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RESEARCH ARTICLE

An individual-based model to quantify the non-breeding season impact of wind farms on seabirds

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Abstract

1. Many countries are developing offshore wind farms to provide renewable energy, yet such developments can harm biodiversity. Seabirds are a highly threatened group of birds and can be impacted by wind farms through lethal collisions and via sub-lethal displacement effects. However, we do not have a comprehensive understanding of the impacts of offshore wind farms on seabird populations, particularly outside of the breeding season.
2. We developed an individual-based model to predict the non-breeding season impacts of offshore wind farms on seabirds. We used long-term tracking data obtained from geolocation-immersion loggers to estimate population-level distributions and activity budgets. We simulated individual behaviour, movement, wind farm interactions (collision and displacement) and any resulting lethal or sub-lethal effects.
3. We demonstrated our model by assessing the impact of 10 simulated offshore wind farms on two populations that breed in Norway: common guillemots *Uria aalge* (Sklinna) and black-legged kittiwakes *Rissa tridactyla* (Ålesund). We quantified collision risk in kittiwakes and sub-lethal displacement effects in guillemots and converted these effects into a change in survival or end of season body mass as a proxy for condition.
4. We predicted that 49.6% of guillemots breeding at Sklinna would experience displacement effects during the non-breeding season. As the energetic impact of displacement is relatively unknown, we modelled a range of possible displacement costs and present several impact scenarios, with adult mortality levels ranging from 0% to 5.32% and end of season body masses of 97.12%–99.84% compared to those resulting from an unimpacted scenario. Despite 98.9% of kittiwakes

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flying through at least one wind farm footprint, we only predicted collisions in 0.055% of the population; this low mortality was primarily driven by low overlap between the modelled height of the turbine rotors and the probable flight height of kittiwakes.

5. Practical implication: Our model provides a tool that can be used to assess the non-breeding season impacts of OWFs on seabird populations, improving sustainability when developing renewable energy infrastructure. We highlight several key limitations as areas of research that are required to reduce uncertainty when predicting impacts. Our model is reproducible and adaptable for use on other species or for other marine threats.

KEYWORDS
agent-based model, black-legged kittiwake, collision, common guillemot, displacement, renewable energy, vulnerability

1 | INTRODUCTION

Many countries are transitioning to alternative energy technologies to reduce carbon emissions and tackle the climate crisis (International Energy Agency, 2021). Offshore wind farms (OWFs) are a useful source of renewable energy for coastal countries, providing reliable energy without taking up land space (Kaldellis & Kapsali, 2013). However, OWFs can have negative impacts on biodiversity through habitat degradation and fragmentation, and by causing disturbance and direct harm to wildlife (Gasparatos et al., 2017). As technology advances, OWF development is expanding further offshore and turbine structures are becoming larger and more powerful (Enevoldsen & Xydis, 2019), yet we do not know how this development will impact biodiversity and bioabundance. In addition, the oceans are already heavily industrialised through activities such as fishing, shipping and fuel and mineral extraction (Cinner et al., 2020; Venegas-Li et al., 2019), thus renewable energy development presents an additional threat to biodiversity. Repeated interaction with marine threats can result in cumulative effects, which are difficult to appropriately assess using traditional impact assessments (Maxwell et al., 2013). Given the need for rapid development, it is crucial to gain a holistic understanding of how these developments will impact marine biodiversity and bioabundance.

Most impact assessments focus on spatial overlap between animals and threats (e.g. Goodale & Milman, 2019). However, overlap analyses do not incorporate the cumulative sub-lethal effects that individuals experience due to interactions with multiple threats or repeated exposure to a single threat. Sub-lethal effects include a reduction in body condition, which can impact survival likelihood or future breeding success and drive population change (Searle et al., 2018). Individual-based models (IBMs) are a useful tool for evaluating cumulative effects of anthropogenic change on individuals, which we can subsequently scale up to the population level. IBMs enable us to create a modelled world where simulated individuals move and behave in ways approximating real-life individuals (Vincenot, 2018). When we change the environment of the modelled world, we can observe how the behaviour of simulated individuals changes and model the resulting impacts on body condition and mortality rates (DeAngelis & Mooij, 2005). IBMs have been used to predict the impacts of wind farms on a variety of taxa, including bats (Ferreira et al., 2015), marine mammals (Gallagher et al., 2021) and raptors (Eichhorn et al., 2012). IBMs also enable us to assess the cumulative effects of multiple threats and determine the timing of threat interaction, which is valuable when considering mitigation efforts.

In seabirds, OWFs can result in direct mortality, via collision with rotor blades or through the sub-lethal effects of displacement. Displacement effects can result in behavioural and energetic changes, including reduced access to foraging habitats (Busch & Garthe, 2016); 'barrier effects', where seabirds have to travel longer distances around a development area (Masden et al., 2010); and disturbance, which can increase the frequency of escape behaviours (Fliessbach et al., 2019). The sub-lethal effects of displacement are difficult to quantify (Drewitt & Langston, 2006) but can impact breeding success and survival (Lane et al., 2020; Searle et al., 2014). As many seabird species are migratory and use different areas throughout the year (e.g. Deakin et al., 2019; Fayet et al., 2017), individuals can encounter several OWFs over their annual cycle, potentially leading to substantial cumulative effects. IBMs have been used to predict the impacts of OWFs on breeding populations of seabirds (i.e. groups of individuals of the same species that breed in the same location) during the breeding season (e.g. Pollock, 2022; Searle et al., 2018; Warwick-Evans et al., 2018), but we are in the early stages of developing such models for the non-breeding season (although see Duckworth, 2023; Soudijn et al., 2025). During the breeding season, seabirds exhibit central-place foraging and are therefore more constrained to remain near their breeding colony to retain their nesting sites, incubate their eggs and provision and protect

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their chicks (Orians & Pearson, 1979). In addition, data (e.g. tracking or observational data) are more readily available during the breeding season, when individuals are more easily accessible and observable, and short-term higher-resolution tracking devices can be deployed. During the non-breeding season, seabirds are less constrained to remain near the breeding colony, and often travel far from their breeding sites. Therefore, data tend to be lower resolution and/or are more difficult to link to breeding populations, which makes it more challenging to relate the impact of human activities to population-level change. However, seabirds that breed in temperate and polar environments typically experience their highest levels of mortality during the non-breeding season (Acker et al., 2021; Harris et al., 2007) and adult mortality is a crucial driver of changes to seabird population size (Layton-Matthews, Reiertsen, et al., 2023). We therefore require a transparent and replicable modelling framework that can be applied to assess impacts of OWFs on seabirds during the non-breeding season.

We developed an IBM to predict the impacts of OWFs on seabirds during the non-breeding season. To assess the lethal and sub-lethal impacts of OWFs on individual seabirds during the non-breeding season, we simulated individual behaviour, movement and OWF interactions (collision and displacement effects). Our approach enables us to highlight key periods of OWF interaction and impact, which may be useful for mitigation approaches. Our model is parameterised using individual-based tracking data from geolocation-immersion loggers ('geolocators'). Although geolocators have lower spatial resolution than for example, GPS loggers, they are useful for understanding broad-scale distribution patterns during the non-breeding season (e.g. Strøm et al., 2021). These loggers also record salt-water immersion data, which can be used to estimate activity budgets and energy expenditure (Burke & Montevecchi, 2018; Fayet et al., 2017), enabling us to predict the sub-lethal effects of displacement on behaviour and energetics. Here, we describe our IBM framework and how it can be applied to assess the non-breeding season impacts of OWFs on seabird populations with geolocator or similar datasets available. We demonstrate our model by simulating the non-breeding season impacts of 10 hypothetical OWFs on two seabird populations in Norway: common guillemots *Uria aalge* ('guillemots') breeding at Sklinna (65.2° N, 10.99° E; Figure 1) and black-legged kittiwakes *Rissa tridactyla* ('kittiwakes') breeding in Ålesund (62.4° N, 5.63° E). Guillemots are considered vulnerable to displacement effects but, due to their low flight height (Cook et al., 2012), they are thought to have low vulnerability to collision (Furness et al., 2013). Kittiwakes are generally considered more vulnerable to collision than displacement effects (Furness et al., 2013), but have shown weak levels of avoidance (i.e. potential displacement) during the non-breeding season (Peschko et al., 2020). Therefore, although kittiwakes may be susceptible to displacement during the non-breeding season, we chose to demonstrate the flexibility of our approach by focusing on collision in kittiwakes and displacement effects in guillemots.

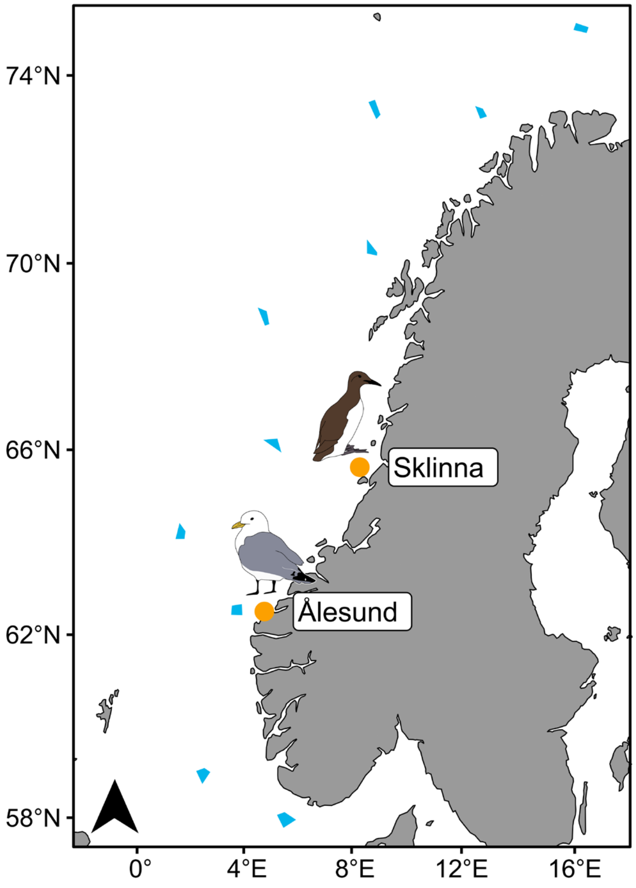

FIGURE 1 The location of the breeding colonies for common guillemots (Sklinna) and black-legged kittiwakes (Ålesund) are shown as orange circles next to illustrations of the relevant study species. The footprints for the hypothetical OWFs are shown in blue.

2 | MATERIALS AND METHODS

We developed a model to simulate seabird movement, behaviour and energetics during the non-breeding season to predict the lethal and sub-lethal impacts OWFs. The model has three submodel: (1) behaviour and movement; (2) displacement and energetics; and (3) collision. A visual overview of the model is provided in Figure 2. The model was run separately for each species. We ran 1000 movement simulations for each population, with each of these 'super-individuals' (Scheffer et al., 1995) representing 100 individuals, for which we simulated OWF impact (resulting in 100,000 total simulated individuals for each population). The Supporting Information contains a detailed model description, following the overview, design concepts and details (ODD) protocol (Grimm et al., 2006, 2020). The model was built in R version 4.4.1 (R Core Team, 2024).

The model contains three types of entities: super-individuals, which are made up of individual seabirds, environmental grid cells, and OWFs. Seabirds are characterised by their species, breeding colony location, dates of leaving the breeding colony and arriving back the following year, grid cell location, behavioural budget, mean flight

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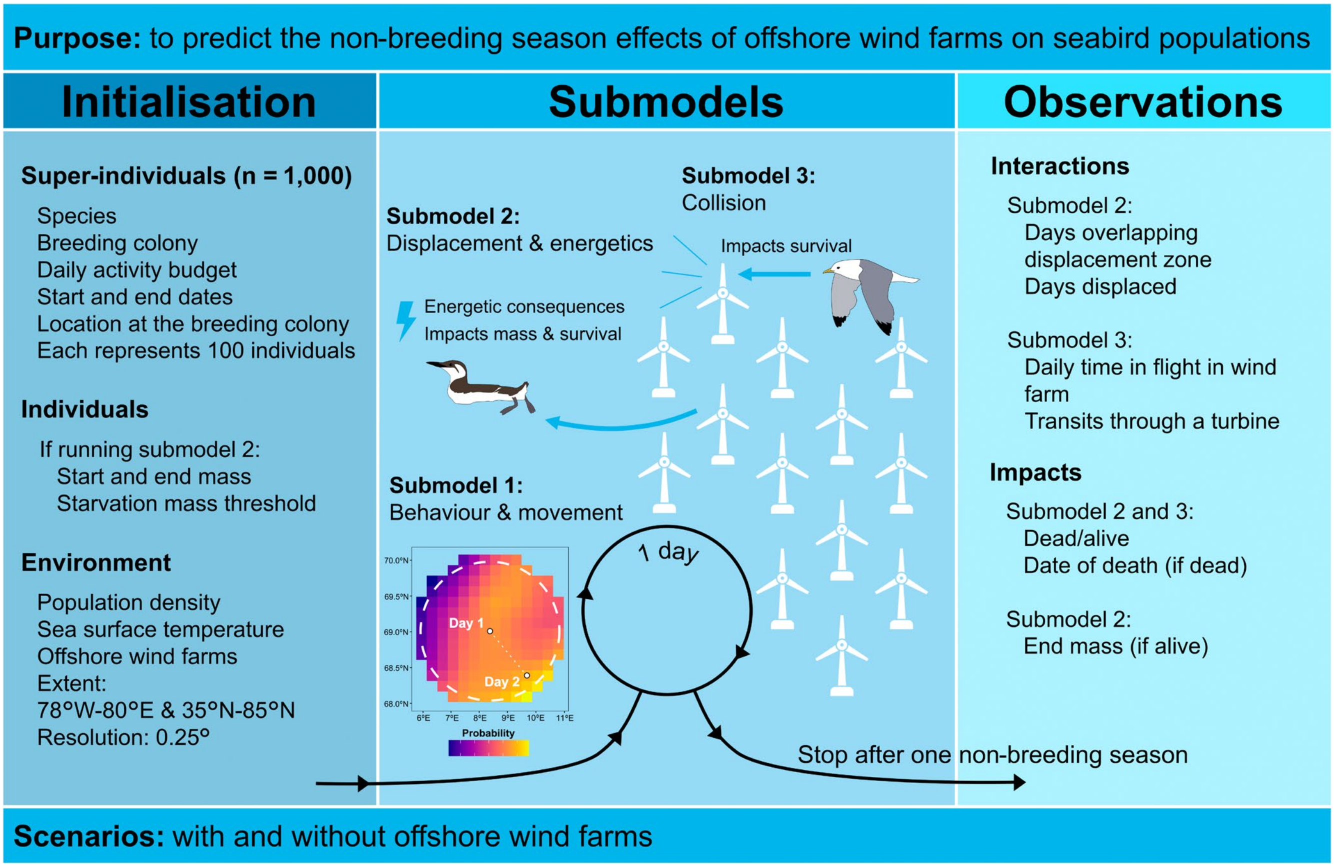

FIGURE 2 Model visualisation using the vODD format (Szangolies et al., 2024). The model's purpose is to predict the impacts of offshore wind farms on seabird populations during the non-breeding season. During model initialisation, super-individuals (each representing 100 individuals) and individuals are initialised, and the landscape is generated. Time steps are 1 day, during which each super-individual is relocated and offshore wind farm interaction submodels run. The simulation ends after one non-breeding season when outputs are generated. The simulations run in two scenarios: with and without offshore wind farms. Detailed submodel processes are visualised in the Supporting Information. Turbine icons are from Freepik.

speed and for guillemots only, mean swim speed, mass and starvation mass. The environment is constructed of 0.25° grid cells (200 × 632 cells) covering the North Atlantic (Supporting Information), with each grid cell characterised by modelled seabird population density and sea surface temperature (SST). These environmental data are updated daily. OWFs are spatial polygons characterised by area covered (km^2), number of turbines, energy output of each turbine (MW), number of blades on each turbine, turbine rotor radius (m), air gap (distance from the sea to the rotor swept area; m), maximum rotor blade width (m), rotation speed (rpm) and blade pitch (°).

Simulation time steps are 1 day long and follow this order: (1) an activity budget is assigned to each super-individual; (2) super-individuals move and interact with OWFs; (3) for guillemots only, energy expenditure is calculated and individual mass is updated, then, for all individuals within each super-individual and for both species, mortality is assessed.

2.1 | Behaviour and movement submodel

We used a large database of seabird tracking data, collected as part of the SEATRACK programme (Strøm et al., 2021), to parameterise our behaviour and movement submodel. SEATRACK has been coordinating wide-scale deployments of leg-mounted geolocators on seabirds across the North-East Atlantic since 2014, with loggers measuring light, salt-water immersion and temperature. Permits to work at Sklinna and Ålesund were obtained from the Local County Governors, with permissions to handle birds and equip them with loggers granted by the Environmental Agency and the Norwegian Food Safety Authority (FOTS IDs: 6291, 8482, 15603, 23259).

2.1.1 | Parameterisation

The SEATRACK database has previously been used to calculate monthly density maps for each of our study populations (Fauchald et al., 2021). Briefly, the maps were created using raw light data to derive locations, following the methods described in Bråthen et al. (2021). These locations were used to develop species distribution models, which were combined with count data to model monthly population density (mean density within each 0.25° × 0.25° grid cell; Fauchald et al., 2021). A summary of the predictor variables used in the species distribution models is

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contained in the Supporting Information but refer to Fauchald et al. (2021) for the full details. We ran a linear interpolation on these monthly population density maps to estimate daily density per grid cell, using a moving window of 30 days. Densities were projected using North Pole Lambert azimuthal equal area Atlantic (EPSG:3574).

We used raw salt-water immersion data to estimate time-in-activity budgets for the population for each day of the non-breeding season. These activity budgets were used to inform the time spent in 'travelling' behaviours each day (kittiwakes: flight only; guillemots: flight and active on water), and thereby the distance that could be travelled in one time step. In guillemots, these budgets were also used to inform daily energy expenditure (DEE). For guillemots, activity budgets were assigned following Buckingham et al. (2025). Each 10-min sampling period was allocated to the following:

- Active on water if the geolocator was ≥92% wet, which included time foraging, pauses between foraging bouts and swimming and preening behaviours. We ensured that there was at least 10 minutes of time active per day.
- Flight if the geolocator was completely dry for ≤30 min during the day (Dunn et al., 2020).
- Resting on land if the geolocator was completely dry for >30 minutes during the day (Dunn et al., 2020) or for the entire night (Sinclair et al., 2017).
- Resting on water if the geolocator was between 0% and 92% wet, indicating that the geolocator-equipped leg was tucked into the plumage while resting on the water. As we could only measure this behaviour when one leg was tucked (the geolocator-equipped one), we accounted for this by subsequently multiplying the time spent in this behaviour by 1.8 (Buckingham et al., 2025) and reduced time active accordingly.

For kittiwakes, activity budgets were allocated following McKnight et al. (2011):

- Flight if the geolocator was completely dry.
- Resting on water if the geolocator was ≥97.5% wet.
- Foraging if the geolocator was between 0 and 97.5% wet, as kittiwakes tend to forage by a flighted search followed by a drop into water, leading to a mixed immersion level.

For each population, we extracted the daily mean and 95% confidence interval (CI) for time spent in each behaviour.

2.1.2 | Simulation

We assigned each super-individual a date for leaving and arriving back at the breeding colony by sampling a range of fledging dates (guillemots: 18 July ±10 days; kittiwakes: 28 July ±16 days) and lay dates (guillemots: 24 May ±10 days; kittiwakes: 20 May ±16 days) (Supporting Information). Super-individuals were also assigned a daily activity budget by sampling values of each relevant behaviour from within their 95% CI for that day, with the remaining time making up the final behaviour. Using the simulated activity budgets, we determined the maximum distance that each super-individual could have travelled during that day based on their mean flight speed (guillemot: 16.6 ms^{-1}, Elliott et al., 2014; kittiwake: 13.41 ms^{-1}, Davies et al., 2024) and swim speed (guillemot: 1.15 ms^{-1}, Merkel & Strøm, 2023) or foraging speed (kittiwake: 6.07 ms^{-1}, Cook et al., 2023).

Subsequently, we assigned each super-individual a daily location, based on the daily density per grid cell and the maximum distance they could travel each day. To constrain movements to areas of predictable consistent use, avoid super-individuals getting 'stuck' in less-frequented outlier areas, and following a sensitivity analysis, we constrained the daily densities to a proportion of the total range (80% for guillemots and 90% for kittiwakes; that is, the area in which 80% and 90% of the population of guillemots and kittiwakes respectively can be found; Supporting Information). On the first day of the non-breeding season, we assigned the location of each super-individual to the grid cell of the daily densities that the breeding colony was located in. We then drew a buffer around the first location, equal to the maximum distance the super-individual could have travelled in that day. We subsequently used the 'mask' function in the 'terra' package in R (Hijmans et al., 2022) to extract the gridded daily densities that were within the maximum possible distance travelled. We then converted the gridded daily densities to probability of occurrence for each grid cell within this maximum distance and used these probabilities to assign the super-individuals to the central point of a new grid cell. If a super-individual got 'stuck' in an area with no grid cells within the maximum distance for that day, we assigned it to the nearest grid cell. We repeated this process for each day of the non-breeding season, assigning a new grid cell and activity budget each day.

2.2 | Displacement effects submodel

2.2.1 | OWF interaction

We assessed overlap between each guillemot super-individual's location with seasonal displacement categories (Table 1; Peschko et al., 2020, 2024). For each day that a location overlapped with an area where displacement was possible (displacement zone), we selected a displacement probability from within the confidence interval for the relevant displacement category, assuming a uniform distribution. As there was a significant area where displacement effects could occur in guillemots, we did not account for barrier effects (i.e. displacement along the movement path) within the guillemot model. If displacement occurred, we relocated the super-individual to another location within the maximum possible distance travelled for that day, using the probabilities of the grid cells within this distance, but outside all displacement zones. If all grid cells that were within the maximum distance travelled were within an OWF displacement zone, we relocated the super-individual to the nearest grid cell that was outside all displacement zones. We assigned 'displacement = true' for that day.

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TABLE 1 Probability of displacement at varying distances from an OWF footprint boundary.

			Probability of displacement		
				95% confidence interval	
Season	Dates	Distance from OWF boundary (km)	Mean	Lower	Upper
Autumn	16 July–30 September	≤1	0.91	0.84	0.94
		≤5	0.8	0.74	0.84
		≤10	0.76	0.71	0.81
		≤19.5[b]	0.79	0.74	0.83
Winter	1 October–29 February	≤1	0.67	0.53	0.77
		≤5	0.54	0.45	0.62
		≤10	0.5	0.41	0.57
		≤16.5[b]	0.51	0.42	0.58
Spring	1 March[a]–6 May	≤3	0.63	0.47	0.74
		≤9	0.49	0.33[c]	0.60[c]

Note: Spring probabilities were extracted from Peschko et al. (2020) and autumn and winter were extracted from Peschko et al. (2024). The smallest distances indicate the distance covered from the OWF boundary but also include the OWF footprint itself.

[a] The start of spring is 21 February in Peschko et al. (2020), but as this overlapped with the winter season from Peschko et al. (2024), we have used the dates for autumn and winter from the most recent publication.

[b] These distances were provided as a range of 18–21 km (autumn) and 15–18 km (winter) in Peschko et al. (2024). Here, we have extracted the mean of this range.

[c] As there was no uncertainty provided for displacement for spring ≤9 km, we used the range of error from the ≤3 km zone to inform this range, resulting in a confidence interval of 0.33–0.60.

2.2.2 | Energetics

Energetics were modelled using the daily activity budgets assigned to each super-individual and SST. We assigned a value of SST for each guillemot super-individual's daily location to inform DEE. Values were randomly selected from the 95% CI of SST during the period of data collection (2006–2021) for the closest value of satellite-derived SST (0.25° resolution, Reynolds et al., 2007). For each individual guillemot within each super-individual, we assigned a mass for the first and last days of the non-breeding season. We used these masses to model an unimpacted mass change throughout the non-breeding season, which we could then compare with disturbance-impacted masses. A linear model of mass change during the breeding season was used to calculate the median and 95% confidence intervals (CIs) for the start and end of the non-breeding season (Supporting Information). We assigned each individual guillemot a mass for the start (i.e. at chick fledging; Mass_F) and end of the non-breeding season (i.e. at egg laying; Mass_L) by sampling from a multivariate normal distribution centred around the median masses at fledging and laying and with a correlation between the two of 0.9. In doing this, we assumed that in an unimpacted scenario, the individual would return to the breeding colony with the mass it had during egg-laying the previous year. Finally, we calculated DEE (kJ) for each individual guillemot using the following equations, which were developed by Elliott and Gaston (2014) and are widely used for these types of datasets. Here, we used an updated version based on Patterson et al. (2022), which corrected an error in the original equation, and Buckingham et al. (2025), based on validation using time depth recorders and which also incorporated a temperature constraint to ensure that the cost of resting at sea never falls beneath the cost of resting at the nest (i.e. the basal metabolic rate):

(a) when the daily mean SST ≤14°C

$$\text{DEE} = 508 \times T_{\text{Flight}} + (118 - 2.75 \times \text{SST}) \times T_{\text{Active}} + 33 \times T_{\text{Rest:at nest}} + (72 - 2.75 \times \text{SST}) \times T_{\text{Rest:at sea}}$$

(b) when the daily mean SST >14°C

$$\text{DEE} = 508 \times T_{\text{Flight}} + (118 - 2.75 \times \text{SST}) \times T_{\text{Active}} + 33 \times \left(T_{\text{Rest:at nest}} + T_{\text{Rest:at sea}}\right)$$

Here, the value of 14°C represents the lower critical temperature; when the SST is below this temperature, individuals must expend energy on thermoregulation.

2.2.3 | Mass

To calculate mass (g) on any given day, we used the following equation adapted from Green et al. (2007, 2009) and further informed by Dunn et al. (2022):

$$\text{Mass}_{\text{Day } n+1} = \text{Mass}_{\text{Day } n} + \frac{T_{\text{Active Day } n} \times \text{FS} \times \text{EF} \times \text{AE} - \text{DEE}_{\text{Day } n}}{\text{ET}} + \alpha \times \left(\text{Mass}_{\text{L}} - \text{Mass}_{\text{Day } n}\right)$$

where T_{Active} = time spent active (min); FS = foraging success (g min^{-1}); EF = energetic density of food (kJ g^{-1}); AE = assimilation efficiency

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(%; DEE = daily energy expenditure [kJ]; ET = energetic density of body tissue [$kJ\,g^{-1}$]). We added a pull (α) of 0.012 ± 0.003 towards the mass during egg laying ($Mass_L$), to ensure that daily mass change was within the expected range and that mass did not become impossibly large or small within the unimpacted scenario due to uncertainty within the other variables in this equation (Supporting Information). This approach was similar to Dunn et al.'s (2022) method, which applied a constraint to the minimum and maximum masses that individuals could reach; however, as our main aim was to create a reproducible and simple model of non-breeding season mass, where individuals could also experience sub-lethal effects that resulted in mortality, we could not limit mass in the same way. In addition, the incorporation of this parameter allowed individuals to compensate for lost foraging time following displacement, enabling them to regain body mass lost resulting from displacement effects that occurred earlier in the season.

As there is limited information on guillemot diet during the non-breeding season, we followed Dunn et al. (2022) and assumed their main prey source was lesser sandeels *Ammodytes marinus*, which is a reasonable assumption for this study species, season, and region. We therefore used the energetic density of lesser sandeels ($5.8 \pm 0.5\,kJ\,g^{-1}$, Wanless et al., 2005), the assimilation efficiency of guillemots (77.52 ± 1.60%, Hilton et al., 2000), and assumed that all tissue compositional changes affected fat, thus assigning the energetic density of tissue as $39.3\,kJ\,g^{-1}$; all as in Dunn et al. (2022). As we had no information on foraging success, we first calculated a daily value of FS assuming that energy intake and expenditure balanced between consecutive days by using the mean values for EF and AE in the following equation:

$$FS_{Day\ n} = \frac{DEE_{Day\ n}}{T_{Active\ Day\ n} \times EF \times AE}$$

Subsequently, when calculating daily mass, we accounted for uncertainty by sampling values of EF and AE from their error ranges and assuming a uniform distribution. To account for uncertainty within ET, we assigned it a gamma prior distribution with a mean of 39.3 and a standard deviation of 0.001, similar to the process in Dunn et al. (2022). This process resulted in a mean daily mass change of ±2.50 g (SD = 1.56 g) within the unimpacted scenario, which was comparable to mass change during the breeding season ($-2.5\,g\,day^{-1}$ during incubation; $-1.5\,g\,day^{-1}$ during brooding, Harris et al., 2000).

2.2.4 | Displacement cost and mortality

There is limited understanding of the mechanism and severity of displacement effects from OWFs in guillemots, particularly during the non-breeding season, yet it is generally considered that guillemots are primarily impacted via habitat loss, resulting in reduced food intake (Dierschke et al., 2016). Therefore, for each day that displacement occurred, we represented a displacement cost (DC) of reduced food intake by applying a proportionate reduction to foraging success for that day. To account for the uncertainty surrounding displacement effects on guillemots, we created a range of displacement impact scenarios where we reduced daily foraging success by a range of DCs (0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9 and 1—i.e. foraging success = 0) when displacement occurred.

To model guillemot mortality during the non-breeding season, we first had to determine the mass at which survival was unlikely. We did not have mass data for guillemots breeding at Sklinna that had died from starvation, yet guillemots are known to vary in body mass both by breeding population (Barrett et al., 2008) and throughout the annual cycle (Harris et al., 2000). We therefore calculated the proportion of breeding season body mass at which mortality was likely, by comparing data from individuals known to have died from starvation with breeding season masses from the region where they likely bred. We used masses of 7 adult guillemots that died from starvation in the North Sea during January–March 2022 (mean = 659 g; SD = 51 g; Christensen-Dalsgaard et al., 2022). As these individuals likely bred at colonies in east Scotland (Buckingham et al., 2022; Christensen-Dalsgaard et al., 2022), we compared these masses to the breeding masses of guillemots on the Isle of May, east Scotland (mean = 947 g; range = 775–1130 g; Harris et al., 2000). We created normal distributions for the starvation masses and the breeding season masses using these values, and sampled 1000 masses from each distribution to create a simulated population distribution. We then divided the breeding season mass distribution by the starvation mass distribution and extracted the 95% CI from this result to estimate the proportion of its breeding season mass at which an adult guillemot would likely die (95% CI = 0.556–0.876). We sampled a value from this range for each individual and assumed that mortality occurred if a guillemot's mass fell beneath this proportion of its fledging mass ($Mass_F$). Using this approach, we found that when we constrained food intake for multiple days in a row (i.e. simulating starvation), it took on average 7.4 ± 1.3 days for an individual to die (Supporting Information), which was in line with predictions from Clairbaux, Mathewson, et al. (2021; October–December: 8.4 ± 0.5 days; January–February: 6.3 ± 0.7 days).

At the end of the simulations, we extracted the number of individuals displaced per day. We calculated the difference in mass between each displacement scenario and the unimpacted scenario for each simulation each day and, where mortality occurred, extracted the date of death for each scenario.

2.3 | Collision submodel

As time spent in flight within the OWF footprint was an important metric for quantifying impact in kittiwakes, we extracted the grid cells that super-individuals moved through between point locations, resulting in a 'movement path'. We assumed that super-individuals travelled in a straight line between the points, and that any tortuosity took place within the grid cells along the movement path, as we did not have information on fine-scale movements between grid cells. Each day, for each movement path that crossed an OWF, we sampled a value of the number of minutes

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spent in flight within any OWF footprint for each individual kittiwake within each super-individual. This value was sampled from a binomial distribution around the total number of minutes spent in flight that day and the proportion of the day's movement path that was within an OWF.

To inform likelihood of interacting with a turbine, we calculated the proportionate turbine coverage of each OWF footprint using the following equation:

$$\text{Turbine coverage} = \frac{2r \times AD \times nT}{\text{Area}_F}$$

where 2r was twice the rotor radius (km), AD was the avoidance distance (km), nT was the number of turbines and Area_F was the total area of the OWF footprint (km^2). The avoidance distance was defined as the distance at which an individual must detect the turbine to avoid collision, estimated to be within 10s of collision (Martin & Banks, 2023). Therefore, based on flight speeds from Davies et al. (2024; 95% CI: $3.75\,\text{ms}^{-1}$, $35.76\,\text{ms}^{-1}$), we sampled a value of avoidance distance from the range: 0.0375–0.358 km. This value informed the likelihood of a ‘transit’, that is, overlap in vertical space between an individual and a wind turbine. One transit could occur for each minute spent in flight within an OWF footprint for each individual kittiwake. If a transit occurred, we selected a probability of collision for a single transit (i.e. ‘pcoll’ in the Band model) from a range of values, simulated using code extracted from the stochLAB R package (Caneco et al., 2022) to run the stochastic Collision Risk Model (sCRM) 1000 times (Band, 2012; Masden, 2015; McGregor et al., 2018). We used the standard values contained within the sCRM for flight height distribution (which are modelled flight heights based on observed data; Johnston et al., 2014; Supporting Information) and kittiwake avoidance rates and gave an equal probability of upwind and downwind approaches. If the kittiwake collided, we assumed mortality occurred. If there was no collision, we repeated this process for each day of the non-breeding season, assigning a new grid cell each day.

At the end of the simulations, we extracted the time spent in flight within an OWF footprint per day, the number of transits and whether lethal collision occurred for each individual.

2.4 | Offshore wind farms

We demonstrate our model by assessing the impacts of 10 hypothetical OWFs distributed in Norwegian waters (Figure 1). We used the turbine parameters in Table 2, which were taken from a proposed development within our study area (Layton-Matthews, Buckingham, et al., 2023).

TABLE 2 The following turbine parameters are those expected to be used within our region, based on the plans for a proposed development within our study area (Layton-Matthews, Buckingham, et al., 2023) and discussions with developers. These were used in the stochastic collision risk model. For a description of these terms, see the Supporting Information.

Parameter	Value
Number of turbines	50
Output of each turbine (MW)	20
Number of blades on each turbine	3
Turbine rotor radius (km)	0.135
Airgap (m)	23–24
Maximum rotor blade width (m)	7.5
Rotation speed (rpm)	6.6
Blade pitch (°)	5.8

3 | RESULTS

Our model predicted that 53.8% of the guillemot population overlapped with an OWF displacement zone at least once during the non-breeding season, resulting in displacement effects for 49.6% of the population (based on displacement probabilities inferred from Peschko et al., 2020, 2024; Figure 3). The number of displacement events per super-individual ranged from 0 to 17 across the season. The number of super-individuals displaced per day varied throughout the year, with peaks during August–September and November–March. We estimated a lower and upper death threshold of 0.556 and 0.876, from which we sampled a value for each individual and multiplied by Mass_F. Mortality rates and end of non-breeding season mass varied with displacement cost (DC), with population-level mortality rates ranging from 0% to 5.32% and end of non-breeding season mass ranging from 97.12% to 99.84% of the unimpacted scenario (Table 3). The model is therefore sensitive to this parameter; yet it is challenging to validate these results because in real populations empirical evidence is lacking for determining the rates and effects of displacement from OWFs and subsequent mortality. We therefore plotted daily mass as a proportion of Mass_F for three DCs, representing lower (0.1), medium (0.5) and higher (1) displacement costs (Figure 4).

Almost all kittiwakes (98.9%) spent at least 1 min in flight within an OWF footprint during the non-breeding season. Daily time spent in flight within a wind farm footprint varied significantly across the population, but was fairly low on average (Figure 5). Most individuals (81.84%) made at least one transit through a turbine, and the number of transits per individual varied from 1 to 39 across the simulation period (Figure 5). However, the stochastic collision risk model predicted a very low risk of collision from a single transit (mean = 0.000198; SD = 0.000482), thus we predicted that only 0.055% of the population would collide with an OWF turbine.

4 | DISCUSSION

Extensive OWF development is expected throughout the north-east Atlantic over the next 15 years (GWEC, 2023). Previous IBMs that have been developed to assess the non-breeding season impacts of

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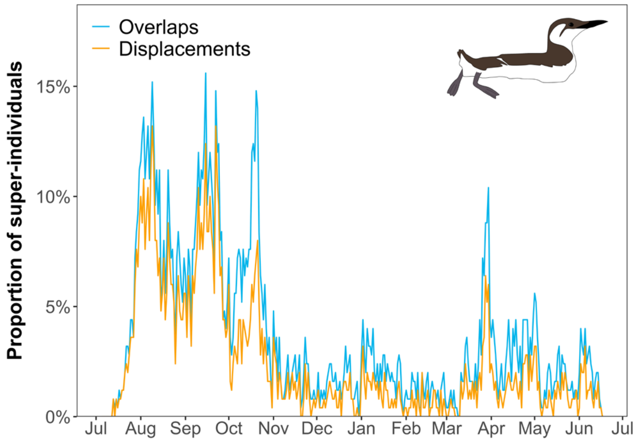

FIGURE 3 Number of daily interactions with OWFs (overlaps and displacements) per super-individual (*n* = 1000) for adult guillemots that breed at Sklinna.

TABLE 3 Mortality rates and end of non-breeding season mass compared to the unimpacted scenario (% of 100,000 simulations) for each modelled displacement costs (the proportionate reduction of foraging success on any day that displacement occurred).

Displacement cost	Deaths (% of population)	End mass compared to unimpacted scenario (%) mean (SD)
1.0	5.32	97.12 (6.82)
0.9	3.91	97.61 (5.92)
0.8	2.66	98.08 (4.94)
0.7	1.64	98.48 (3.97)
0.6	0.85	98.83 (3.03)
0.5	0.35	99.11 (2.19)
0.4	0.08	99.33 (1.49)
0.3	0	99.51 (1.03)
0.2	0	99.67 (0.68)
0.1	0	99.84 (0.34)

OWFs on seabirds have either incorporated individual-level energetics, with no spatial component (Duckworth, 2023), or have been parameterised using counts of seabirds at sea rather than data from individuals of known breeding colonies (Soudijn et al., 2025). Here, we have presented a spatial and energetic model that can predict the cumulative effects of OWFs during the non-breeding season and links these effects with breeding populations. This linkage is a crucial step, as it provides the potential to combine changes in mortality and body condition with demography data and predict the impact on population trends over time (Layton-Matthews, Buckingham, et al., 2023). The impacts of any additional developments will be combined with the impact of OWFs that are already operational (Masden et al., 2010), and of co-existing threats, such as fisheries bycatch (Christensen-Dalsgaard et al., 2019), oil spills (O'Hanlon et al., 2023), competition for prey with fisheries (Searle et al., 2023) or climate change (Reiertsen et al., 2021). Our model provides a framework with the potential to incorporate the lethal and sub-lethal effects of other threats, thereby providing a more realistic analysis of the changes that further development may have on seabird populations (Horswill et al., 2022). The approach we have developed could also be applied to compare options for planned OWFs, for example to compare the impacts of various potential wind farm locations or turbine parameters. Alternatively, the model could help identify the areas where preventing future development would have the most impact, and which may benefit from a protected status (e.g. a marine protected area; MPA).

We predicted potentially significant impacts of displacement effects on guillemots breeding at Sklinna. The energetic cost of displacement is a key metric when predicting the effects of OWFs on guillemots, yet the pathway and true value of this cost are poorly known. Here, we assumed that displacement affected individuals via foraging success (Dierschke et al., 2016), rather than through behavioural changes such as increased time in escape behaviours (i.e. flight or diving; Fliessbach et al., 2019) or reduced time foraging or resting. The model could be readily adapted to incorporate energetic impacts from behavioural changes, should our understanding of displacement pathways improve, but here we have accounted for the uncertainty within the energetic impacts of displacement by presenting the potential impacts of a range of displacement costs. Research into the energetic cost of displacement is therefore urgently required to enable accurate calculations of the impacts of displacement on guillemots and other vulnerable seabird species (Soudijn et al., 2025), and our modelling framework is designed to be adaptable as our knowledge on this topic advances. Further research on this topic would also improve our understanding of the impacts of displacement on individuals that have not themselves been displaced but which experience displacement effects indirectly, such as through an influx of displaced individuals causing increased competition for food. This aspect is not currently included in our model but could be accounted for if suitable information becomes available. Within our model, we inferred displacement probability from studies of fixed-turbine wind farms in the southern North Sea (Peschko et al., 2020, 2024); however, most OWF developments in Norwegian waters are likely to be floating (NVE, 2023). The impacts of floating OWFs are particularly poorly understood (Maxwell et al., 2022) and, as the turbines used for floating OWFs are typically taller and more widely spaced than for fixed OWFs, it is possible that the risk of displacement from floating OWFs will be different to those estimated by Peschko et al. (2020, 2024). Furthering our understanding of the impacts of floating OWFs on seabirds (such as through pre- and post-construction surveys) would therefore increase the reliability of our model.

We used data from geolocators to estimate activity budgets and energy expenditure in guillemots, which we then used to predict OWF interactions and displacement effects. Although these data have relatively low spatial and temporal resolution, they provide a reasonable comparison of activity budgets and energy expenditure

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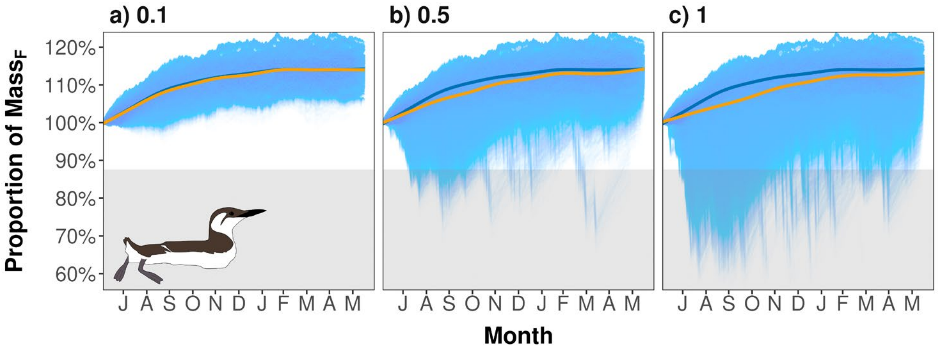

FIGURE 4 Daily mass compared to the start of the non-breeding season (Mass$_F$) for individual guillemots ($n = 100{,}000$). A selection of displacement costs are plotted, representing lower (panel a), moderate (b) and higher (c) displacement costs. Light blue lines are daily mass for each individual (ending at either death or the end of the non-breeding season), with the population-level mean unimpacted mass in dark blue and the population-level mean impacted mass in orange. The grey box highlights the range within which mortality can occur.

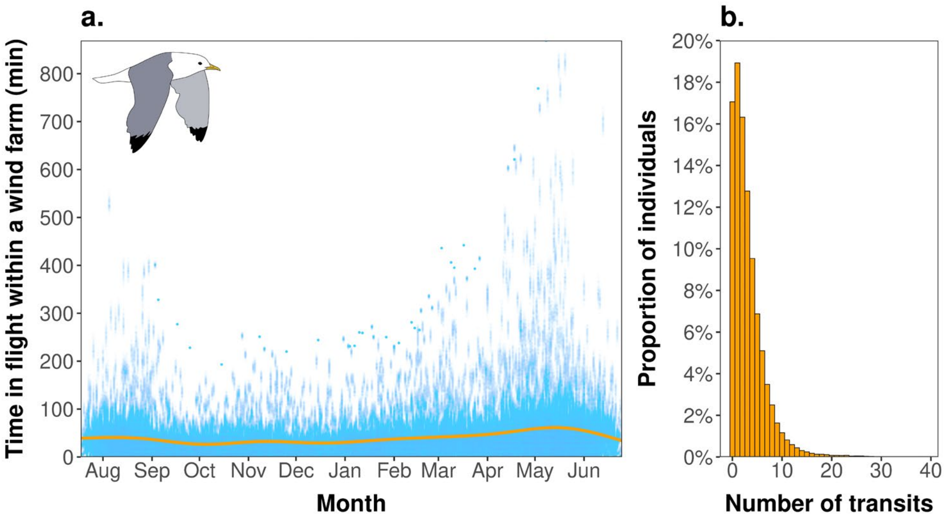

FIGURE 5 (a) Minutes spent in flight within a wind farm footprint per day (blue points) with the population-level mean in orange and (b) total number of transits for each individual kittiwake ($n = 100{,}000$).

between individuals and populations (e.g. Buckingham et al., 2023; Dunn et al., 2020), and are the best source of data currently available for our study species outside the breeding season. We then used activity and energy expenditure to model mass change throughout the non-breeding season. We were unable to validate our predictions with measured values as there are limited mass data for healthy adult guillemots of known breeding population at this time of year; however, our predicted masses were within the expected range for our study species and fit with measured masses of individuals from an unknown breeding population within our study region (Harris et al., 2000) and modelled masses using similar approaches (Dunn et al., 2022). Our observed pattern of high rates of mass increase during the early non-breeding season also fits with our expectation of mass change during the winter, as auks such as guillemots tend to spend this period feeding up while they complete their post-breeding moults (Harris & Wanless, 1988). Additionally, the aim of this study was not to estimate true mass values, but rather to investigate differences in predicted mass between impacted and unimpacted individuals.

Although most simulated kittiwakes interacted with at least one OWF, we predicted very few collisions, primarily driven by a low vertical overlap between kittiwake flight height (Johnston et al., 2014; Supporting Information) and the rotor height used in this study; therefore, collision was unlikely even when multiple turbine transits were made. The rotor height we used was informed by discussions with OWF developers within our region, and is our best estimate for development within Norwegian waters (Layton-Matthews, Buckingham, et al., 2023). As collision risk for each transit was derived directly through the sCRM (Band, 2012; Masden, 2015; McGregor et al., 2018), we did not run a sensitivity analysis of the impacts of rotor height on collision risk, but we highlight that detailed plans (such as specific footprints and turbine parameters) are required to accurately assess the impacts of development. We assessed collision risk only during directed flight, rather than during foraging activities, when kittiwakes undertake short flights interspersed with dips into or rests on the water. However, as flight heights are typically lower during foraging behaviour than during

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directed flight, collision vulnerability during foraging is significantly lower (Davies et al., 2024); we therefore chose to model collision risk during directed flight only. Additionally, we followed an established method for allocating activity budgets in kittiwakes from geolocation-immersion data (McKnight et al., 2011), which did not distinguish between time in flight and resting on land. It is probable that kittiwakes spend at least some time on land during the non-breeding season, thus we have likely overestimated time in flight within our model. However, as we have modelled very few turbine collisions, we feel that this has had a negligible impact on our model results. Additionally, it is outside the remit of this paper to review methods of allocating activity budgets from geolocation-immersion data, but as our modelling framework is adaptable, these inputs could be modified easily as updated methods and data sources become available. Similarly, seabird distributions are likely to change due to climate change (Clairbaux, Cheung, et al., 2021) and, as OWFs are expected to be operational for around 25 years, seabird distributions may not be consistent throughout the development's lifespan. Nevertheless, as the model requires seabird density maps as environmental input data, maps of predicted seabird distribution could be incorporated to assess the longer-term impacts of OWFs on seabirds under different climate scenarios.

5 | CONCLUSIONS

We developed an individual-based model to assess the non-breeding season impacts of marine threats on seabird populations, which we applied to assess the cumulative impacts of 10 simulated OWFs. The model is designed to be easily applied to other populations and species with similar data, and the model could also be applied to assess the effects of other marine threats. Overall, we believe this model makes an important contribution as a useful tool for gaining a better understanding of the non-breeding season impact of additional human activity on threatened seabird populations.

AUTHOR CONTRIBUTIONS

Lila Buckingham, Signe Christensen-Dalsgaard, Per Fauchald, Elizabeth A. Masden and Tone K. Reiertsen conceived the ideas; Lila Buckingham, Signe Christensen-Dalsgaard, Per Fauchald, Elizabeth A. Masden, Kate Layton-Matthews, Tone K. Reiertsen, Kate R. Searle and Arnaud Tarroux designed the methodology; Ingar S. Bringsvor, Signe Christensen-Dalsgaard, Nina Dehnhard and Svein-Håkon Lorentsen collected the data; Lila Buckingham, Vegard Sandøy Bråthen, Per Fauchald, Kate Layton-Matthews, Elizabeth A. Masden and Arnaud Tarroux processed and analysed the data; Lila Buckingham led the writing of the manuscript and created all visualisations. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data are available from Zenodo (Buckingham et al., 2026a), and all codes are available in the associated GitHub repository (Buckingham et al., 2026b).

STATEMENT ON INCLUSION

The lead author and most of the authorship team were based in Norway, where the data collection for this study was carried out. Whenever possible, our research was discussed with local interested parties to seek feedback on the questions to be tackled and the approach to be considered. Whenever relevant, literature published by scientists from the region was also cited, including relevant work published in the local language. All authors were engaged early on with the research and study design.

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Figure S1. Model visualisation using the vODD format (Szangolies et al. 2024).

Table S1. State variables for each seabird super-individual.

Table S2. Additional state variables for each individual within each super-individual.

Table S3. State variables of offshore wind farms.

Table S4. State variables of the global environment, consisting of 0.25° grid cells.

Figure S2. The global environment for the guillemot model, aggregated into two-month periods (Fauchald et al., 2021). The colour of the sea depicts the density (individuals km^{-2}) of adult guillemots that breed at Sklinna (indicated by a white circle).

Figure S3. The global environment for the kittiwake model, aggregated into two-month periods (Fauchald et al., 2021). The colour of the sea depicts the density (individuals km^{-2}) of adult kittiwakes that breed in Ålesund (indicated by a white circle).

Figure S4. Visualisation of submodel processes. Submodel 1 (behaviour and movement) runs first; if there is an OWF interaction, submodel 2 (displacement and energetics) or 3 (collision) runs depending on the species and the impact being assessed.

Figure S5. Graphic of submodel 1: behaviour and movement. In both panels, the black circle shows the current location of a super-individual, with the white dashed circle showing the maximum distance the individual can move during the next time step (1 day), according to the time spent in 'travelling' behaviours.

Table S5. Number of geolocator datasets for each species, tag type and non-breeding season.

Figure S6. Graphic of the displacement relocation process.

Table S6. Probability of displacement at varying distances from an OWF footprint boundary. Spring probabilities were extracted from Peschko et al. (2020) and autumn and winter were extracted from Peschko et al. (2024).

Table S7. Estimates for the intercept (α, mass at median fledging date), linear trend in mass over the breeding season (β_{Day}) and individual (σ_i^2), year (σ_t^2) and observation effect variances (σ^2_{mass}) for guillemots breeding at Sklinna.

Figure S7. Predicted relationship between body mass and date for common guillemots breeding at Sklinna.

Table S8. Mass change parameters.

Figure S8. Graphic of offshore wind farm interactions for kittiwakes.

Table S9. Parameters used in the stochastic Collision Risk Model.

Figure S9. Modelled flight heights from Johnston et al. (2014), extracted from the stochLAB R package (Caneco et al., 2022).

Table S10. The proportionate densities that were retained that had the top ten most similar population-level distributions (BA) to the input data for guillemots.

Table S11. The proportionate densities that were retained that had the top ten most similar population-level distributions (BA) to the input data for kittiwakes.

Figure S10. A selection of simulated tracks without behavioural inputs for guillemots breeding at Sklinna. Locations are coloured by month and the breeding colony is shown as a white circle.

Figure S11. A selection of simulated tracks without behavioural inputs for kittiwakes breeding at Ålesund. Locations are coloured by month and the breeding colony is shown as a white circle.

Figure S12. A selection of simulated tracks using the final model for common guillemots breeding at Sklinna. Locations are coloured by month and the breeding colony is shown as a white circle.

Figure S13. A selection of simulated tracks using the final model for kittiwakes breeding at Ålesund. Locations are coloured by month and the breeding colony is shown as a white circle.

Table S12. The strength of the pull (α) towards Mass$_L$ and mean difference (ΔMass) in end of simulation mass compared with Mass$_L$.

Figure S14. Patterns of mass change during the non-breeding season for individuals (light blue lines; $n=500$) and the population-level means for different strengths of the pull (α) towards Mass$_L$.

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