Popul Biol* 36:267–280. [https://doi.org/10.1016/0040-5809\(89\)90034-8](https://doi.org/10.1016/0040-5809(89)90034-8)
61. Wood S (2020) Mixed GAM Computation Vehicle with Automatic Smoothness Estimation. Version 1.8–33. <https://cran.r-project.org/web/packages/mgcv/index.html>

Figures

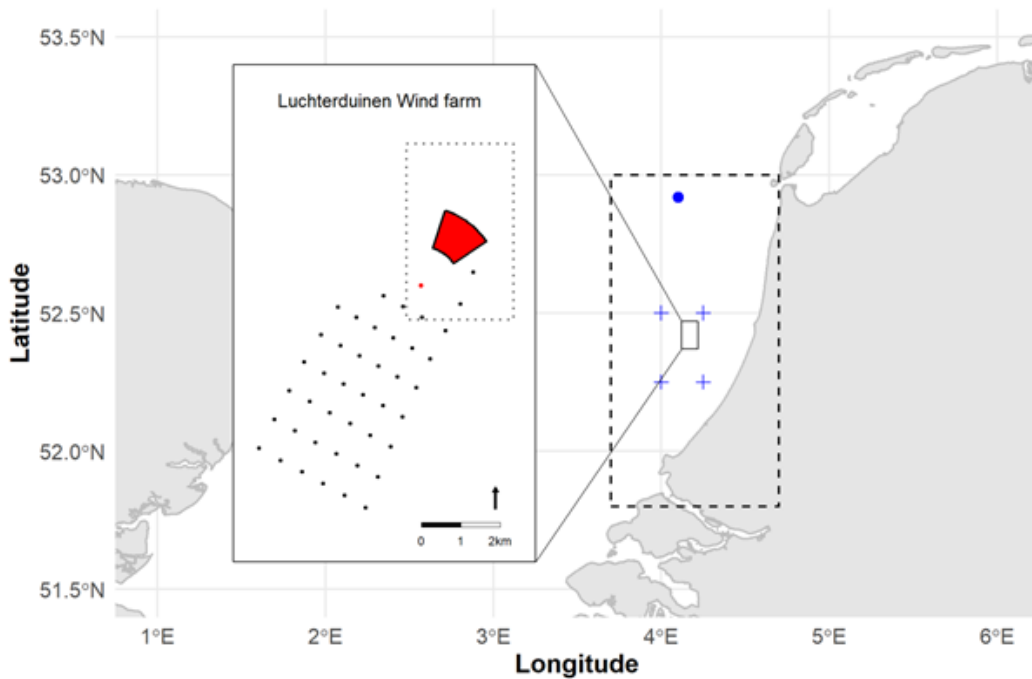


Figure 1

Overview of the sample area and Luchterduinen offshore wind farm (box) and the position of the radar in relation to the coast of the Netherlands (map). Map: tidal water height was measured at Hoorn platform (blue dot, 52.92064°N, 4.09822°E), blue plusses indicate the resolution grid of ERA5 data (0.25° Lon-Lat grid), and ESAS5.0 species observation data was sampled between 51.8°N-53°N and 3.7°E-4.7°E (dashed black square). Box: black dots show the individual turbines, the red dot shows the turbine that has the radar-system installed (52.42783°N, 4.18535°E). The 1km² area of interest is shown in red with black lining; it is delimited by the 1000 and 2000m ranges and the 22.5° and 60.7° azimuth angles from the radar. The dotted grey square shows the grid cell from which ERA5 reanalysis data were sampled Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

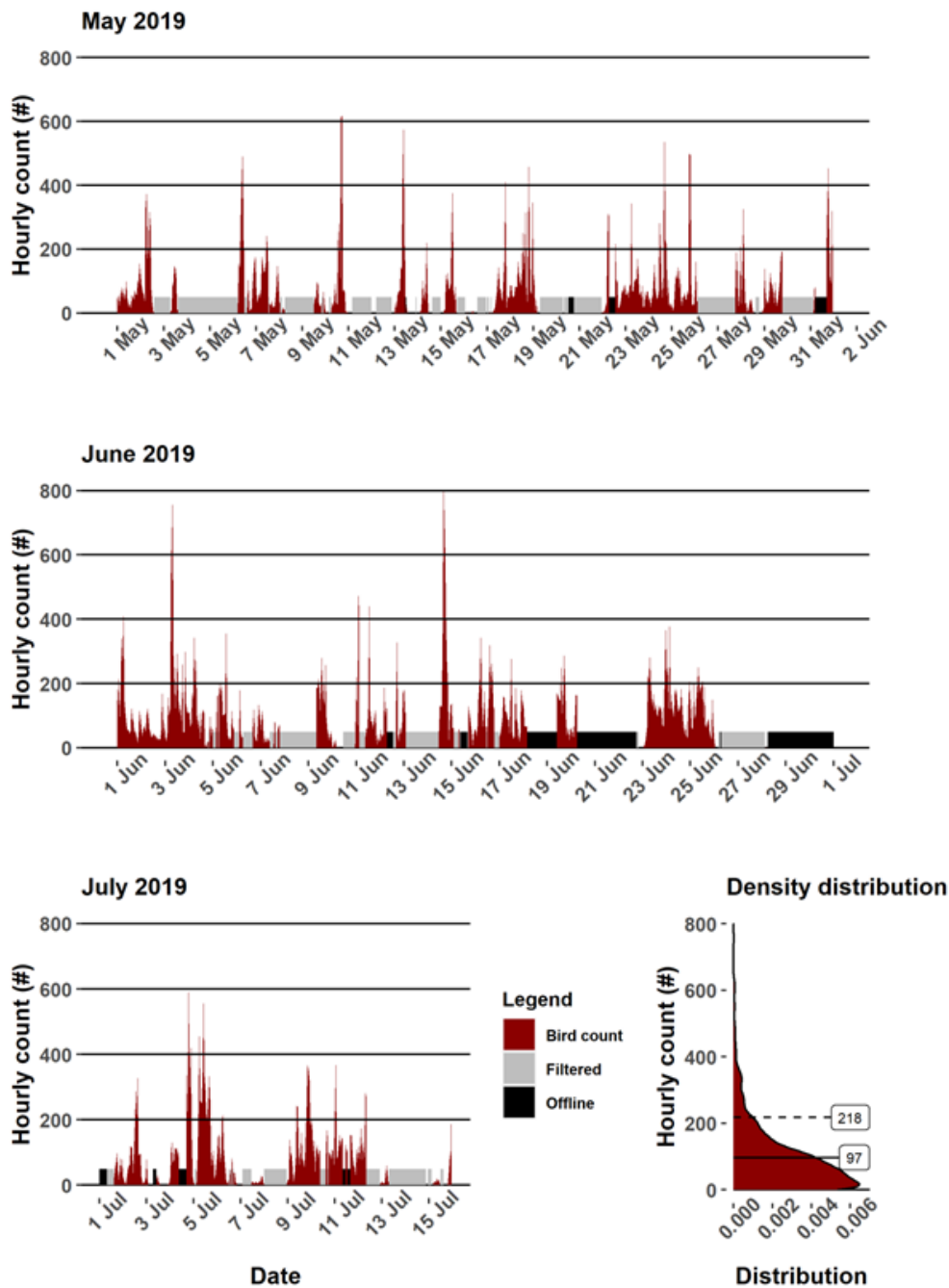


Figure 2

Overview of hourly bird abundance in 2019 (in dark red) per month, with kernel density distribution of the data (bottom-right corner). Grey columns show hours in which filter activity was too high for accurate recordings, while black columns show hours the radar was offline. The Y-axis of all figures is limited to 800 birds h-1 for better interpretation; one outlier (2019-06-14 1600, 1401 birds) is therefore capped to 800 birds. The horizontal black lines in the density distribution graph show the mean (black line) and 90th percentile (dashed black line) of the distribution

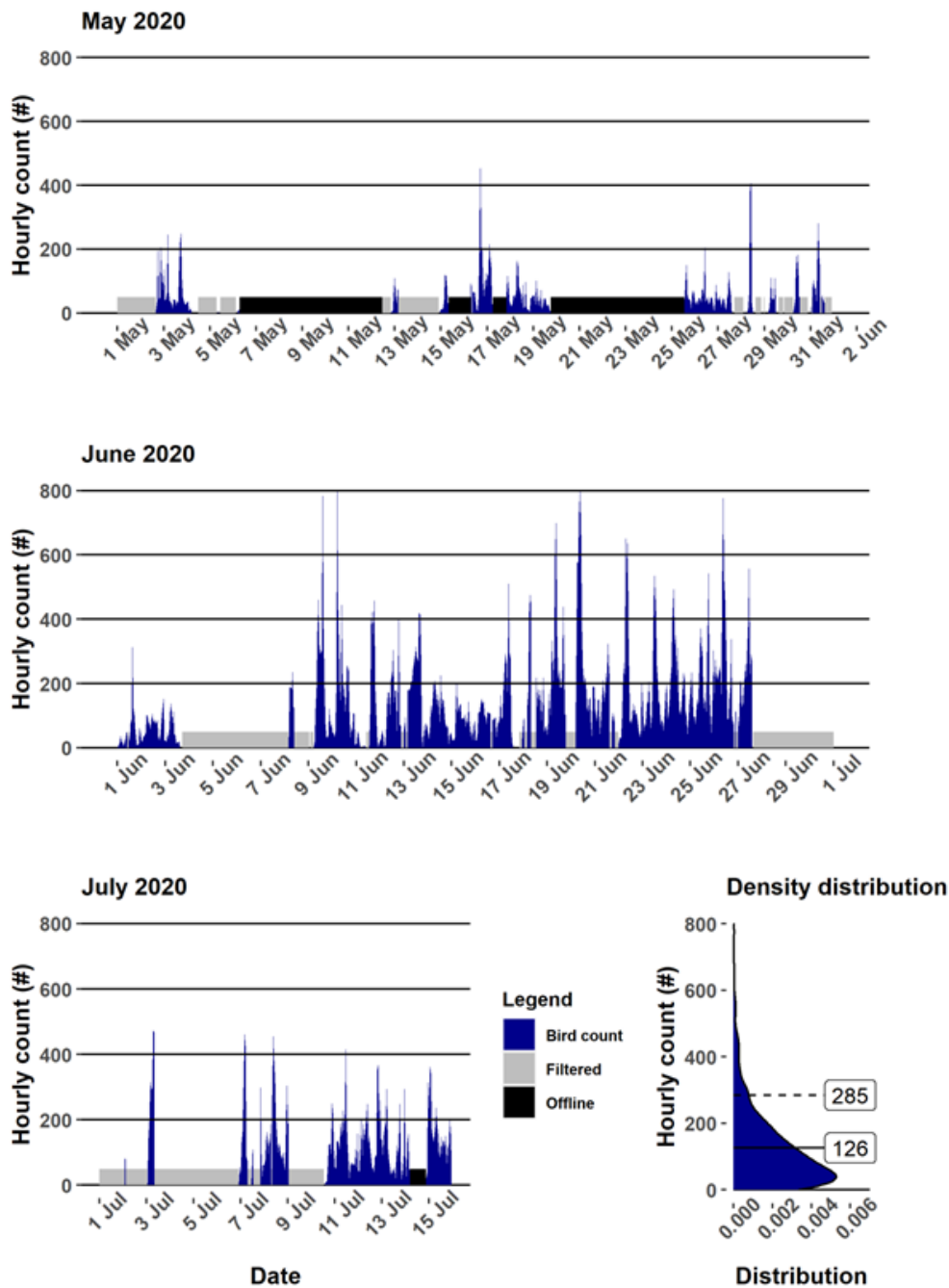


Figure 3

Overview of hourly bird abundance in 2020 (in dark blue) per month, with kernel density distribution of the data (bottom-right corner). Grey columns show hours in which filter activity was too high for accurate recordings, while black columns show hours the radar was offline. The Y-axis of all figures is limited to 800 birds h⁻¹ for better interpretation; two outliers (2020-06-10 0500, 804 birds; 2020-06-20 0900, 820 birds) are therefore capped to 800 birds. The horizontal black lines in the density distribution graph show the mean (black line) and 90th percentile (dashed black line) of the distribution

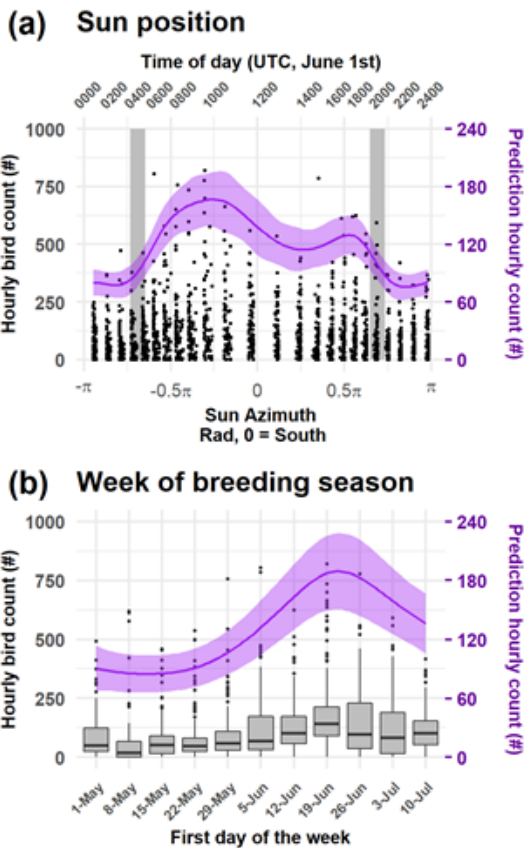


Figure 4

Smoothed effects of the significant individual predictors in the hourly abundance model. Left Y-axis shows hourly bird count (black dots / boxplots), whereas the right Y-axis shows predicted hourly bird count (purple line = mean, area = mean ± 2 se). a) Effect of sun position (sun azimuth). Azimuth in radians from South (bottom X-axis). Sunrise occurs between Azimuth = $-.73\pi$ to $-.64\pi$, sunset between Azimuth = $.64\pi$ to $.73\pi$, indicated by the grey areas. For readability, associated timestamps (UTC) for June 1st are displayed on the top X-axis. B) Effect of week in the breeding season, date indicates the first day of each week (bottom X-axis)

Supplementary Files

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- [ESM4JvEAbundancepatterns.docx](#)