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Challenges in quantifying the responses of Black-legged Kittiwakes *Rissa tridactyla* to habitat variables and local stressors due to individual variation

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ABSTRACT

Capsule: Strong individual variation was observed in the responses of Black-legged Kittiwakes *Rissa tridactyla* to environmental covariates related to foraging behaviour and habitat selection, and in the overlap with nearby offshore windfarms (OWFs).

Aims: To determine whether environmental covariates consistently drive Kittiwake foraging behaviour and how this may influence overlap with local potential stressors at the population and individual levels.

Methods: We used two complimentary methods (Hidden Markov Models and Step Selection Functions) to classify the at-sea behaviour of Kittiwakes and identify environmental covariates associated with foraging at a colony in northeast Scotland during the 2021 breeding season. We also calculated the overlap, by behaviour, of individuals with several operational and proposed OWFs within the vicinity.

Results: We found no evidence for habitat selection at the population level, with uncertainty in which conditions were linked to foraging, due to considerable variation in the responses of individuals to local environmental conditions. This was attributed to unmeasured intrinsic variation among individuals and high competition among conspecifics and other seabird species. We also observed variation among individuals in the extent of overlap with a local stressor, OWFs, by behaviour.

Conclusion: Individuals within a population that do not respond consistently to environmental conditions will likely vary in their vulnerability to local stressors, in this case to OWFs. This could lead to unforeseen population-level consequences if not accounted for. Therefore, it is important to identify and understand variation among individuals to better establish population-level consequences of different foraging areas and overlap with stressors to reduce uncertainty in current impact assessments.

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Seabirds are the most threatened group of birds globally, with nearly a third of species classified as threatened due to global population declines, and many species facing multiple threats across the annual cycle (Dias *et al.* 2019). To understand how seabirds interact with stressors in the marine environment we need to understand how species are distributed. Seabird at-sea distributions are largely driven by prey availability and predictability, which drives where individuals forage in time and space (Stephens & Krebs 1986, Staniland *et al.* 2009). In turn, prey availability is driven by various static and dynamic environmental conditions that concentrate prey in areas where seabirds can access them in the water column (Worm *et al.* 2005,

Waggitt *et al.* 2018), with accessibility to prey also being influenced by the species' foraging strategies (i.e. plunge divers versus surface feeders).

During the breeding season, seabirds are central-place foragers, therefore their distribution at-sea will be further influenced by breeding status, distance to the colony and the density of intra- and inter-specific competitors that might compete for prey, with individuals frequently making repeat trips to productive foraging areas during this period (Orians & Pearson 1979, Furness & Birkhead 1984, Camphuysen *et al.* 2015). Whilst prey availability is a strong driver of seabird foraging behaviour, we often lack data on prey at appropriate spatial and temporal

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resolutions to model species distributions. Instead, we rely on environmental covariates, such as sea surface temperature (SST), salinity, front locations and sea surface substrate as proxies for prey availability (Embling *et al.* 2012, Scales *et al.* 2014, Wakefield *et al.* 2017). However, there are still challenges with this approach as there is often a spatial mismatch between these measures of high marine productivity and the distributions of prey species and therefore their predators (Grémillet *et al.* 2008). Scale can also play an important part, as large physical processes might concentrate prey to specific areas but at smaller scales other factors influence the distribution and availability of prey, such as local interactions between currents and sea depth, as well as competition and predation (Fauchald 2009). Furthermore, individuals can take cues from other marine predators rather than prey directly, especially at larger scales (Tremblay *et al.* 2014). Individuals can also respond differently to cues with some of this variation attributed to intrinsic factors such as sex, age and individual specialization (Phillips *et al.* 2017).

Establishing seabird distributions at-sea can help identify overlap with specific stressors and how this might influence a species' demography (Wakefield *et al.* 2017). Therefore, understanding drivers of distribution, particularly foraging areas, has important implications for conservation and marine spatial planning (Grémillet & Boulinier 2009, McGowan *et al.* 2013), such as the effective implementation and management of marine protected areas (MPAs; Davies *et al.* 2021) and likely interactions with marine renewable developments based on whether they show connectivity with features of Special Protection Areas (Thaxter *et al.* 2015). Seabird foraging areas can be identified from positional data alone by detecting behaviour associated with foraging activity, e.g. area-restricted search movements characterized by short step lengths and regular changes in direction (Fauchald & Tveraa 2003, Sims *et al.* 2008). Modern biologging technology, particularly global positioning system (GPS) tracking, can provide data on fine-scale movements of seabirds, which can be used to identify important foraging areas and, potentially, the environmental conditions associated with these (Wilson *et al.* 2002, Burger & Shaffer 2008). By coupling information on foraging areas with spatio-temporal data on environmental conditions, it may be possible to predict how populations will respond to changes in environmental conditions and the implications of that for interactions with specific stressors.

The Black-legged Kittiwake *Rissa tridactyla* (hereafter Kittiwake) has undergone significant population declines and is classified as vulnerable on

the European and global red lists of the International Union for Conservation of Nature (IUCN) and red-listed as a Bird of Conservation Concern in the UK (BirdLife International 2021, Stanbury *et al.* 2021). Having been adversely affected by climate change and fisheries, resulting in reduced breeding success and survival (Frederiksen *et al.* 2004), Kittiwakes are also sensitive to the impacts associated with offshore windfarms (OWFs), particularly the risk of collision (Furness *et al.* 2013).

Environmental variables have been used to successfully model the at-sea distributions of Kittiwakes (Wakefield *et al.* 2017) and, therefore, where they may interact with OWFs. However, predicting the environmental conditions that are associated with foraging areas that Kittiwakes target is more challenging (Embling *et al.* 2012). Kittiwakes are surface foragers that exploit prey, generally small fish, in the top 1 m of the sea surface (Burt 1974, Coulson 2011). In the North Sea, they typically specialize in Lesser Sandeels *Ammodytes marinus* (Lewis *et al.* 2001, Olin *et al.* 2020), but are known to alter their foraging behaviour to match the availability of prey species, especially outside the North Sea (Bull *et al.* 2004, Chivers *et al.* 2012). At the larger scale, ocean fronts associated with upwellings of nutrient-rich water can concentrate resources and prey that Kittiwakes are known to target, as does mean standardized sea surface temperature (SST), a measure of thermal stratification (Wakefield *et al.* 2017, Trevail *et al.* 2021). The proportion of gravel and the sand-to-mud ratio in seabed sediment affects habitat selection and distribution of sandeels and therefore seabirds (Wright *et al.* 2000, Wakefield *et al.* 2017). At a local scale, sea depth and seabed slope can influence the distribution and aggregation of prey in the water column, especially in relation to tidal processes (Embling *et al.* 2012, Wakefield *et al.* 2017, Trevail *et al.* 2021). To better understand the impact of stressors, such as OWFs, on specific populations it is, therefore, necessary to understand how these environmental conditions influence the availability of sandeels and other prey species. However, associations can be complex, complicated by colony and individual differences in habitat use (Trevail *et al.* 2019, 2021).

We used GPS tracking data to establish connectivity of Kittiwakes listed as a feature of a Special Protection Area with several operational and proposed OWFs (Thaxter *et al.* 2012). To investigate the influence of environmental covariates known to affect Kittiwake distributions and behaviour, and how this may influence interactions with this potential stressor, we used three complementary approaches. Firstly, we used hidden

Markov models (HHMs) to define discrete states that reflect ecologically relevant at-sea behaviours and determine whether environmental covariates influenced switches between these states (McClintock & Michelot 2021). Secondly, we used integrated step selection functions (iSSFs) to determine: (i) the direct effect of environmental covariates on Kittiwake movement at the local scale via the distribution of steps and turns and (ii) habitat selection at the population and individual scale (Avgar *et al.* 2016). We used these multiple approaches as each provides useful information over different spatial scales, with HHMs providing information at the population level over the larger scale of the entire foraging range (McClintock & Michelot 2021), whilst iSSFs provide information at the finer scale of each step, from the individual-level perspective, which can be averaged to provide information at the population level (Avgar *et al.* 2016, Michelot *et al.* 2019). If individuals consistently target similar environmental conditions to one another for foraging, we expect strong habitat selection at the population level, potentially enabling us to predict future foraging areas and how these may alter the population's vulnerability to local stressors, such as OWFs. If different individuals respond differently to environmental conditions, we expect weaker population-level habitat selection, making future predictions challenging, and implying that individuals may be affected differently by local stressors, with implications for demographic rates and population dynamics.

Methods

Data collection

Kittiwakes were captured at Whinnyfold, UK (57° 23'07"N, 001°52'11"W) on the 23rd and 26th June 2021 during late incubation/early chick rearing (Figure 1). Whinnyfold is part of the Buchan Ness to Collieston Coast Special Protection Area, which holds approximately 11 000 apparently occupied nests of Kittiwakes (Seabird Monitoring Programme database, 2021; <https://app.bto.org/seabirds>; online Figure S1). A total of 42 breeding adults were caught on the nest from two cliff faces, within 400 m of each other, using a noose-pole. UvA-BiTS (University of Amsterdam Bird Tracking System) GPS devices (Model 2CDse; Bouten *et al.* 2013) were deployed onto 21 individuals, with an equal number of 21 untagged controls. These solar-powered GPS devices remotely downloaded data to a central base station. All tagged and control individuals were fitted with a unique metal and alpha-numeric colour ring, had biometrics taken (maximum wing chord, body mass, total head length, bill length

to feather and bill depth at gonys) and were dye marked on the nape and rump plumage to improve detectability during monitoring (Tagged – Picric Acid, Control – Silver Nitrate).

Tag deployment

Glue-mounting was used to attach devices (dimensions: 7.5 g, 52 × 22 × 9 mm) to individuals. A small piece of muslin extending 5–10 mm from the sides of the GPS device was superglued (cyanoacrylate) to each device base prior to deployment in the field. Once an individual had been captured, we trimmed an area of mantle feathers in the centre of the back to about 5 mm, corresponding to the size of the muslin footprint, and exposing some skin to ensure the device was attached close to the body. We wiped the area with acetone to remove any grease and help create a strong bond with the glue. Using superglue, we attached the device and muslin firmly to the area of trimmed feathers, with the front of the device in line with the grey mantle feathers meeting the white of the neck feathers, careful to mould the muslin to the shape of the back and ensuring no sharp or raised edges were left once dried.

The combined mass (mean ± SD) of the GPS device, attachment material and any additional identifying marks was 10.03 ± 0.06 g ($N = 21$). This represented 2.25–2.73% of the tagged Kittiwakes' body mass. The time taken to glue mount the devices was 9–15 minutes. The total time between capture and release was 20–50 minutes, including additional holding time in individual compartments for the plumage dye to dry. Control individuals typically flew immediately back to the nesting cliff following release whilst tagged birds headed to sea to preen, however, most were seen back on the nest during the same catching session and frequently within 30 minutes. All activities were carried out with approval from the Special Methods Technical Panel, part of the British Trust for Ornithology Ringing Committee.

The GPS devices were programmed to take a positional fix every 10 minutes. This increased to every 10 seconds if an individual entered pre-defined geo-fences associated with the operational offshore wind farms within the vicinity of the colony, where the battery life of the device was at a high enough level.

Monitoring potential device effects

To check for any adverse effects of device deployment we monitored the productivity of individuals that were tagged ($N = 21$), marked control individuals that

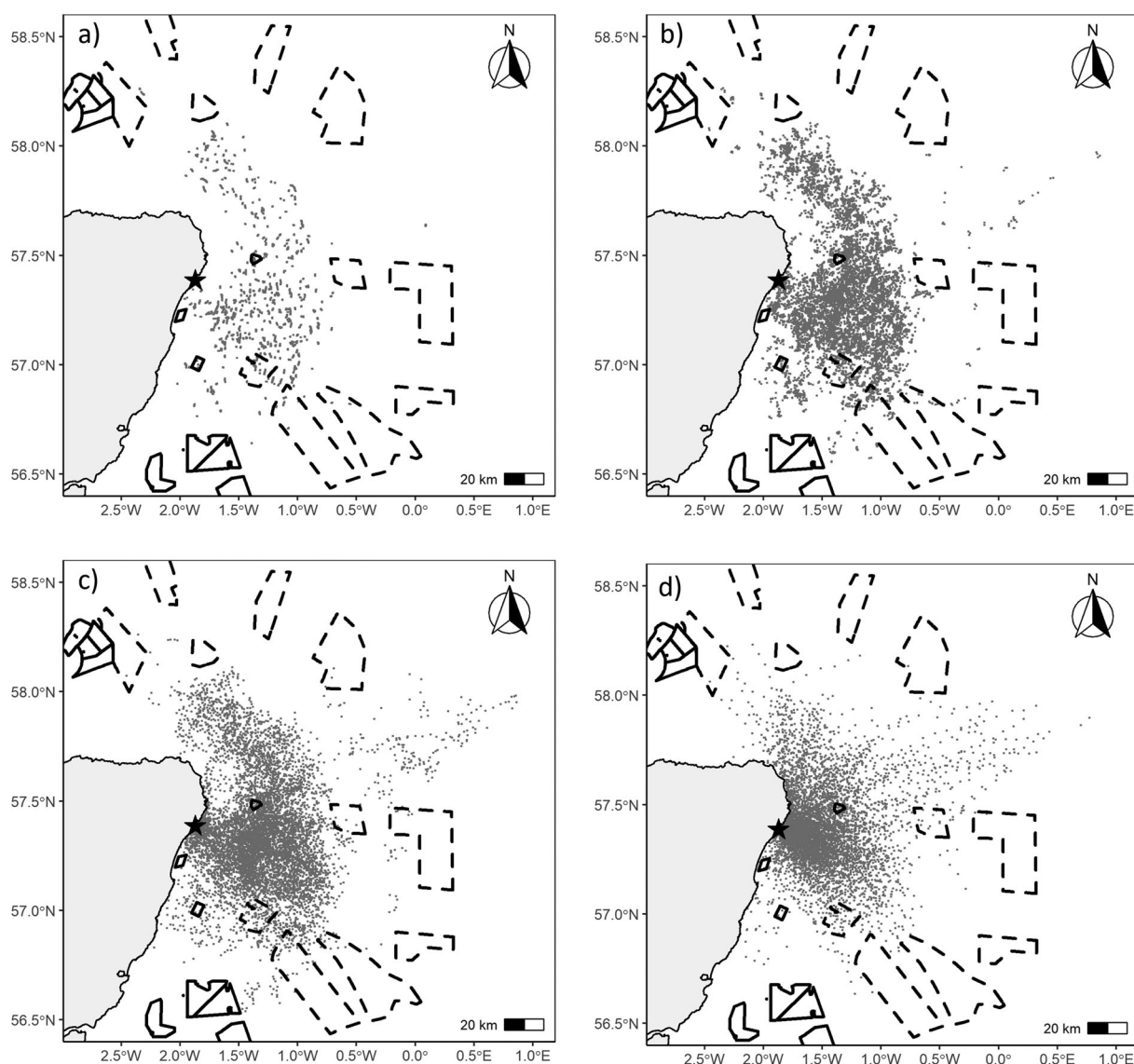


Figure 1. Location of the study area in northwest Scotland with the Kittiwake ($n = 20$) fixes at 10-minute resolution by behaviour classified by a 4-state HMM: (a) resting/bathing/floating on the sea surface, (b) resting/foraging, (c) foraging flight/searching and (d) commuting. Also shown are the operational offshore wind farms at the time of the study (black solid outline: Aberdeen Bay Demo, Hywind Scotland Pilot Park and Kincardine Wind Farm) and the ScotWind Lease Areas under option agreements (black dashed outline). The black star depicts the location of the Whinnyfold Kittiwake colony ($57^{\circ}23'07''N$, $001^{\circ}52'11''W$).

were caught but not tagged ($N = 21$) and unmarked control individuals that were not caught ($N = 42$). Whilst monitoring the productivity of tagged and marked control individuals we also recorded whether tagged, marked control or unmarked individuals were present on the nest. The nests of tagged and marked control individuals were identified by watching released birds return to their nests and by scanning the colony with a telescope and digital camera. Nests of unmarked control individuals were selected in the vicinity of the nests of tagged birds to limit biases in productivity associated with nest location. We made 14 visits to the colony across daylight hours between

24 June 2021 and 4 August 2021. From vantage points overlooking the colony to prevent disturbance, we recorded nest contents (number of eggs and chick and the size of chicks) and whether tagged, marked control or unmarked individuals were present on the nest. We recorded two measures relating to productivity: (i) whether a nest failed or was successful and (ii) the minimum number of fledged young from each nest (based on the maximum count of young during the last three monitoring visits with large primary feather growth).

We also visited the colony between 4 July 2022 and 8 July 2022 to resight returning birds. Of the 42 Kittiwakes

that were colour-ringed (21 tagged and 21 marked controls), we observed 32 (76%) individuals that were attending nests during this period. Unfortunately, due to the distances involved, it was challenging to read ring numbers to identify individuals and, therefore, whether they were tagged or marked control birds. Of 12 colour-rings that were read, 6 were tagged individuals and 6 were marked controls.

Data processing

All data processing and analyses were carried out in R version 4.1.2 (R Core Development Team 2021; see online Figure S2 for our analytical workflow). Throughout, we report means and standard deviations (SD). The raw GPS position data downloaded from the deployed tags were cleaned to remove erroneous positions, identified by trajectory (ground) speeds more than 30 ms^{-1} , or where GPS positions were obtained from three or fewer satellites due to the accuracy of geographical location being reduced.

Defining trips

To define foraging trips, we created a 500 m buffer around the centre of the colony (Paredes *et al.* 2012), with sequential trips identified when an individual left and re-entered this buffer. All GPS positions were, therefore, either classified as at the colony (when within this buffer) or on a foraging trip (when outside this buffer). Trips that were classified without leaving or re-entering the colony buffer were classified as incomplete, with trips labelled sequentially where gaps of an hour between fixes occurred due to battery failure or missed fixes. Only complete trips were used to calculate trip statistics (online Table S2).

Behavioural classification – Hidden Markov models

We used Hidden Markov models (HMMs) to classify the behaviour of Kittiwakes during foraging trips, using the R package *momentuHMM* (McClintock & Michelot 2021). We fitted a continuous-time movement model through the Kittiwake tracks to interpolate positions along a predicted route at a 10-minute re-sampling interval using *momentuHMM::crawlWrap* (McClintock & Michelot 2021) and *crawl::crwMLE* (Johnson *et al.* 2018).

We specified a four-state HMM with two data streams or input variables (step lengths and turning angles) using the R package *momentuHMM* (McClintock & Michelot 2021). We initially ran a

three-state model based on behavioural knowledge that commuting would be associated with long step lengths and small turning angles (representing relatively fast and directed flight), aerial-based foraging would be associated with shorter step lengths and high turning angles, and resting/bathing or foraging on the sea would be associated with short step lengths and low turning angles (Redfern & Bevan 2014, Trevail *et al.* 2019). However, a four-state HMM was a better fit for the data, based on visual observations and Akaike's information criterion (AIC; Patterson *et al.* 2017). The additional state had intermediate step length and turning angles to resting/foraging and commuting indicating more aerial foraging and search-like behaviour based on visual evaluation of the data. We applied a gamma distribution for step lengths (mean \pm SD) and a von Mises distribution (μ = mean, κ = concentration factor) for turning angles (McClintock & Michelot 2021). Specifically, our starting parameter values were: (i) step length: 50 ± 20 m and turning angle: $\mu = 0$, $\kappa = 1$ for resting/bathing behaviour or foraging on the sea surface; (ii) step length: 500 ± 100 m and turning angle: $\mu = 0$, $\kappa = 1$ for foraging; (iii) step length: 2000 ± 1000 m and turning angle: $\mu = 0$, $\kappa = 1$ for searching and (iv) step length: 6000 ± 3000 m and turning angle: $\mu = 0$, $\kappa = 20$ for commuting. To assign the most likely state to each Kittiwake position we used the Viterbi algorithm within *momentuHMM* (McClintock & Michelot 2021). HMMs were fitted across all individuals at the trip level. Model residuals were checked to ensure model assumptions relating to residual autocorrelation and normality were met.

Environmental covariates

To determine the drivers of Kittiwake at-sea distribution we obtained data on environmental covariates that were expected to influence movement and habitat selection of Kittiwakes based on previous studies (Wakefield *et al.* 2017, Trevail *et al.* 2019, 2021). The distance of an individual to the colony (km) of each GPS position was calculated in R. Sea depth (m) was obtained from ETOPO1 Global Relief Model at 0.016° resolution (NOAA 2009). Seabed slope ($^\circ$) was estimated from the ETOPO1 data using *terrain* in the *Raster* R package (Hijmans 2022). The proportion of gravel index and the ratio of sand to mud index in seabed sediments was derived from British Geological Survey 1:250 000 offshore seabed sediment maps (based on sediment classification by Folk 1954), rasterized to 1 km resolution following Wakefield *et al.* (2017). SST ($^\circ\text{C}$) and ocean front data

at 1.2 km resolution were obtained from the Earth Observation Data Acquisition and Analysis Service (NEODAAS, Natural Environment Research Council; <https://data.neodaas.ac.uk/visualisation>). SST and ocean fronts are dynamic variables that vary over time, therefore we used the mean mid-point value from 7-day composite maps across the season (rolling by 1 day; Miller 2009). This gave us a daily value that incorporates the mean value of SST or ocean front values on that day as well as from the previous and subsequent three days. Three variables relating to ocean front data were considered: front density (a local neighbourhood average of frontal gradient), the distance of an individual to the closest simplified front (km) and front persistence (the fraction of cloud-free observations of a pixel for which a front is detected; Miller 2009, Scales *et al.* 2014, Miller *et al.* 2015). Given that Kittiwake foraging decisions are also known to be influenced by the tides (Embling *et al.* 2012, Trevail *et al.* 2019), we extracted tidal height data from the British Oceanographic Data Centre (BODC; https://www.bodc.ac.uk/data/hosted_data_systems/sea_level/uk_tide_gauge_network/) tidal gauge located at Aberdeen (30 km southwest of Whinnyfold) at a temporal resolution of 15 minutes. We converted the tidal height data to elevation in relation to Mean Sea Level (MSL), which could then be used to categorize the tidal elevation data into four phases: low tide, where 80% or more of negative elevations were below MSL; flood, where less than 80% of elevations were above and below MSL of increasing value; high tide, where 80% or more of positive elevations were above MSL; and ebb where less than 80% of elevations were above and below MSL of decreasing value (Cox *et al.* 2013, Johnston *et al.* 2022b).

The size of conspecific breeding colonies, and those of other seabirds, along the coast can influence the foraging decisions of Kittiwakes at specific colonies through competition (Wakefield *et al.* 2017). We considered including the predicted at-sea density of all Kittiwake colonies in the region, which considers colony size, using a foraging radius approach (Critchley *et al.* 2018, 2019) in our analysis. However, as this measure weights values by the inverse log distance from the breeding colony, the resulting at-sea Kittiwake density estimates were significantly positively correlated with distance from the colony therefore we did not include this variable in our analysis (online Figure S1).

All environmental covariate rasters were converted to the same resolution (0.01×0.01 degrees), and extent, covering the study area (online Figure S3) in the *raster* R package (Hijmans 2022). For each GPS

position, we extracted environmental covariate values using *raster::extract* (Hijmans 2022). SST was standardized on a monthly basis by subtracting the mean 7-day SST composites across the study area for each month and dividing by its standard deviation, which provides an alternative index of stratification; with high values indicating thermally stratified (warmer) waters and low values indicating mixed (cooler, and typically more productive) waters (hereafter sSST; Wakefield *et al.* 2015, 2017). All remaining continuous environmental covariates were standardized by subtracting the mean and dividing by the standard error. To check for multi-collinearity between the environmental variables we checked pairwise correlations and variance inflation factor (VIF) values, with all variables having a $VIF < 3$ (Zuur *et al.* 2010).

Habitat influences on behaviour – Hidden Markov models

To determine whether the transitions from one behavioural state to another (i.e. from commuting to foraging flight/searching) were associated with external environmental conditions we re-ran the four-state HMM and included the above environmental covariates that were expected to influence Kittiwake behaviour at-sea. We first ran separate univariate four-state HMMs including each environmental covariate as an input variable, along with step lengths and turning angles, to determine which should be retained in a multivariate HMM and, therefore, were likely associated with changes in behavioural states based on AIC values compared to the null model. Seabed slope, distance to fronts, sand-to-mud ratio and proportion of gravel were removed. Therefore, distance to the colony, depth, mean standardized SST (sSST), front persistence, front density and distance to the nearest front were included in the full multivariate HMM. We fitted all potential models ($n = 31$, made up of all possible combinations of the six remaining covariates) and carried out model selection using Akaike's information criterion (AIC), with the most parsimonious models being those with $\Delta AIC < 2$.

Integrated step selection functions

To understand how environmental covariates influenced Kittiwake habitat selection and movement patterns, from the perspective of the individual, we used integrated step selection functions (iSSFs). The iSSFs consider movement by comparing habitat use at the level of steps between two consecutive fixes (Avgar

et al. 2016). We extracted environmental covariate values at the start (to determine their influence on Kittiwake movements) and end (to determine their influence on Kittiwake habitat selection) of each observed and random available step using the `amt::extract_covariates` and `extract_covariates_var_time` functions, for static and dynamic covariates respectively (Signer *et al.* 2019). For each observed step, we generated 10 random available steps using the `amt::random_steps` function (Signer *et al.* 2019).

We first ran an iSSF model to determine how the environmental variables might influence the movement of individual Kittiwakes using all positions from the four-state HMM (run with no environmental covariate data, at the 10-minute sampling rate). To determine whether Kittiwakes moved slower and in a less directed way in certain environmental conditions (indicating area-restricted search behaviour rather than commuting) we ran a conditional logistic regression model using `amt::fit_issf` (Signer *et al.* 2019). Three movement parameters were included as main effects: step length, log of the step length and the cosine of turn angles. We also included two-way interactions with these movement parameters and distance to colony, sea depth, front density and sSST (using values extracted at the start of each step). These four environmental covariates were included given that they were retained in the four-state HMM and were therefore expected to influence Kittiwake movements (see results). Stratum identity was also included as a covariate to pair each observed step with the 10 generated random available steps. Whether steps were observed (1) or available (0) was included as a binomial response variable.

The second iSSF was run to establish whether Kittiwakes showed a preference for specific environmental covariates (habitat selection). For this habitat selection analysis, we removed all positions that were classified as commuting to focus on which features individuals might be selecting for foraging. We ran the conditional logistic regression model with sea depth, front density, distance to the nearest major front, front persistence, seabed slope, sSST and proportion of gravel included as main effects (using values extracted at the end of each step) along with the stratum identity. Sand to mud ratio was removed from the model due to issues with convergence, likely due to most of the area within the Kittiwakes foraging range having a value of 3. Whether steps were observed (1) or available (0) was included as a binomial response variable. Given that tidal state may influence Kittiwake habitat selection we also subset the observed and random steps per individual by the four

tidal states and re-ran the above conditional logistic regression model for each subset of data.

Connectivity with offshore windfarms

To determine the amount of time Kittiwakes overlapped, or showed connectivity, with the offshore windfarms within their foraging ranges we obtained the footprints of operational windfarms from EMODnet (2022). At the time of the study, there were three operational offshore windfarms within the foraging range of the Buchan Ness to Collieston Coast Special Protection Area: Aberdeen Bay Demo, Hywind Scotland Pilot Park and Kincardine Wind Farm (Figure 1, online Figure S1). We also obtained the polygons of proposed ScotWind Offshore Wind Leasing areas within the region (Crown Estate Scotland 2022; Figure 1, online Figure S1).

The states classified by the four-state HMM were used to estimate the proportion of time (temporal overlap) that individuals spent in each of the operational and proposed offshore windfarms within the foraging range of the colony. To calculate the time individual Kittiwakes spent in each OWF footprint we extracted the number of GPS positions that fell within each OWF polygon using the `over` function in the `sp` R package (Pebesma & Bivand 2005), for all positions, and by behaviour (resting/bathing/floating, resting/foraging, foraging flight/searching and commuting).

Results

Data were successfully transmitted to the base stations for 20 of the 21 deployed tags. No data were downloaded for one individual due to device failure. The GPS tags were deployed on the remaining 20 Kittiwakes for a mean of 30 ± 9 days (range 17–45) during late incubation and early chick rearing of the 2021 breeding season (24 June to 10 August, online Table S2). After cleaning, this resulted in 220934 GPS positions across all individuals at a mix of 10-second and 10-minute sampling rates.

Potential tag effects

We found no significant difference in the rate of nest failures between tagged, control marked and control unmarked individuals (Pearson's Chi-squared test: $\chi^2_2 = 3.231$, $P = 0.199$), nor in the minimum number of fledglings (Kruskal–Wallis chi-squared test: $\chi^2_2 = 1.66$, $P = 0.436$). Attendance rate over the breeding season was lower for tagged (0.36 ± 0.14) compared to marked control individuals (0.45 ± 0.17), however, this

difference was not statistically significant (Kruskal–Wallis chi-squared test: $\chi_1^2 = 3.22$, $P = 0.073$, online Table S1). When we considered each of the two cliff faces separately, there was a significant difference in attendance rate over the breeding season with lower attendance for tagged than marked control individuals for one cliff face (Kruskal–Wallis chi-squared test: $\chi_1^2 = 5.43$, $P = 0.020$, online Table S1), but not the other cliff face nor for the other measures at the cliff face level ($P > 0.14$). Effects of tag deployment on foraging behaviour, but not fitness in terms of breeding success or survival, have been observed in several species (Harris *et al.* 2012, Gillies *et al.* 2020). Our trip statistics should, therefore, be interpreted with care, however, we do not believe this influenced our wider results. The effects on our measure of nest attendance were largely noticeable after the tags had been deployed for two weeks. It is, therefore, important that the potential effects of tags glue-mounted for this length of time continue to be monitored for different species and sites.

Trip statistics

Based on the cleaned data, we obtained data on a total of 1002 foraging trips across all 20 individuals (mean per individual: 50 ± 17 , range: 24–85, online Table S2). The mean maximum distance travelled from the colony by individuals on foraging trips was 38.64 ± 27.52 km, whilst the mean total distance travelled per trip was 106.63 ± 83.70 km (online Table S2). The mean trip duration across all 20 individuals was $8:36 \pm 5:26$ hours. Across all trips, the mean distance offshore Kittiwakes travelled was 26.68 ± 18.79 km.

Behaviour classifications

After fitting the continuous-time movement model to interpolate GPS positions at a 10-minute re-sampling, we had 26 543 positions (range: 609–2526 per individual). The HMM classified these Kittiwake positions into four states (Figures S4, S5) that we inferred as resting/bathing/floating (step length: 290 ± 146 m; turning angle: $\mu = 0$, $\kappa = 6.8$), resting/foraging (step length: 740 ± 626 m; turning angle: $\mu = 0$, $\kappa = 0.4$), foraging flight/searching (step length: 3034 ± 1473 m; turning angle: $\mu = 0$, $\kappa = 1.4$), and commuting (step length: 6000 ± 1496 m; turning angle: $\mu = 0$, $\kappa = 17$). Whilst there was variation between individuals, the HMM resulted in a mean of 7% ($\pm 3\%$, range 3–15%) of GPS positions classified as resting/bathing/floating, 38% ($\pm 6\%$, range 24–50%) as resting/

foraging, 31% ($\pm 4\%$, range 20–38%) as foraging flight/searching, and 24% ($\pm 6\%$, 15–41%) as commuting (Table S3).

Environmental variables influencing changes in behaviour – Hidden Markov models

For the four-state HMM including environmental covariates, the most parsimonious model included distance to colony, sea depth, sea surface temperature and front density. As Kittiwakes travelled further from the colony, the probability of continuing commuting behaviour declined up to distances of around 85 km from the colony (standardized values of 2, Figure 2 (a)). At greater distances from the colony, there was considerable uncertainty, potentially due to these values only representing 2% of fixes (Figure 2(a)). In contrast, the probability of continuing in resting/foraging behaviour, and to a lesser extent foraging flight/searching, increased with distance from the colony, especially within 85 km (which involved 98% of fixes). Overall, the retained environmental covariates had a stronger effect on foraging flight/searching and commuting behaviours, with minimal influence on continued resting/ bathing/floating behaviour. The probability of continuing in foraging flight/searching behaviour decreased with greater sea depths (Figure 2(b)), whilst the probability of continuing in resting/foraging or commuting behaviour increased slightly. Individuals had a greater probability of continuing in foraging flight/searching behaviour with higher SST, whilst the probability of commuting declined (Figure 2(c)). The pattern was more complex with front density, with greater uncertainty across all behaviours especially associated with stronger fronts (Figure 2(d)). At the lowest values of front densities, the probability of continuing in foraging flight/searching or resting/foraging behaviour declined slightly with increasing front density, whilst the probability of continuing commuting behaviour increased.

Movement processes – step selection functions

We found no significant interactions between the four included environmental covariates (distance to colony, sea depth, front density or sSST) and turning angles or log step length, indicating that the environmental conditions individuals started in did not influence how directed their subsequent movements were (Figure S6). There was an influence of the covariates on step length, however, there was considerable individual variation in the responses to starting

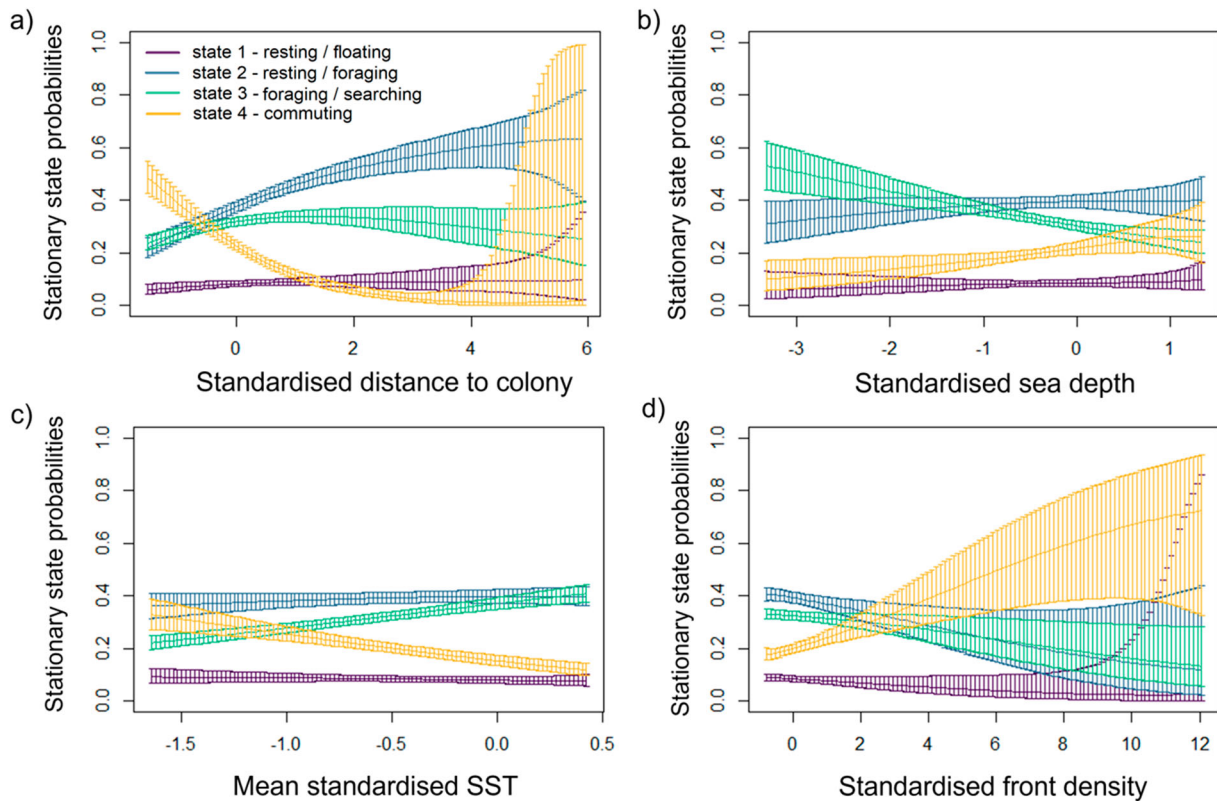


Figure 2. Stationary state probabilities of the 20 tracked Kittiwakes, with 95% confidence intervals, showing the probability of being in each state for (a) standardized distance to colony (corresponding to 0.12–176 km), (b) standardized sea depth (corresponding to –178–0 m), (c) mean standardized sea surface temperature (sSST, a measure of thermal stratification), and (d) standardized front density. All environmental covariate values are standardized. The legend is the same for all subplots.

conditions. Across all individuals, step lengths were longer at greater sea depths. In areas of increasing distance to the colony and sSST most individuals reduced their step lengths, potentially indicating more area-restricted search-type movements. However, for some individuals, the opposite relationship occurred. For front density, the pattern was very mixed with many individuals showing no response.

Habitat selection – step selection functions

The SSF model run on non-commuting behaviours revealed variation in resource selection coefficient estimates among individuals (Figure S7). Estimates for sSST, and to a lesser extent distance to fronts, were particularly variable. Some individuals showed a preference for warmer, stratified waters and areas more distant to major fronts, whilst others showed a preference for cooler, mixed waters and areas closer to major fronts. Most individuals showed a preference for deeper water and locations closer to the colony. There was limited evidence for preference in any direction for front density, front persistence, proportion of gravel or seabed slope. Therefore, at the

population level, we found no overall selection for any of the included environmental covariates.

There was no indication that Kittiwake habitat selection was influenced by tidal state at the population level (Figure S8). Estimates of individual selection coefficients showed a similar pattern across tidal states, with potential individual variation in selection for some variables (i.e. particularly, sSST, and to a lesser extent distance to fronts), whilst for most variables there was again limited evidence for any preference/avoidance at the individual level.

Temporal overlap with offshore wind farms

Of the 20 tracked Kittiwakes, 15 were recorded to overlap with the footprint of at least one of the 3 operational windfarms, however, the amount of time spent in the windfarms varied considerably by individual (Figure 3, online Figure S9). Overall, the tracked Kittiwakes spent only 0.56% of the time away from the breeding colony within the three operational windfarms, across all individuals and behaviours. Most of this time was classified as resting/foraging behaviour, largely on the sea surface, (0.19%), followed by resting/ bathing/

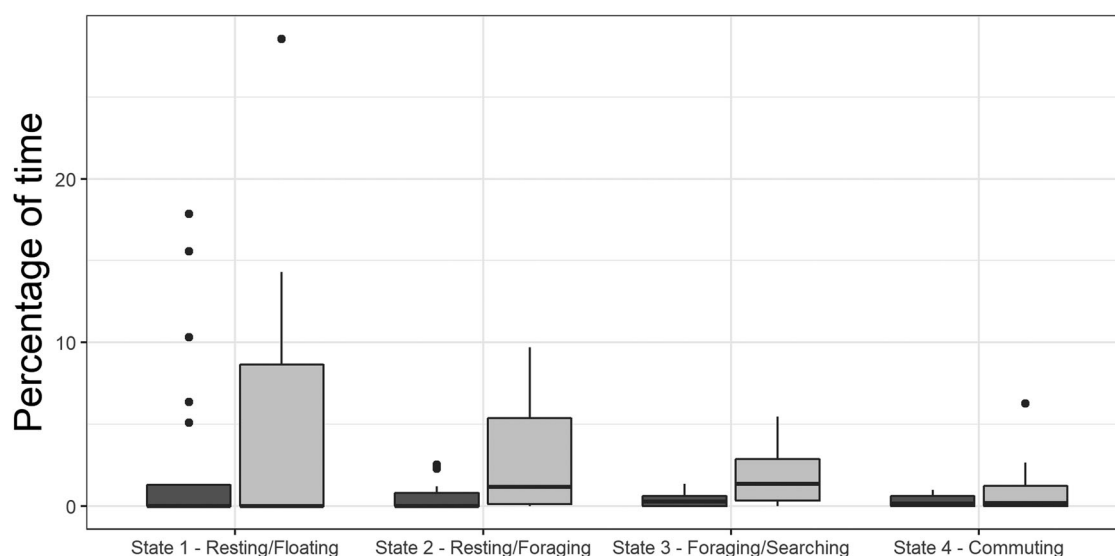


Figure 3. Boxplot highlighting the temporal overlap of the 20 tracked Kittiwakes by behaviour with operational (dark grey) and proposed (light grey) offshore wind farm areas in the vicinity of the breeding colony indicating considerable variation among individuals and behaviours. Percentage of time refers to the percentage of the total time each individual spent in each behaviour within the operational or proposed offshore wind farm areas: i.e. for commuting, the amount of time an individual spent commuting within the offshore wind farm areas as a percentage of the total time that individual spent commuting when away from the colony. Boxplots show median (horizontal line), inter-quartile ranges (box), and minimum and maximum values (whiskers). Points represent outliers.

floating on the sea surface (0.16%), foraging flight/searching behaviour (0.14%), and commuting (0.08%). Seventeen of the tracked Kittiwakes also overlapped with the proposed ScotWind lease areas, spending a total of 2.32% of the time away from the breeding colony within these locations, which again varied by individual and behaviour (Figure 3, online Figure S9).

In terms of the relative importance of the operational and proposed OWF areas by each behaviour, individuals spent 2.32% of their time away from the colony resting/bathing/floating on the sea surface within the footprint of the operational OWFs (range: 0–18%, 2.76 ± 5.53 , Table S4) and up to 3.98% of this time in the proposed lease areas (range: 0–29%, 5.02 ± 7.71 ; Table S5). The relative importance of the operational OWFs for individuals resting/foraging, foraging flight/searching or commuting when away from the colony was much less (0.49%, 0.45% and 0.32%, respectively). However, eight individuals spent between 4% and 7% of their resting/foraging time within the proposed lease areas, with these same individuals spending an additional 4–29% of their resting/bathing/floating on the sea surface time within these areas (Figure 3, online Figure S9, online Tables S4 and S5).

Discussion

Using data from GPS tracking we identified the at-sea distribution of Kittiwakes, by behaviour, during the

breeding season from a single colony in northwest Scotland. Kittiwakes were distributed across a large area arching around the coastline to the east and south of the colony, largely within 30 km of the coast. The distribution of Kittiwakes was weakly related to several marine environmental covariates that are frequently used as proxies of prey availability, with no consistent population-level habitat selection. Instead, we found strong individual variation in habitat preferences and in the use of OWFs within the vicinity of the colony. This individual variation makes it difficult to identify important foraging areas at the population level. It also means that vulnerability to local stressors, such as OWFs, likely varies among individuals (Peschko *et al.* 2020b, 2021).

Individual variation in responses to environmental covariates

Understanding the environmental drivers of at-sea distributions of individuals is vital for sustainable marine spatial planning and limiting adverse impacts on species of conservation concern (Grémillet & Boulinier 2009, McGowan *et al.* 2013). Within the North Sea, the key concern to Kittiwake populations, outwith climate change and prey availability, is the presence of multiple operational, and proposed, OWFs (Furness *et al.* 2013, Burthe *et al.* 2014). Identifying

how individuals use the marine environment can, therefore, provide useful insights into how offshore renewable developments might influence a species.

However, as individuals did not respond consistently to environmental conditions, we were unable to identify specific conditions and foraging areas that were important to Kittiwakes at the population level. At the individual level, foraging behaviour was generally associated with locations close to the colony, as would be expected from central-place foragers (Orians & Pearson 1979). There was also a tendency for individuals to forage over relatively deeper depths. Kittiwakes generally associate with shallow depths where increased vertical mixing occurs which increases the availability of prey at the surface (Carroll *et al.* 2015). However, the preferred depth of foraging Kittiwakes has previously been found to relate to the local bathymetry around a colony (Trevail *et al.* 2019, 2021), indicating that preferences for depth are confounded by what depths are available close to the colony. At colonies surrounded by shallow water Kittiwakes preferred shallower depths, whilst at those surrounded by deeper water they preferred greater depths, with the latter also being observed at Whinnyfold during an earlier study (Trevail *et al.* 2019, 2021).

There was high uncertainty around the influence of front density on foraging behaviour, likely attributed to individuals responding inconsistently to the presence of fronts. Seabirds, including Kittiwakes, are expected to be attracted to strong front areas as these are typically associated with productive, nutrient-rich waters that aggregate prey (Hunt *et al.* 1999, Bost *et al.* 2009, Scales *et al.* 2014). However, Kittiwakes can be outcompeted at strong fronts by larger marine predators, resulting in individuals foraging in areas of weaker, and less persistent, fronts (Scales *et al.* 2014, Trevail *et al.* 2021). Given the large number of surrounding colonies, it is likely that high levels of competition from conspecifics and other seabird species contributed to the variation in the responses of individuals to fronts, and to the other included environmental conditions (Wakefield *et al.* 2017, Trevail *et al.* 2021). Prey availability may have also differed between areas associated with different front strengths, but we were unable to test that here.

We also found substantial variation in the response of individuals to mean standardized SST, a measure of thermal stratification, with no clear pattern of preference or avoidance. Being surface feeders, Kittiwakes are reliant on features that increase mixing in the water column and bring prey species to the surface, such as seabed morphology (slope), SST and

tidal or thermal stratification (Scott *et al.* 2010, Embling *et al.* 2012, Cox *et al.* 2013, Wakefield *et al.* 2017). Previous studies have found that Kittiwakes prefer cooler sea surface temperatures and more mixed waters, which are also typically associated with higher marine productivity (Carroll *et al.* 2015, Trevail *et al.* 2021). However, variation in preferences for SST can also occur between colonies (Trevail *et al.* 2021), which may indicate differences in colony-specific local prey ecology related to SST and thermal stratification. We found no evidence for habitat selection associated with sea slope or tidal cycle at the population or individual level. However, we only focused on tidal state, rather than tidal stratification, which is known to influence Kittiwake movement and foraging decisions (Embling *et al.* 2012, Trevail *et al.* 2019, 2021). Marine environments are complex, therefore it is challenging to account for all factors that influence where seabirds are distributed and drive foraging behaviour. Time of day may influence when and where Kittiwakes forage especially where diurnal patterns affect prey availability (Daunt *et al.* 2002, Engelhard *et al.* 2008, Embling *et al.* 2012). Breeding stage may also influence foraging behaviour. When chicks are newly hatched (1–8 days after hatching) adults typically make short, regular trips to bring back small prey items. During this early chick-rearing stage, the influence of environmental conditions may differ or be weaker than when foraging on larger prey items for themselves or larger chicks (Humphreys *et al.* 2006, Kotzerka *et al.* 2009). We found no evidence within our data of a bimodal pattern in foraging trip duration or distance travelled, nor any pattern in the number of foraging trips made per day across the breeding season. Foraging trip duration and distance travelled did weakly decline ($r < -15.00$) with day of the year, indicating slightly shorter trips on average as chick demand for food increased, but there was still much variation in trip length and duration across individuals and the breeding season.

It is likely that intrinsic variation among tracked individuals, associated with sex, age, experience, and individual specialization, contributed to the considerable individual variation observed (Phillips *et al.* 2017, Harris *et al.* 2020). These intrinsic-driven differences may be particularly evident when foraging conditions are poor and therefore may not be consistent within or between years due to variations in environmental conditions and prey availability (Ishikawa & Watanuki 2002). Although all individuals tracked were of breeding age and, therefore, likely to be at least four-years old we did not know their exact ages or sexes. This is important to consider in future

to understand variation in habitat use and overlap with stressors driven by intrinsic factors.

Uncertainty around habitat selection and drivers of foraging behaviour at the population level may also be attributed to a mismatch in the environmental covariates at the spatial and temporal scale we included in our analysis and what was occurring at lower trophic levels, specifically prey availability. Finer-scale data on environmental features or forage fish species may provide better predictions of where seabirds target, however, this data is typically limited in availability at suitable temporal and spatial scales (Scott *et al.* 2010, Michelot *et al.* 2017, Bertrand *et al.* 2021, Langton *et al.* 2021). Our ability to identify links between Kittiwake at-sea distributions and the environmental covariates may also have been restricted by the ability of the HMM to accurately classify biologically meaningful states, and therefore adequately distinguish between assumed behaviours; especially associated with foraging due to Kittiwakes having several feeding techniques that include plunge diving and feeding from the sea surface (Coulson 2011). We also did not account for the influence of weather, particularly wind speed and direction, which can influence seabird at-sea distribution and behaviour, as well as prey availability (Christensen-Dalsgaard *et al.* 2018, Lane *et al.* 2019, Jakubas *et al.* 2022). For example, based on data from the tracked Kittiwakes in this study, Davies *et al.* (2023) found that as windspeeds increased, individuals were less likely to commute and more likely to rest on the sea surface.

Consequences for overlap with anthropogenic stressors

The extensive individual variation we observed in drivers of behaviour and foraging distribution made it difficult to interpret the responses of individuals, and populations, to commonly measured environmental covariates. Consequently, we were unable to predict how populations might be affected by local stressors, such as OWFs, with changing environmental conditions, either naturally or under anthropogenic-driven climate change.

Overall, tracked Kittiwakes spent a relatively small amount of time within the footprints of operational OWFs, although there was considerable variation among individuals, and by behaviour. When considering the proposed lease areas, the time associated with OWF footprints increased nearly fivefold. In terms of behaviour, the proportion of time spent foraging and commuting within operational

OWFs was low but increased slightly when considering the proposed OWFs, particularly for foraging. The proportion of time spent resting/bathing/floating on the surface within OWFs was higher, especially within the footprint of proposed lease areas. Understanding the behaviour of Kittiwakes within OWFs can help determine how this stressor might manifest itself in demographic rates and through what mechanisms individuals might be affected i.e. through increased mortality due to collision risk or reduced productivity due to loss of foraging areas (Peschko *et al.* 2020b, Johnston *et al.* 2022a). For example, individuals who are commuting or in foraging flight within operational OWFs will be at higher risk of collision than if floating or foraging on the sea surface. Furthermore, the Kittiwakes tracked in this study had lower flight heights when searching / in foraging flight than when commuting, indicating a lower risk of collision for individuals in searching/foraging flight behaviour when within operational wind farms, specifically in the rotor-swept area (Davies *et al.* 2023). Given that the resting/bathing/floating behaviour was largely associated with the existing and particularly the proposed OWFs away from the coast, this behavioural state may be associated with foraging, either directly or indirectly through waiting for foraging opportunities near fronts or foraging aggregations (Camphuysen 2000). The development of the proposed lease areas could, therefore, result in displacement from foraging habitat if individuals subsequently avoid these areas (Cook *et al.* 2018, Peschko *et al.* 2020a). Alternatively, if individuals continue to forage there, they may be at risk of collision with turbines (Peschko *et al.* 2020a).

We documented the extent to which tracked individuals overlapped with operational and proposed OWFs during a single breeding season, largely associated with chick rearing. However, the foraging areas of seabirds, including Kittiwakes, can vary considerably within and among years due to changing environmental conditions and prey availability, which can alter key foraging areas and commuting patterns (Pettex *et al.* 2012, Robertson *et al.* 2014, Fijn *et al.* 2017). This can result in variation in the extent to which seabirds overlap with OWFs within and among years (Thaxter *et al.* 2015). Therefore, it is very likely that the overlap with OWFs we observed in this study will change in subsequent seasons and years. Where it is not possible to predict the distribution of seabirds in response to future temporal and spatial variation in environmental conditions, and therefore how populations will overlap with stressors, data from multiple seasons and years will be necessary

(Robertson *et al.* 2014, Thaxter *et al.* 2015). Given the considerable individual variation we observed in response to environmental covariates and overlap with OWFs, it is also important to identify and understand drivers of intrinsic variation among individuals. Intrinsic-driven variation that affects resource use and habitat selection can subsequently influence an individual's vulnerability or response to anthropogenic stressors (Gianuca *et al.* 2017, Genovart *et al.* 2018). This intrinsic-driven variation has conservation and management implications as variation in foraging strategies that affect individual fitness will impact population dynamics (Caswell 2001), particularly if fitness costs differ with differential exposure to stressors (Genovart *et al.* 2018). Identifying the extent of variation among individuals can also help us understand a population's resilience to environmental change. If individuals within a population have plasticity in their foraging behaviour, they can likely target alternative resources or locations if one habitat or area is lost (Bolnick *et al.* 2003, Nussey *et al.* 2007), although there may be implications dependent on the quality of alternative resources and associated density-dependent competition.

We identified several challenges and limitations that prevented us from predicting at-sea distributions of Kittiwakes to adequately assess the potential population-level impacts of nearby operational and proposed OWFs. Specifically, we found clear evidence of individual differences in response to environmental variables and of interactions with OWFs. Where modelled results relating to foraging decisions and habitat selection are averaged across individuals to focus on population responses, the impact of operational and proposed OWFs on some individuals is likely to be under or overestimated. Underestimating this impact may particularly lead to unforeseen consequences on demographic rates and population dynamics if this individual variation is not accounted for. It is important that future studies should incorporate data on intrinsic factors such as age, sex, breeding status, body condition and personality (Phillip *et al.* 2017, Harris *et al.* 2020) to identify drivers of individual variation in at-sea distributions and overlap with potential stressors. Collecting data from multiple colonies and species within a region may also help elucidate the influence of intra- and inter-specific competition on at-sea foraging decisions and movements (Wakefield *et al.* 2017). Combining data on intrinsic factors with spatially explicit models that include fine-scale data on environmental conditions, competition and prey availability will improve our ability to understand

population-level consequences of individual-responses on population dynamics and plasticity to change, and reduce uncertainty surrounding predicted impacts of stressors, such as OWFs.

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