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Avoidance of offshore wind farms by Sandwich Terns increases with turbine density

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ABSTRACT

The expanding use of wind farms as a source of renewable energy can impact bird populations due to collisions and other factors. Globally, seabirds are one of the avian taxonomic groups most threatened by anthropogenic disturbance; adequately assessing the potential impact of offshore wind farms (OWFs) is important for developing strategies to avoid or minimize harm to their populations. We estimated avoidance rates of OWFs—the degree to which birds show reduced utilization of OWF areas—by Sandwich Terns (*Thalasseus sandvicensis*) at 2 breeding colonies in western Europe: Scolt Head (United Kingdom) and De Putten (the Netherlands). The foraging ranges of birds from each colony overlapped with multiple OWFs. We modeled GPS tracking data using integrated step selection functions (iSSFs) to estimate the relative selection of habitats at the scale of time between successive GPS relocations—in our case, 10 min, in which Sandwich Terns traveled ~2 km on average. Besides the effects of OWFs and the direct surroundings of OWFs, iSSFs considered distance from the colony and habitat characteristics (water depth and sediment grain size) as well as movement characteristics. Macro-avoidance rates, where 1 means complete avoidance, were estimated at 0.54 (95% CI: 0.35, 0.7) for birds originating from Scolt Head and 0.41 (95% CI: 0.21, 0.56) for those from De Putten. Estimates for individual OWFs also indicated avoidance but were associated with considerable uncertainty. Our results were inconclusive with regard to the behavioral response to the areas directly surrounding OWFs (within 1.5 km); estimates suggested indifference and avoidance, and were associated with large uncertainty. Avoidance rate of OWFs significantly increased with turbine density, suggesting that OWF design may help to reduce the impact of OWFs on Sandwich Terns. The partial avoidance of OWFs by Sandwich Terns implies that the species will experience risks of collision and habitat loss due to OWFs constructed within their foraging ranges.

Keywords: integrated step selection functions, macro-avoidance, movement, offshore wind farms, Sandwich Terns, seabirds, *Thalasseus sandvicensis*

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LAY SUMMARY

- To assess the effect of offshore wind farms (OWFs) on seabirds, we need to know whether birds enter OWF areas or avoid them.
- We studied the movements of GPS-tracked Sandwich Terns (*Thalasseus sandvicensis*) from 2 colonies in western Europe, where multiple OWFs are within the distance that the terns usually travel on their daily trips. We calculated how likely they were to venture into the OWF areas, while accounting for how fast and winding they usually fly.
- Based on the tracked movements, Sandwich Terns reduced their use of the OWF areas by an average of 41% at one colony and 54% at the other, compared to what we expected. They avoided wind farms more when the turbines were closer together.
- The results can be used to calculate how many Sandwich Terns fly through an OWF, which is important for calculating the number of potential collision victims. Our study indicates that the impact of OWFs on the space use of Sandwich Terns can be reduced by building OWFs outside their regular foraging range and by placing turbines farther apart.

La evitación de las granjas eólicas marinas por parte de *Thalasseus sandvicensis* aumenta con la densidad de las turbinas

RESUMEN

La creciente utilización de parques eólicos como fuente de energía renovable puede afectar a las poblaciones de aves debido a colisiones y otros factores. A nivel mundial, las aves marinas son uno de los grupos taxonómicos de aves más amenazados por los disturbios antropogénicos; evaluar adecuadamente el impacto potencial de las granjas eólicas marinas (GEMs) es importante para desarrollar estrategias que eviten o

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minimicen el daño a sus poblaciones. Estimamos las tasas de evitación de GEMs—el grado en el que las aves muestran una reducción en la utilización de áreas de GEMs—por parte de *Thalasseus sandvicensis* en dos colonias de cría en Europa occidental: Scolt Head (Reino Unido) y De Putten (Países Bajos). Los rangos de forrajeo de las aves de cada colonia se superponían con varias GEMs. Modelamos los datos de seguimiento por GPS utilizando funciones de selección de pasos integradas (FSPIs) para estimar la selección relativa de hábitats a la escala de tiempo entre sucesivas reubicaciones de GPS; en nuestro caso, cada 10 minutos, en los cuales los individuos de *T. sandvicensis* se desplazaron en promedio ~2 km. Además de los efectos de las GEMs y de sus alrededores directos, las FSPIs consideraron la distancia desde la colonia y las características del hábitat (profundidad del agua y tamaño de los granos de sedimento), así como las características del movimiento. Las tasas de evitación a nivel macro, donde 1 significa una evitación completa, se estimaron en 0.54 (95% IC: 0.35, 0.7) para las aves originarias de Scolt Head y 0.41 (95% IC: 0.21, 0.56) para las de De Putten. Las estimaciones para las GEMs individuales también indicaron evitación, pero estuvieron asociadas con una considerable incertidumbre. Nuestros resultados no fueron concluyentes con respecto a la respuesta conductual a las áreas que rodean directamente a las GEMs (dentro de 1.5 km); las estimaciones sugirieron indiferencia y evitación, y estuvieron asociadas con una gran incertidumbre. La tasa de evitación de las GEMs aumentó significativamente con la densidad de las turbinas, lo que sugiere que el diseño de las GEMs puede ayudar a reducir el impacto de las GEMs en *T. sandvicensis*. La evitación parcial de las GEMs por parte de *T. sandvicensis* implica que la especie experimentará riesgos de colisión y pérdida de hábitat debido a las GEMs construidas dentro de sus áreas de forrajeo.

Palabras clave: aves marinas, funciones de selección de pasos integradas, granjas eólicas marinas, macro-evitación, movimiento, Thalasseus sandvicensis

INTRODUCTION

Antropogenic infrastructures can impact birds through increased direct mortality and habitat loss. For example, seabirds can be impacted by offshore wind farms (OWFs) through increased collision risk and displacement through habitat loss if birds avoid OWFs (Stienen et al. 2007, Furness et al. 2013, Dierschke et al. 2016, Welcker and Nehls 2016). With the expansion of OWF development by countries worldwide to meet renewable energy targets (GWEC 2022), the potential for adverse effects of OWFs on seabirds will increase, which could eventually lead to population declines (Dierschke et al. 2016). Seabirds are among the most threatened taxonomic groups among birds globally (Croxall et al. 2012); thus, measuring the effects of current OWFs on seabirds is important to inform predictions of the cumulative effect of future OWFs on seabird populations.

An important driver of both collision rates and habitat loss is the degree to which seabirds show avoidance of, or attraction to OWFs (Dierschke et al. 2016). Avoidance behavior is usually characterized at three spatial levels: macro-scale (avoidance of the entire OWF), meso-scale (avoidance of the turbines, once a bird has entered the OWF), and micro-scale (avoidance of individual rotor blades once the bird is approaching the rotor-swept area) (May 2015, Cook et al. 2018), and attraction can be conceptualized at the same spatial scales (Vanermen et al. 2019). Since the construction of the first OWFs, efforts have been made to estimate avoidance and attraction rates, the decreased or increased utilization relative to a reference situation such as the pre-construction period or a reference area (Cook et al. 2018). Nevertheless, due to logistic and methodological difficulties, robust estimates of avoidance and attraction rates, even at coarse macro-scales, are lacking for many seabird species, including those of high conservation concern or those vulnerable to OWFs (Furness et al. 2013). The lack of macro-avoidance rates hampers accurate assessment of potential impacts from OWFs.

Besides the location where OWFs are developed, the design of individual turbines and of the whole OWF is likely to also determine the impact on birds. For example, OWFs with larger, but more widely spaced wind turbines may be associated with lower collision risks as larger wind turbines rotor swept zone is positioned higher and therefore overlaps less with flight heights of birds (Krijgsveld et al. 2009, Johnston et al. 2014). In addition, more widely spaced turbines may be associated with lower macro-avoidance rates (Masden et al. 2012), which reduces the degree of habitat loss, but may be associated with higher collision rates. Showing an association between turbine density and macro-avoidance rates is challenging, as it requires data from multiple OWFs with a range of turbine densities, uniform data collection protocols, and sufficiently high bird densities (cf. Zuur 2018).

Macro-avoidance or attraction rates can be estimated from seabird densities within and outside the OWF, preferably before and after construction of the OWF to quantify the effect of location. Responses can be estimated from ship-based seabird surveys (Leopold et al. 2013, Welcker and Nehls 2016), aerial surveys (Bradbury et al. 2014), radar data (Krijgsveld et al. 2011, Skov et al. 2018), or tracking data of individual seabirds (Peschko et al. 2020, Johnston et al. 2022). Tracking data provide continuous information in time and space about the presence of individuals, but no direct information on the areas not used. Therefore, to use tracking data within a habitat-selection framework, models must be specified that compare conditions (e.g., the presence of an OWF) at positions visited by the animal ("used" positions, that is the tracking data) with those at positions that were available to the animal, but not used at that time ("available" positions) (Boyce and McDonald 1999). The relationships between used and available positions can then be modeled as a function of environmental characteristics, such as distance from the colony, as well as the presence of an OWF. The coefficients from habitat-selection models indicate the preferential use or avoidance of locations with certain characteristics, such as habitat conditions or the presence of an OWF. From the several types of habitat-selection models available, integrated step selection functions (iSSFs) model both the habitat selection process and the movement process. This is achieved by comparing used locations to the locations available to the individual from its previous location, taking into account distance and turning angles between subsequent positions (Avgar et al. 2016). Providing a sufficient sample size of individuals tracked for long enough times, iSSFs are also suitable for estimating macro-avoidance and attraction because they provide unbiased and robust parameter estimates and can be fitted using freely available and open-source software (Avgar et al. 2016; Fieberg et al. 2021; Mercker et al. 2021).

One of the species for which current estimates of macro-avoidance rates could be improved is the Sandwich Tern (*Thalasseus sandvicensis*). The Sandwich Tern is a colonially breeding seabird, usually foraging at sea targeting pelagic fish, in particular Atlantic herring (*Clupea harengus*), European sprat (*Sprattus sprattus*), and sandeel (*Ammodytidae* spp.) (Veen 1977, Stienen et al. 2000). Foraging trips from the colony are mostly restricted to ~40 km from the colony, but longer trips are occasionally made for foraging and prospecting other colonies (Fijn et al. 2017, Kralj et al. 2023). Foraging behavior is associated with shallow water and coarse sediments (Fijn et al. 2022), which are preferred by sandeel (Baerwald and Barclay 2016). The species has been identified as being potentially sensitive to OWFs, showing partial avoidance behavior and thus reduced abundances within those areas (Dierschke et al. 2016, Harwood et al. 2017), and the high predicted number of collisions (using Collision Risk Models; Band 2012) of this species have led to refusal of planning consent for one OWF in British waters (Broadbent and Nixon 2019). Although most studies indeed report partial avoidance of OWFs by Sandwich Terns (Dierschke et al. 2016, Harwood et al. 2017), attraction to OWFs, at least to their fringes, has also been suggested to occur, because turbulence potentially creates foraging opportunities (Vanermen et al. 2013, Lieber et al. 2019). Using iSSFs and GPS tracking data collected at 2 colonies in the southern North Sea, we (1) estimated the macro-scale response of breeding Sandwich Terns to operational OWFs and their direct surroundings, (2) compared responses to OWFs between 2 colonies with different bathymetry and sediment distribution around the colonies, and (3) tested for relationships between characteristics of the 7 OWFs studied (distance from colony, OWF surface area and turbine density) and avoidance/attraction rates. Considering earlier studies, we predicted partial avoidance of OWFs, with higher avoidance at the denser OWFs.

METHODS

Fieldwork

Adult Sandwich Terns were captured on the nest, using walk-in traps, in the colonies of De Putten, Camperduin, the Netherlands (N52°44′ E4°39) in 2019–2021 and at Scolt Head, Norfolk, United Kingdom (N52°59′ E0°40) in 2016–2019 (Figure 1), during the second or third week of incubation. Individuals weighing >220 g were selected for GPS-logger deployment. In total, 63 individuals were tagged at De Putten and 43 at Scolt Head. Additional data were included from 2 individuals GPS-tagged at the Slijkplaat, Zuid-Holland, the Netherlands (N51°48′ E4°09) in 2021 that relocated for a second breeding attempt at De Putten in that year (Fijn and van Bemmelen 2023). In addition, data were obtained from 7 individuals tagged in 2021 in the Netherlands that bred at De Putten in 2022.

Ecotone GPS-UHF loggers with solar panels (Ecotone, model PICA, ~4.5 g, 35 × 12 × 8 mm) were attached using a full-body harness constructed from fishing elastic (Preston Innovations Slip Elastic, diameter: 1.4–2.2 mm), which disintegrated over ~1.5 months, or, in 2021, from 2 mm wide Teflon, which is relatively permanent. The combined weight of the logger, harness, and rings was 6.3 g, which represented 2.3%–2.8% of the body mass, thus staying below the generally accepted limit of 3% (Phillips et al. 2003, Vandenabeele 2013). GPS loggers were pre-set to record positions between 5:00 and 21:00 local time, taking positions at intervals of 5, 10, or 15 min, depending on year, location, and the battery voltage. GPS loggers automatically transmitted the tracking data to base stations positioned at each colony.

Avoidance of and Attraction to OWFs

Integrated step selection functions were used to assess the degree to which Sandwich Terns avoided or were attracted to offshore wind farms, because they provide unbiased and robust parameter estimates and can be fitted using freely available and open-source software (Avgar et al. 2016; Fieberg et al. 2021; Mercker et al. 2021). Discrete-time step selection functions require regular time intervals between subsequent positions. Selecting an appropriate time interval involves balancing the number of interpolated positions with the spatial and temporal resolution. Here, we regularized tracking data to time intervals between positions of 10 min (with each set of 2 subsequent positions called a "step"), considering most data were collected at intervals of 5 or 10 min (15 min data concerned only some loggers at De Putten in 2019), with linear interpolation of positions across time gaps no longer than 35 min (thus, a maximum of 2 positions). In addition, 10-min intervals were chosen because at this time interval, most step lengths were <5 km, and OWFs will—under most weather circumstances—be easily visible to the birds at this range. For each used step, random steps from the first position were generated from the sea (as none of the used positions were on land) using the random_steps function from the amt package (Signer et al. 2019), which first fits a gamma distribution to the observed step lengths and a von Mises distribution to the observed turning angles and subsequently samples from these distributions. Whereas usually about 10–20 random steps per used step suffices in SSFs, estimating the selection strength of relatively rare habitats requires larger samples (Thurfjell et al. 2014). We generated 50 random steps per used step, which produced parameter estimates that were stable across model runs. At the endpoint of each used or available step, water depth (EMODnet website, www.emodnet.eu, data from 2018, spatial resolution of 1/16 × 1/16 arc min or about 115 × 115 m), median grain size (D_{50}) of the bottom sediment (Bockelmann et al. (2018), spatial resolution of 1852 × 1852 m, obtained from, hereafter referred to as "sediment") and the distance to the colony (avoiding overland routes) were extracted. Sediment was heavily left-skewed and therefore log-transformed. Water depth and sediment were included in the iSSFs following the study by Fijn et al. (2022), which indicated that these were the most important factors in explaining the switch to foraging behavior in Sandwich Terns; we therefore expect they also drive movement patterns in the terns in our study. Water depth, sediment, and distance to the colony were standardized within the data sets for each colony to allow comparison of effect sizes within models. To avoid overfitting of models, no additional environmental variables were added other than our primary interest, the presence in or proximity to OWF. Wind turbine positions were obtained from Zhang et al. (2021) and turbines from Lincs, Lynn, and Inner Dowsing OWFs were combined for statistical analyses as these OWFs border each other and buffers would overlap. Around the outer row of turbines of each OWF, a convex hull was drawn, as well as a distance band of 0–1.5 km around the convex hull. The distance of 1.5 km was selected considering the scale at which turbulence around turbines may attract terns (tens to hundreds of meters; Lieber et al. (2019), Schultze et al. (2020)) and to obtain a large enough sample size of bird positions within the distance band. OWFs were only included when tracking data positions fell within their perimeters (Figure 1). These OWFs were Eneco Luchterduinen, Prinses Amaliawindpark, and Egmond aan Zee near De Putten and Sheringham Shoal, Race Bank, Dudgeon, and Lincs/Lynn/Inner Dowsing wind farms near Scolt Head. Other operational OWFs were not

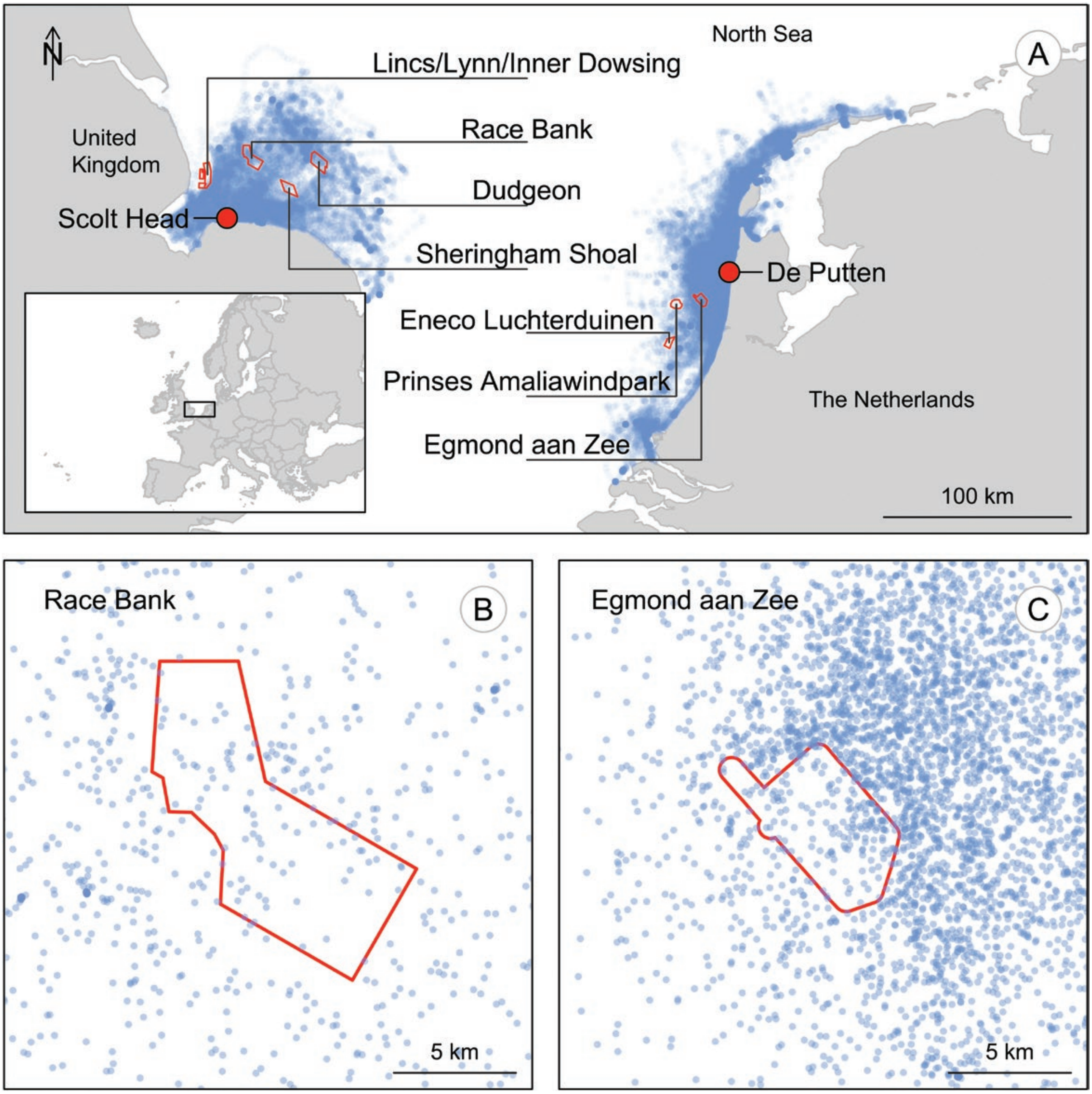

FIGURE 1. (**A**) Tracking data of Sandwich Terns (small dots) breeding in the Scolt Head (United Kingdom) and De Putten (the Netherlands) colonies (large dots) and offshore wind farms (OWFs; outlined polygons): 6 OWFs (of which 3 were combined for analyses) near Scolt Head and three near De Putten. Note that in the integrated step selection functions (iSSFs), only steps have been included in which at least one of the used or available positions were within 10 km of an OWF. This causes the rather sharp cut-off of positions north of De Putten. The inset shows the study area within Europe. Enlarged examples of 2 OWFs: (**B**) Race Bank OWF (United Kingdom) and (**C**) Egmond aan Zee OWF (OWEZ, the Netherlands).

considered as they were far outside the foraging ranges of the 2 colonies (>100 km) and no bird positions were recorded within these OWFs.

We aimed to quantify the overall avoidance/attraction rates of OWFs and their 1.5 km distance bands, as well as avoidance/attraction rates per OWF. Only steps were selected in which at least one of the used or available positions was within an OWF or distance band, thus where the OWF or its distance band were available. Given the environment (e.g., bathymetry) is rather different between the two colonies, and therefore the habitat selected by Sandwich Terns potentially as well, separate models were fitted for each colony.

Two iSSFs were fitted per colony (Equation (1)). The first iSSF included a categorical fixed effect with 3 levels indicating whether a position was outside OWFs and distance bands (the base level), within OWF perimeters (β_1) or within a OWF distance band (β_2). In the second iSSF, this categorical fixed effect included either 7 levels (De Putten, with 3 OWFs) or 9 levels (Scolt Head, with 4 OWFs) indicating a position was outside any OWFs and distance bands (the base level), within which OWF perimeters ($\beta_{1a,1b,\ldots,1n}$), or in within which OWF distance bands ($\beta_{2a,2b,\ldots,2n}$). iSSFs included the available (coded as 0) and used (coded as 1) steps as the response variable. In addition

TABLE 1. Sample size of tracking data for each colony, within 10 km from offshore wind farms (OWFs).

Colony	Number of individuals	Number of positions	Number of positions in OWFs	Number of positions in distance bands
De Putten	60	47,024	99	382
Scolt Head	32	11,694	150	270

to the effect of OWFs and their distance bands, water depth (wd), sediment median grain size (gs), and distance to the colony (dc) (all standardized) were also included as fixed effects. Finally, step length (sl), the log of step length, and the cosinus of the turning angle (ta) were included as fixed effects, as including these tends to reduce bias in parameter estimation (Forester et al. 2009). Step ID s was included as a random intercept u_s, with the variance of the random intercept for step ID fixed at 10^6 (Muff et al. 2020), which renders the likelihood of this model equivalent to a conditional logistic regression model (Aarts et al. 2012, Fithian and Hastie 2013). For all covariates, random slopes $u_{1–4}$ were included per individual i, with penalized complexity priors with scale parameter 3 and probability parameter 0.05 for their precisions. Models were fitted as Poisson models using integrated nested Laplace approximation as implemented in the R-INLA *package* version 21.02.23 (Lindgren and Rue 2015). All calculations were performed in *R* version 4.2.2 (R Core Team 2022).

$$y_i \sim \exp\begin{pmatrix}\beta_0 + \beta_1\mathrm{OWF}_{is} + \beta_2\mathrm{band}_{is} + \beta_3 dc_{is} + \beta_4 wd_{is} + \beta_5 gs_{is} + \beta_6 sl_{is} + \\ \beta_7\log(sl_{is}) + \beta_8\cos(ta_{is}) + u_s + u_{1i}\mathrm{OWF}_i + u_{2i}dc_i + u_{3i}wd_i + u_{4i}gs_i\end{pmatrix} \tag{1}$$

The relative use of OWFs and distance bands compared to the surrounding sea (within the distribution of used and available positions) was calculated following instructions by Fieberg et al. (2021), to calculate the relative selection strength (RSS) of OWFs by exponentiating regression coefficients of OWFs (β_1) and their distance bands (β_2). RSSs of OWF and distance band effects represent relative intensities within OWFs versus outside OWFs when availability of locations inside and outside OWFs, as well as habitat characteristics, are equal. Avoidance rate (AV) was calculated from regression coefficients as 1 – exp(β), which indicates attraction if negative.

We also investigated to what degree the OWFs footprints were avoided or preferred by Sandwich Terns due to the location-specific environmental conditions related to availability of sandeel, specifically sediment grain size (Baerwald and Barclay 2016). To what degree Sandwich Terns avoided OWFs due to differences in sediment grain size (while ignoring the effect of the OWF) was calculated using the parameter estimate for the effect of sediment β_{sd} from the iSSFs and the mean sediment grain size within the OWF $\overline{sd}_{\mathrm{OWF}}$ and outside the OWF $\overline{sd}_{\mathrm{out}}$ for areas with the same water depth and distance to the colony (Equation (2)). The avoidance rate due to differences in sediment is additional to the avoidance rate of the OWFs. Credible intervals were attained by repeating the calculation using 1,000 posterior samples of β_{sd}.

$$\mathrm{AV} = 1 - \frac{\exp(\beta_{sd}\overline{sd}_{\mathrm{OWF}})}{\exp(\beta_{sd}\overline{sd}_{\mathrm{out}})} \tag{2}$$

Relationship of Avoidance Rate to OWF Characteristics

Avoidance rates obtained from the iSSFs were related to 3 characteristics of OWFs: (1) distance from the colony in kilometers (km), (2) surface area of the OWF in km^2 and (3) turbine density of OWFs in n/km^2. Estimates of the relation between avoidance rates and the three characteristics were obtained by bootstrapping from a linear model relating the OWF avoidance estimates to all 3 OWF characteristics using 1,000 posterior samples from the iSSFs with parameters per OWF. Significance was assessed by checking whether 0 was within the 95% credible intervals (95% CIs).

RESULTS

Sample Size

The final dataset used for the iSSFs comprised 58,718 positions of 92 individuals (Table 1). The median number of positions per individual was 265 (range: 33–981) for Scolt Head and 546 (range: 43–3,879) for De Putten. All OWFs had at least one position of a Sandwich Tern within its perimeter, ranging from 1 position of 1 individual in Eneco Luchterduinen to 95 positions of 30 individuals in Egmond aan Zee. Steps entering the OWFs comprised 1.3% of the used steps for Scolt Head and 0.2% for De Putten. Similarly, used steps entering the distance bands surrounding the OWFs comprised <1% of the positions for Scolt Head and <1% for De Putten.

Avoidance of and Attraction to OWFs and Distance Bands

Step length and turning angle distributions were similar between Scolt Head and De Putten. Median step length was 3.14 km (95% CI: 0.01, 8.91) for Scolt Head and 3.23 km (95% CI: 0.03, 7.66) for De Putten (Supplementary Material Figure 1A). Most flights were strongly directional (Supplementary Material Figure 1B).

The performance of the iSSF for Scolt Head with parameters for each OWF or distance band was equivalent to the model with a single parameter for OWFs and one for distance bands (ΔDIC = 2), suggesting no substantial differences in the effects of each OWF. Conversely, for De Putten, the model with a single parameter for all OWFs performed best, with the model with parameters for each OWF or distance band having a higher DIC (ΔDIC = 3.4), indicating differences in the effects of each OWF and distance band.

Avoidance rates of OWFs by Sandwich Terns were 0.54 for Scolt Head (95% CI: 0.35, 0.7) and 0.40 for De Putten (95% CI: 0.21, 0.56; Figure 2, Table 2). In models with parameters for each OWF, all parameters indicated avoidance of OWFs, but estimates were associated with large credible intervals. The parameters for Prinses Amaliawindpark and Dudgeon had 95% CIs overlapping with 0, indicating indifference to these OWFs cannot be fully excluded, although the mean

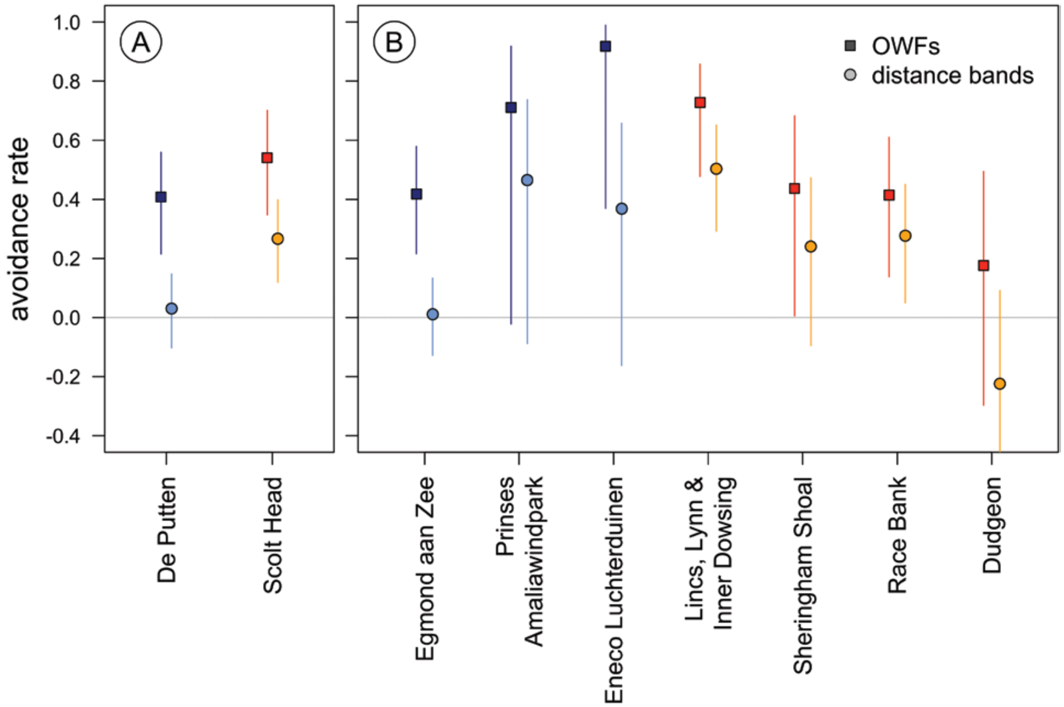

FIGURE 2. Sandwich Terns partially avoided entering OWFs but estimates of their response to OWF distance bands were inconsistent. Avoidance rates of OWFs (squares) and 1.5 km distance bands around OWFs (dots) are shown for 2 colonies (De Putten, blue/light blue, and Scolt Head, red/orange), estimated by iSSFs from GPS tracking data. Values close to 0 indicate indifference, positive values indicate avoidance and negative values indicate attraction. (**A**) Estimates for the overall avoidance rate of OWFs each colony. (**B**) Estimates of avoidance per OWF and their distance bands. Error bars show 95% credible intervals.

TABLE 2. Sandwich Terns partially avoided entering offshore wind farms (OWFs). Mean and 95% credible intervals of raw parameter estimates and of avoidance rates of OWFs by Sandwich Terns, and the approximate distance from each OWF to the corresponding Sandwich Tern colony. Estimates for the overall effect of OWFs (from models with a single parameter for all OWFs) for each of the 2 colonies are given in bold. Negative values of avoidance estimates indicate attraction.

Colony/OWF	Estimate	Avoidance rate	Distance to colony (km)
OWFs near De Putten	–0.52 (–0.82, –0.24)	0.41 (0.21, 0.56)	
Egmond aan Zee	–0.54 (–0.87, –0.24)	0.42 (0.22, 0.58)	21
Prinses Amaliawindpark	–1.24 (–2.51, 0.02)	0.71 (–0.02, 0.92)	33
Eneco Luchterduinen	–2.5 (–4.55, –0.46)	0.92 (0.37, 0.99)	49
OWFs near Scolt Head	–0.78 (–1.21, –0.43)	0.54 (0.35, 0.7)	
Lincs-Lynn-Inner Dowsing	–1.3 (–1.95, –0.65)	0.73 (0.48, 0.86)	58
Sheringham Shoal	–0.57 (–1.15, –0.01)	0.44 (0.01, 0.68)	35
Race Bank	–0.54 (–0.94, –0.15)	0.41 (0.14, 0.61)	24
Dudgeon	–0.19 (–0.68, 0.26)	0.18 (–0.3, 0.5)	37

estimates of 0.71 and 0.18, respectively, are well above 0 (Figure 2, Table 2).

The avoidance of distance bands was consistently lower than that of OWFs (Figure 2, Supplementary Material Table 1). With 95% credible intervals overlapping with 0, there was no evidence of avoidance or attraction for OWF distance bands of OWFs near De Putten, although the distance bands around Prinses Amaliawindpark and Eneco Luchterduinen had estimates well above 0. For OWFs near Scolt Head, OWF-level parameters show inconsistent patterns, with apparent avoidance of distance bands of Race Bank and Lincs, Lynn and Inner Dowsing, and avoidance suggested for the distance band of Sheringham Shoal and attraction for the distance band around Dudgeon, albeit with 95% credible intervals overlapping with 0 for the distance bands of the latter two OWFs.

The distribution of water depth, sediment and distance to the colony of GPS-positions was substantially wider for terns tracked from Scolt Head compared to De Putten (Supplementary Material Figure 2), which was reflected in different effect sizes in the iSSFs between colonies. Only at De Putten, all 3 variables had an important effect with 0 well outside the 95% credible intervals, whereas at Scolt Head the estimated effect sizes were very small with 95% credible intervals overlapping with 0 (Supplementary Material Table S2). At De Putten, Sandwich Terns preferably moved to shallower

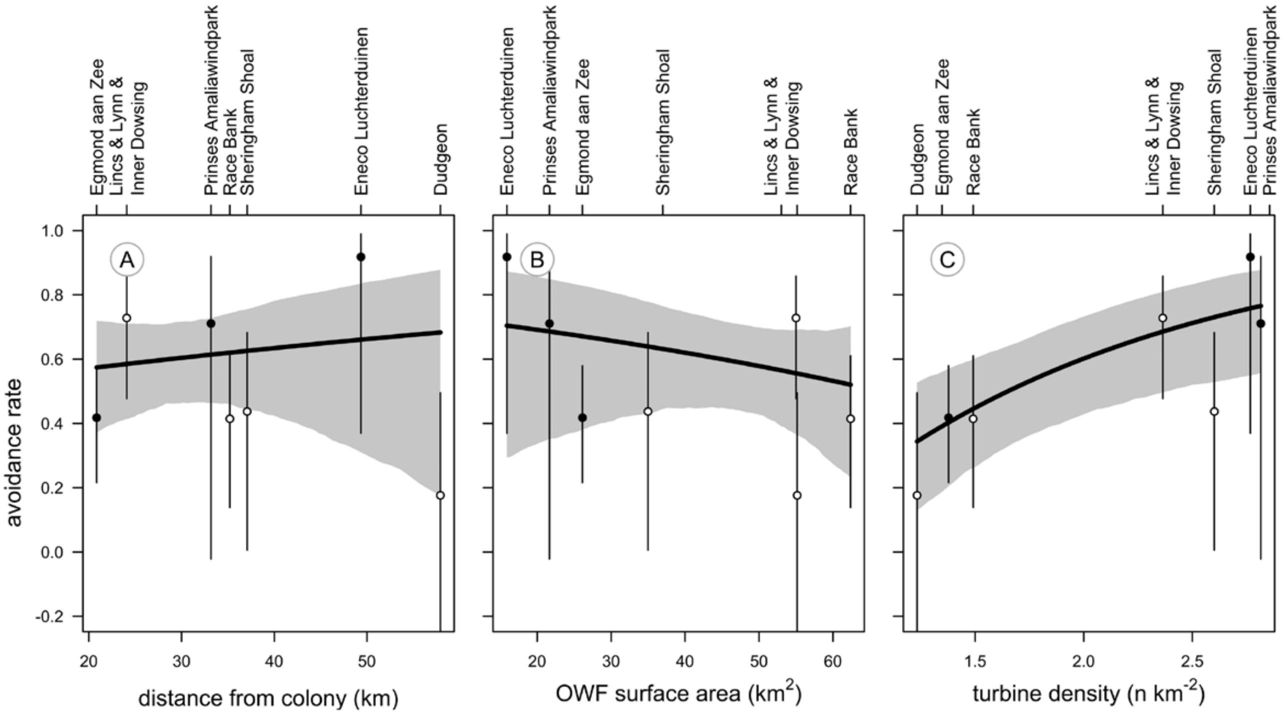

FIGURE 3. Avoidance rate of OWFs by Sandwich Terns did not correlate with (**A**) distance to the colony or (**B**) OWF surface area, but increased with (**C**) turbine density. Open circles refer to OWFs near Scolt Head, filled circles to OWFs near De Putten. Some labels on the upper x-axis have been shifted to avoid overlap.

areas (β_4 = –0.28, 95% CI: –0.33, –0.23) closer to the colony (β_3 = –0.12, 95% CI: –0.23, –0.01) and to coarser sediments (β_5 = 0.11, 95% CI: 0.05, 0.16).

Sandwich Terns avoid OWFs near De Putten partly due to finer sediments in OWF areas compared to courser sediments at locations at the same water depth and distance from the colony and outside the OWFs, with avoidance rates of the 3 OWF areas due to sediment between 0.02 and 0.04. For Sandwich Terns breeding at Scolt Head, where sediment was not important for movements and similar between OWF areas and surrounding areas, sediment did not result in avoidance (Supplementary Material Figure 3).

Relationship of Avoidance Rate to OWF Characteristics

The avoidance rate of OWFs showed no relation with distance from the colony (β = 0.008, 95% CI: –0.024, 0.038) or surface area of the OWF (β = –0.01, 95% CI: –0.035, 0.014). However, avoidance was generally higher for OWFs with a higher density of turbines, or, in other words, with less space between turbines (β = 0.478, 95% CI: 0.2, 0.639) (Figure 3).

DISCUSSION

Using iSSFs to model GPS tracking data of Sandwich Terns from 2 colonies, we showed evidence for macro-avoidance of OWFs by Sandwich Terns during the breeding season. Our estimates indicated macro-avoidance rates of 0.54 for OWFs near the Scolt Head colony and 0.41 for OWFs near the De Putten colony, at the scale of the step lengths of ~2 km. Avoidance rate estimates for single OWFs ranged from 0.42 to 0.92 for De Putten and 0.18 to 0.73 for Scolt Head, but most of these estimates were associated with substantial uncertainty that precluded firm conclusions. Furthermore, our results are inconclusive with regard to the behavioral response to the areas directly surrounding OWFs; estimates suggested indifference and avoidance, and were associated with large uncertainty. While the uncertainty in our estimates of avoidance was relatively low for estimates for the overall effect of OWFs and OWF distance bands per colony, it was substantially larger for most OWF-specific estimates. This uncertainty would be reduced if larger samples of GPS positions in and round OWFs were available.

Although our results generally indicate avoidance by Sandwich Terns of OWFs, previous studies showed mixed results. Sandwich Tern was classified as weakly avoiding OWFs in the literature review by Dierschke et al. (2016), with "continued use of a marine area after the construction of the OWF, but to a lesser degree or at a lower abundance." Indeed, following the criteria of Dierschke et al. (2016), the avoidance rates estimated in our study classify the Sandwich Tern as weakly (<50% macro-avoidance) to strongly avoiding OWFs. Studying the response of visually tracked individual Sandwich Terns from Scolt Head to the Sheringham Shoal OWF, Harwood et al. (2017) reported a decrease of Sandwich tern abundance of 30% within the OWF relative to pre-construction densities. This estimate is lower than our estimate of 44% avoidance of Sheringham Shoal, as well as to our overall estimate for OWFs near Scolt Head of 41%, but within the credible intervals of our estimates. Other studies used ship-based or aerial surveys to infer avoidance from differences or changes in densities. Densities of terns (of which about half were Sandwich Terns) were ~75% lower inside the Alpha Ventus OWF in Germany than outside (Welcker and Nehls 2016). Tern densities inside the Horns Rev II OWF in

Denmark were reduced by ~30% following its construction, but this was statistically not significant (Petersen et al. 2006). Some other studies were also unable to detect a difference or change in abundance of Sandwich Terns within versus outside the OWFs (Leopold et al. 2013) or between pre- and post-construction periods (Gill et al. 2008), due to low bird densities. The low bird densities in the study by Leopold et al. (2013), which focused on 2 of the same OWFs (Egmond aan Zee and Prinses Amaliawindpark, near De Putten; Eneco Luchterduinen was not yet built at that time), are likely explained by the fact that the closest breeding colony was located at a distance of ~55 km at that time, thus outside the normal foraging range of Sandwich Terns of ~40 km (Fijn et al. 2017, Kralj et al. 2023). In contrast, the closest breeding colony in our study was ~25 km, with accordingly higher abundances in and around these OWFs. However, with Alpha Ventus OWF at ~66 km and Horns Rev II OWF at ~26 km from the nearest Sandwich Tern colonies, the distance from and size of the nearest colony and the resulting local abundance in and around the OWF may not always explain whether an effect of the OWF on tern densities was detected. The differences between these studies may also have resulted from differences in the number of surveys and the statistical approach: all these studies used different statistical tests to estimate the OWF effect on tern density.

According to Dierschke et al. (2016), the observed variation in responses of Sandwich Terns among studies of different OWFs may be related to differences in food supplies (i.e., that better foraging conditions inside the OWF result in lower avoidance rates). Unfortunately, none of the earlier studies of avoidance behavior in Sandwich Tern considered food availability or habitat characteristics. In our study, sediment grain size was used as a proxy of food availability, considering it is known to be positively related to the occurrence of sandeel (Baerwald and Barclay 2016), an important prey type (Holland et al. 2005), and to foraging behavior (Fijn et al. 2022). The finer sediments within OWFs compared to areas at the same water depth and distance to the colonies outside of OWFs led to an avoidance of OWFs of 0.02 to 0.04 in addition to the avoidance rates of OWFs as presented in Figure 2, which assume equal covariates and availability inside and outside OWFs. However, additional avoidance due to sediment was found only for De Putten, where Sandwich Terns preferred coarser sediments. Birds breeding at Scolt Head showed no important effect of sediment on the movements of Sandwich Terns, and no additional avoidance due to sediment. The available foraging area within the range of Sandwich Terns breeding at Scolt Head covers a more level bottom and with considerably finer sediment than at De Putten (Supplementary Material Figure 2).

Different avoidance rates of Sandwich Terns among OWFs could also be caused by OWF characteristics such as spatial configuration and the size of turbines. Indeed, in our study, avoidance rates of OWFs by Sandwich Terns increased with turbine density. A relation between turbine density and avoidance rates by seabirds has been proposed in earlier studies (Masden et al. 2012, Leopold et al. 2013), but has, to the best of our knowledge, never been substantiated. Although turbine density is probably confounded by turbine design, with larger turbines placed further apart, in our study the response of Sandwich Terns to turbine density of OWFs highlights the possibility that OWF effects on habitat use of Sandwich Terns (and potentially other species) may be reduced by careful design of turbine density and/or size in OWFs. Whether the configuration of OWFs also affects meso-scale avoidance behavior and how the interplay of macro- and meso-scale avoidance with OWF configuration ultimately affects habitat loss and collision risks are important topics for future studies.

Sandwich Terns may also profit from vertical structures in the sea such as wind turbines when foraging is facilitated by predictable water turbulence in the wake of turbines that increases availability of fish at the surface (Lieber et al. 2019, Slingsby et al. 2022). Indeed, attraction to a single row of six turbines was reported by Vanermen et al. (2013) and a high percentage of foraging individuals at the edge of the Egmond aan Zee OWF was reported by Krijgsveld et al. (2011). Our study was largely inconclusive with respect to whether Sandwich Terns show avoidance, indifference or attraction to the outer perimeter of the OWFs, with mean estimates of avoidance/attraction ranging from −0.22, suggesting attraction, to 0.5, suggesting avoidance, and most credible intervals overlapping with 0. Only for Lynn, Lincs, and Inner Dowsing and Race Bank, we found support for avoidance of the area within 1.5 km from the OWF, which is in line with the avoidance of 1.5 km around a German OWF by terns (Sandwich, Common [*Sterna hirundo*], and Arctic [*S. paradisaea*] terns) (Welcker and Nehls 2016). However, avoidance the outer perimeter of the OWFs does not exclude the possibility that Sandwich Terns that do venture in or close to the OWF may target turbulence in the wake of turbines for foraging.

Our study follows a series of recent publications that use tracking data to estimate macro-avoidance rates of OWFs by seabirds (Peschko et al. 2020, 2021, Johnston et al. 2022). These studies estimated macro-avoidance by modelling used and available positions but differed in how the available positions are generated. Although Mercker et al. (2021) already provided a thorough comparison of most methods (where iSSFs performed best), a comparison of the merits of the methods to estimate macro-avoidance, also including the method by Schaub et al. (2020) wherein a null distribution is generated by random rotation of trip trajectories, would be valuable. In addition, how estimates of macro-avoidance rates are affected by the lack of data from before the construction of the OWFs should be quantified; something that is also unclear in our study where we also lacked preconstruction data. Ultimately, a unified approach to estimate macro-avoidance rates would facilitate direct comparisons between studies, OWFs and species, and can be used to estimate the avoidance/attraction rates for the large number of species for which such estimates are currently lacking.

Our macro-avoidance estimates fill an important knowledge gap in assessing the effects of OWFs on Sandwich Terns, which is important for both conservation of the species and economic analysis, such as assessment of future proposals for OWF construction. The avoidance behavior indicates that OWFs within foraging ranges of colonies will lead to habitat loss, but also to fewer collisions compared to a situation with no avoidance behavior. However, as our data were collected during the breeding period, to what extent Sandwich Terns avoid entering OWFs during other phases of the annual cycle is still an open question. A next step to refine predictions of the effects of OWFs on Sandwich Terns is to estimate avoidance rates at the meso- and micro-scales, for example through Collision Risk Models (Band 2012, Masden and Cook 2016), but this would ideally be based on tracking data at high temporal resolution. Higher temporal sampling rates are already achievable with bigger GPS-loggers that were too heavy to fit on Sandwich Terns in this study (Bouten et al. 2013). With the further advances that are ongoing in the miniaturization of loggers, collecting high-resolution data will likely become possible for this species and other similar birds.

Supplementary material

Supplementary material is available at *Ornithological Applications* online.

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Ethics statement

Tracking of Sandwich Terns in the Netherlands was performed under project licence for animal procedures AVD401002015102 of the Central Authority for Scientific Procedures on Animals and ringing permits from the Vogeltrekstation. Tracking of Sandwich terns in the UK was performed under the appropriate Special Methods Licences, and ringing permits issued by the BTO, as well as Schedule 1 licenses issued by Natural England.

Conflict of interest statement

The authors declare no conflict of interest.

Author contributions

R.S.A.vB. and R.C.F. conceived the idea. R.S.A.vB., R.P.M., M.P.C., J.J.L., C.B.T., R.M.W.G., and R.C.F. collected the data. R.S.A.vB., with help from C.B.T. and R.C.F., wrote the paper. R.S.A.vB. and J.J.L. analyzed the data.

Data availability

Analyses reported in this article can be reproduced using the data provided by van Bemmelen et al. (2023).

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