

Predicting the impacts of wind farms on seabirds: An individual-based model

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Natural Environment Research Council;
Alderney Commission for Renewable Energy

Handling Editor: Steve Votier

Abstract

1. Individual-based models (IBMs) are a powerful tool in predicting the consequences of environmental change on animal populations and supporting evidence-based decision making for conservation planning.
2. There are increasing proposals for wind farms in UK waters and seabirds are a vulnerable group, which may be at risk from these developments.
3. We developed a spatially explicit IBM to investigate the potential impacts of the installation of wind farms in the English Channel and North Sea on body mass, productivity and mortality of a breeding population of Northern gannets for which we have tracking data.
4. A baseline model with no wind farms accurately represented the status of a sample of tracked gannets at the end of the 90-day chick-rearing period, and the behaviour-time budget was similar to that of tracked gannets.
5. Model simulations in the presence of wind farms indicated that installations should have little impact on the gannet population, when either avoidance behaviour or collision risk scenarios were simulated. Furthermore, wind farms would need to be ten times larger or in more highly used areas in order to have population-level impacts on Alderney's gannets.
6. *Synthesis and applications.* Our spatially explicit individual-based models (IBM) highlight that it is vital to know the colony-specific foraging grounds of seabirds that may be impacted, when identifying potential wind farm sites, in order to account for cumulative impacts from multiple sites. Avoiding areas highly used for foraging and commuting, and avoiding large-scale developments should be effective in limiting gannet mortality as a result of collision, competition and energy expenditure. Our IBM provides a robust approach which can be adapted for other seabird populations or to predict the impacts from other types of spatial change in the marine environment.

KEYWORDS

collision risk, evidence-based decision making, individual based models, *Morus bassanus*, Northern gannets, offshore development, predictive modelling, seabirds, wind farms

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1 | INTRODUCTION

The marine environment is under increasing pressure from anthropogenic activities including overfishing, climate change and offshore developments such as wind farms (Halpern et al., 2012). These installations may enhance the environment by creating de facto no fishing zones (Inger et al., 2009), but there is concern about the negative impacts they may have on Europe's breeding seabirds (Garthe & Hupop, 2004). These impacts may include direct mortality from collisions (Drewitt & Langston, 2006), as well as indirect effects such as altering energy budgets by forcing birds to travel further to forage (Masden, Fox, Furness, Bullman, & Haydon, 2010), or increasing competition in alternative foraging areas. However, robust and consistent knowledge regarding seabird behavioural responses to wind farms is sparse (Fox, Desholm, Kahlert, Christensen, & Krag Petersen, 2006); some birds show avoidance behaviour, whereas others are attracted to these sites (Lindeboom et al., 2011; Poot, Horsssen, Collier, Lensink, & Dirksen, 2012). As an example of this uncertainty, Furness, Wade, and Masden (2013) assessed that Northern gannets *Morus bassanus* are one of the most vulnerable species to collision mortality from wind farms, although empirical evidence suggests that gannets often avoid wind farms entirely (Krijgsveld et al., 2011; Petersen, Clausager, & Christensen, 2004). Indeed, few studies exist that are based on empirical evidence from existing wind farms (e.g. Krijgsveld et al., 2011; Lindeboom et al., 2011), due to the relatively small number currently operating and the difficulty and cost of monitoring them (Fox et al., 2006). Green, Langston, McCluskie, Sutherland, and Wilson (2016) conclude that the current methods to predict the impacts of offshore wind farms on seabirds are inadequate, and this demonstrates a demand to establish a robust methodology which can be used by planners to mitigate the impacts on seabirds, when identifying wind farm sites.

Evidence-based decision making is the preferred approach when responding to such pressures (Solesbury, 2001), but may be challenging when there is little empirical evidence as to how systems will respond to environmental change (Botsford, Micheli, & Hastings, 2003). Predictive modelling can fill this gap and individual-based models (IBMs; Grimm & Railsback, 2013; Sutherland, 1996) are widely used in many disciplines to model complex systems, for example, to predict the impacts of environmental change on shorebirds, seabirds and pinnipeds (Boyd et al., 2016a,b; Harwell et al., 2012; Langton, Davies, & Scott, 2014; McDonald, Searle, Wanless, & Daunt, 2012; Stillman et al., 2003; West & Caldow, 2006). They differ from conventional models by modelling autonomous entities, and each individual's behavioural and physiological traits determine the properties of the system, for example, taking into account individual variation and an individual's interaction with the environment (Grimm, 1999). For example, the functional response (relationship between intake rate and prey density) is often a key relationship underpinning IBMs, thus the individual's behaviour is a result of its own decision making which, in turn, is a result of its physiological state (Stillman, 2008). Individual-based models (IBMs) provide a powerful approach to predict the consequences of environmental change in a variety of systems as the modelled individuals

reflect real animal behaviour (Stillman, 2008). Most importantly, they scale-up individual-level impacts to population-level impacts, and take into account the cumulative impact of spatially explicit disturbances within the home range of a population. Thus, IBMs are superior to methods currently used to predict the impact from wind farms, which focus solely on monitoring at development sites (Drewitt & Langston, 2006), although they do not necessarily recognize impacts of specific developments across multiple colonies.

In an effort to address this critical gap in our understanding of the impacts of proposed offshore wind farms, we have developed a novel, spatially explicit IBM. Our model allows us to predict at a high spatial and temporal resolution how proposed wind farms in the English Channel and North Sea may impact the mortality and breeding success of a population of Northern gannets breeding in the English Channel. We simulate the population both with and without wind farms, allowing (a) the gannets to perform complete avoidance behaviour and (b) allowing them to enter the wind farm areas with a risk of collision when doing so. We also assess the impact of variation in the size and the location of wind farms since these factors and the extent of their overlap with seabird foraging and commuting areas are likely to have a substantial impact, which can be taken into account during planning processes. The framework that we outline could be modified both for other species of mobile marine organism and other environmental pressures.

2 | MATERIALS AND METHODS

2.1 | Data collection

Fieldwork, licensed by the States of Alderney, to determine the behaviour and habitat use of Northern gannets took place at the breeding colony (c. 5,000 pairs), on Les Etacs, Alderney, Channel Islands (49°42'N, 2°14'W) during the early chick-rearing period in June of 2011 and 2013–2015. Adults with chicks c. 2–4 weeks old were caught at their nest using a noose pole. Global positioning system (GPS) data recorders, logging positions every 2 min (IgotU GT 120 or IgotU GT-600, Mobile action technology), were sealed in heat shrink plastic and attached to the base of the tail using tesa extra power tape ($n = 17, 16, 13, 17$ birds and 34, 78, 81, 102 trips respectively). In 2013, nine birds were also fitted with a tri-axial accelerometer ($\times 6-2$, Gulf Coast data concepts), set to record at 25 Hz. The weight of the devices was <2% of the birds' body mass (GPS 33 g; GPS + accelerometer 44 g). The loggers were removed 2–3 weeks later.

2.2 | Data processing and analysis

GPS positions were interpolated to every 10 s using the *adehabitatLT* package (Calenge, 2006) in R (ver. 3.0.2, R Core Team, 2016). The R package *Trip* (Sumner, 2011) was used to calculate the time spent (s) in each 5×5 km cell of a pre-defined grid around the colony for each bird for each year (Time-in-area or TIA grid). In order to identify important foraging areas a second grid was created (foraging grid) by filtering the data for track tortuosity, which represents searching behaviour

(Wakefield et al., 2013). The tortuosity index was calculated as a ratio of the straight line distance to the total distance travelled over a 16-min duration (Wakefield et al., 2013). Individuals were defined as searching where GPS points had a tortuosity index of <0.9 and a speed >1 m/s. The cells in this grid comprising the top 25% of time spent undertaking searching behaviour for all individuals combined were identified as key foraging areas (Warwick-Evans et al., 2015; Figure 1). A third grid (behaviour grid) was generated from the other two grids by expressing a value for each cell as the proportion of points classified as searching behaviour from the total number of points in the cell. This was used to determine the probability of foraging in each cell, rather than flying straight through it. All grids were created independently for years 2013–2015 and for all years combined. The year 2011 was not modelled independently as the number of trips recorded was insufficient to represent the home range of the population (Warwick-Evans et al., 2016).

Ethographer for IGOR Pro (Sakamoto et al., 2009) was used to extract behaviours from the acceleration data automatically, based on unsupervised cluster analysis of the acceleration signals as described in full in Warwick-Evans et al. (2015). We were able to classify all periods within the first 5 days of data per bird as foraging, flying, resting on the water and diving. These were used to understand the time budgets of the gannets, in order to create the behaviour decision trees, and to assist in model validation.

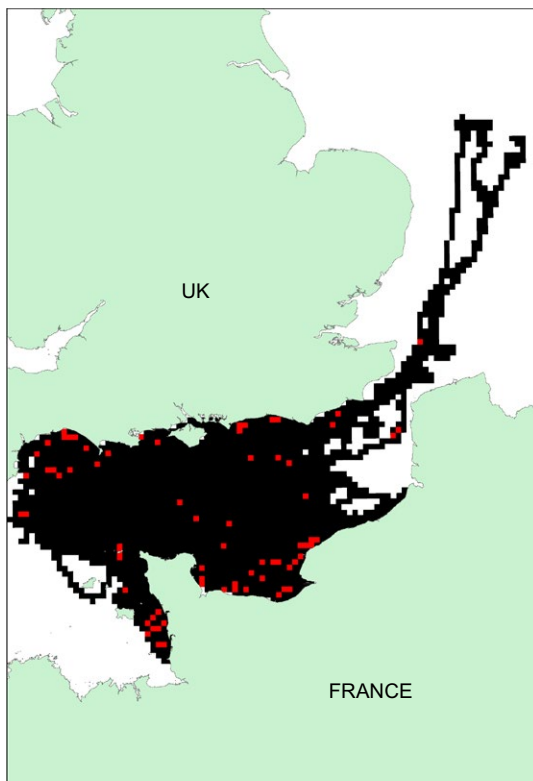


FIGURE 1 Locations visited by Alderney's population of Northern gannets tracked in 2011–2015 (black). Red cells represent the top 25% of areas where gannets spend most time [Colour figure can be viewed at wileyonlinelibrary.com]

2.3 | Model

2.3.1 | Model description

The 4 years of tracking data were combined with key parameters from peer-reviewed literature (Table 1) to design a spatially explicit model using NetLogo (Wilensky, 1999). We describe the model using the overview, design concepts and details (ODD) protocol (Grimm et al., 2010), and provide the script (Appendix S1). Our model builds on the IBM for guillemots devised by Langton et al. (2014) by incorporating fine-scale characteristics of the surrounding environment, direct interactions between birds and prey, and intraspecific competition.

2.3.2 | Purpose

The purpose of the model is to predict how the construction of proposed wind farms in the English Channel and North Sea (Figure 2; Appendix S2) may impact the body mass, mortality rate and breeding success of Northern gannets.

2.3.3 | State variables and scales

The model is composed of 5,000 family groups, each comprising an adult male, an adult female and a chick. The landscape is a grid of 5 km by 5 km patches, each with attributes such as number of fish and probability of foraging. The key state variables are described in Table 2 (see Appendix S3 for all state variables). The model runs in 6-min timesteps, with 240 timesteps per day. The first 200 timesteps in a day are day-time, the remainder are night-time, corresponding with early June at the study location. The model runs for the 90 day chick-rearing period.

2.3.4 | Process overview and scheduling

The main processes in the model are decision making, performing behaviours and updating mass. Behavioural processes are undertaken by all adults in the same order each timestep, at which point behaviour counters are updated. The number of prey items is updated between individuals, that is, if an individual forages successfully the prey in the patch is adjusted accordingly. Adult and chick mass are updated during the last minute of each day. Adult mortality occurs if body mass drops below a specific threshold (1,800 g). Mortality in chicks occurs if on day 90 body mass has not attained a specific threshold (1,800 g).

2.3.5 | Design concepts

Basic principles

The state and mortality rate of adults and chicks throughout the chick-rearing period are impacted by the energy and time budgets of the adults which, in turn, are affected by the amount and distribution of prey. Energy is gained through food intake and lost through maintenance and activity. Northern gannets are long-lived and prioritize their own survival above that of the chick.

TABLE 1 Parameter estimates used in the individual-based models (IBM). See Appendix S8 for justification

Parameter	Value	Source
Initial mass of adults (g)	3286 ± 226	Wanless and Okill (1994)
Initial mass of chicks (g)	79.3 ± 11.2	Montevecchi, Ricklefs, Kirkham, and Gabaldon (1984)
Full (maximum mass of food the adult can hold in gut, g)	745	Garthe, Grémillet, and Furness (1999)
Flyfull (maximum amount of food adult can hold in gut and be too full to commute, g)	550	Derived through iteration
Nearly empty (the mass of food in the stomach above which the gannet will remain resting during the initial long rest period, g)	150	Derived through iteration
Fish size (g)	100 ± 10	Garthe et al. (1999)
Chick-food-max (g)	Calculated daily	Montevecchi et al. (1984)
Assimilation efficiency	0.76	Cooper (1978)
Production efficiency	0.75	Montevecchi et al. (1984)
Basal metabolic rate ($\text{J s}^{-1} \text{g}^{-1}$)	0.0027	Birt-Friesen, Montevecchi, Cairns, and Macko (1989)
Energy density of adult gannet tissue (kJ/g)	13	Montevecchi et al. (1984)
Energy density of gannet chick tissue (kJ/g)	Calculated daily	Derived from Montevecchi et al. (1984)
Energy density of prey (kJ/g)	7	Lewis, Sherratt, Hamer, Harris, and Wanless (2003)
Metabolic rate at nest ($\text{kJ g}^{-1} \text{min}^{-1}$)	0.0007	Birt-Friesen et al. (1989)
Metabolic rate at rest ($\text{kJ g}^{-1} \text{min}^{-1}$)	0.0007	Birt-Friesen et al. (1989)
Metabolic rate at flight ($\text{kJ g}^{-1} \text{min}^{-1}$)	Calculated each timestep	Pennyquick (1998)
Metabolic rate at forage ($\text{kJ g}^{-1} \text{min}^{-1}$)	Calculated each timestep	Pennyquick (1998)
Flight speed (m/s)	15.3	Hamer, Phillips, Wanless, Harris, and Wood (2000)
Foraging efficiency	0.75	Hennicke et al. in Ropert-Coudert et al. (2004)
Mass below which adult is dead (g)	1,800	Garthe et al. (2012)
Mass below which chick is dead (g)	1,800	Garthe et al. (2012)
Digestion rate (proportion of intake per hr)	0.1	Derived from (Jackson, 1991)

Adaptation

Behavioural decisions are based on the physical state of the adult and the attributes of the surrounding environment and are made using decision trees (Appendix S4).

Objectives

The adults aim to brood a chick to fledging while maintaining their own state at a healthy level.

Awareness and sensing

Adults have a memory of their behaviour during the previous timestep. They are aware of their own stomach content, whether they have previously been full during the current trip, if their chick has been fed and if it has been given the maximum food intake for the day. If an adult is on the nest they are aware of whether their partner is on the nest and who has been there longer. Adults are aware of how much food is in the patch they are on, the probability that they should forage there and if it is day- or night-time. In avoidance scenarios they are also aware of the location of wind farms, and calculate a path to their foraging location which does not enter these cells.

Interaction

The adults interact directly with the chick during feeding events and indirectly with one another via intraspecific competition for food as prey availability decreases following foraging success.

Stochasticity

Initial masses of adults and chicks are drawn randomly from normal distributions based on the literature (Table 1). The success or failure of catching a fish, and the mass of the fish is stochastic, based on information from the literature (Table 1). The destination an adult is given when leaving the nest is randomly selected from the foraging grid. It is clear from the tracking data and other studies (Pettex, Bonadonna, Enstipp, Siorat, & Grémillet, 2010) that gannets fly straight through some patches (commuting behaviour), whereas searching behaviour occurs in others. The behaviour grid gives the probability of a gannet foraging there, with higher probability of foraging in patches where increased searching behaviour was observed. After a gannet has reached its foraging destination the probability of moving in a given direction is determined by the amount of time tracked birds spent in the surrounding patches from the TIA grid. If a gannet enters a wind farm area, there is a probability of collision mortality.



FIGURE 2 Wind farms proposed for development in the English Channel and North Sea (Appendix S2 for specifications). Only wind farms within the range of gannets tracked from Alderney, and used in the model, have been included. The colony is marked in blue (star) [Colour figure can be viewed at wileyonlinelibrary.com]

Observation

Adult and chick mortality rate and mass are the main outputs. Trip length and behaviour budgets of adults are used for model validation.

2.3.6 | Initialization

The first minute of the model is the first minute of daylight on the day the chicks hatch (the model assumes all chicks hatch on the same day). Individuals start on the nest and all behaviour counters and stomach contents initialize at zero except for the duration at the nest for males. This initializes at 1 min in order to be higher than that of the female, instigating the departure on a foraging trip by males.

2.3.7 | Input data

The attributes of patches, such as the probability of movement between patches (from the TIA grid), the probability of heading to a particular patch (from the foraging grid) and the probability of foraging (from the behaviour grid) were input into the model. Areas where gannets spend more time represent areas of increased foraging, and hence areas of higher fish availability (Warwick-Evans et al., 2015). The distribution of fish among the patches was therefore assigned by multiplying the TIA grid by a numerical constant (Appendix S5). This value was assigned iteratively in the baseline models until the physiological

TABLE 2 Key state variables for the model entities

Globals	
Day-night	Daytime or night-time
Minute	Minute of the day
Day	Day of the simulation
Chick-food-max	Maximum mass of food the chick can consume this day
Adults	
Pair	Identifies the partnership of the individual
Chicknum	Identifies the chick belonging to each pair
Gender	Sex of the individual
Mass	Body mass on the current day
Stomach-content	Mass of food in the stomach (g)
Behav	Behaviour the bird is performing this timestep
Duration-nest	Minutes the adult has been on the nest (without leaving)
Flight	Minutes flying on this trip
Rest	Minutes resting on this trip
Forage	Minutes foraging on this trip
Forage-type	Whether the adult is foraging for itself or the chick
Catch	Mass of the fish caught (g)
Fish-counter	Total number of fish caught this trip
Food-given-to-chick	Total amount of food given to chick that day (g)
Energy-gain	Energy gain of adult that day (kj)
Tot-energy-expend	Total energy expended that day (kj)
Chicks	
Pair	Pair number of the chicks parents
Chick-mass	Mass of the chick (g)
Energy-tissue-chick	Energy density of chick tissue that day (kj/g)
Egain	Energy gained by the chick that day (kj)
Eexpend	Energy expended by the chick that day (kj)
Patches	
Use	Use of the patch (i.e. home, wind farm)
Fish-number	Number of fish currently in each patch
Start-fish	Number of fish each patch started with
Tortuosity	Tortuosity (proportion of time searching behaviour was observed in the patch)
Probnorth	Probability of heading north when leaving each patch
Probeast	Probability of heading east when leaving each patch
Probsouth	Probability of heading south when leaving each patch
Probwest	Probability of heading west when leaving each patch

state of both adults and chicks at the end of the breeding season represented values observed in natural populations.

2.3.8 | Sub-models

Sub-models were created to decide and perform behaviours of adults, and to calculate the maximum quantity of food a chick can consume each day, the amount of energy expended by the adults, the amount of food in the stomach, and the mass of the adult and chick at the end of each day (Appendix S6).

2.3.9 | Model validation

To test the performance of the model, we compared the body mass of adults and chicks with values from the literature, and the trip length of adults with those from our tracked birds. Additionally, the proportion of the simulated birds performing each behaviour (on the nest, flying and foraging combined, and resting on the water) was plotted against time of day, and compared to the time budgets of birds fitted with accelerometers.

2.3.10 | Simulations

Initially baseline models were simulated using the tracking data from all 4 years combined, which represents the mean state of the population over the 4 years without wind farms. Subsequently, model simulations were carried out independently for each year, parameterized using year-specific tracking data. Both the baseline and the year-specific models were run in the presence and absence of wind farms. For the simulations in which the wind farms exist, the birds either show complete avoidance behaviour or are able to enter this area but risk mortality due to collision with a turbine as described below.

Avoidance

When the birds show avoidance behaviour they are unable to enter patches with wind farms.

Collision risk

Collision risk was calculated individually for each wind farm site using the extended Band model (Band & Band, 2012; Appendix S7). It was not possible to calculate exact values for each site, as some information (e.g. the amount of time the turbines would be operational) was unavailable. Furthermore, the micro-avoidance rates (avoidance of individual turbines when in the wind farm area) of gannets are unknown and industry standard values are used (Cook, Humphreys, Masden, & Burton, 2014). Thus, we created a best- and worst-case scenario for each wind farm site. The best case is with the lowest operational rate (64%) and the highest avoidance rate (99.5%), and the worst case is the highest operational rate (90%) and the lowest avoidance rate (98.9%).

In order to extend the predictions under alternative scenarios of variation in the location and size of proposed wind farms, the model was altered in three ways: (1) Current proposed sites were scaled up in size (multiplied by 2, 5, 10, 15, 20), (2) current proposed sites were

replaced by placing sites in the most used 5%, 10 15%, 20% and 25% of the home range area, (3) current proposed sites were replaced with sites in random cells, covering the same extent as those in scenario 2.

2.3.11 | Sensitivity analysis

To determine the robustness of the model and the parameters that impacted most on the mortality rate and body mass of the adults and chicks, an individual parameter perturbation sensitivity analysis was carried out. Multiple simulations were carried out on the baseline model, where each of a key subset of the model parameters were varied singly and sequentially by a standard variability of $\pm 10\%$, while maintaining the initial values for all other variables. To account for stochasticity in the outputs, simulations were repeated three times, and the mean and standard deviation of mortality rate and body mass for both adults and chicks was calculated and expressed as the percentage difference from the baseline model. Subsequently, a best-case and worst-case scenario were simulated, where all values of model parameters which resulted in an increase/decrease in mortality or body mass were adjusted by $\pm 10\%$ respectively.

3 | RESULTS

3.1 | Model validation

The baseline model accurately represented the mortality rate and physiological state of the tracked gannets at the end of the 90-day chick-rearing period (Table 3). Gannets are undoubtedly subject to mortality from other causes, however, for the purposes of this model, we use zero mortality for both adults and chicks as a baseline from which to quantify increased mortality from the installation of wind farms. Against this baseline, the model can predict increased mortality only as a result of direct collision with turbines, or due to starvation as a consequence of the addition of wind farms, acting through alteration to the energy budget or increased competition. Both simulated and tracked birds spent similar amounts of time per day engaged in the key behaviours of being on the nest, in flight and resting on the water (Figure 3). The diel

TABLE 3 Mean ($\pm SD$) mortality rate and physiological state of natural and simulated gannets. Mortality rate is a measure of increased mortality from collision or starvation as a result of the addition of the proposed wind farms, thus for the baseline model simulation, and empirical data this value is zero. Literature values for adult and chick mass were used, and trip duration taken from Warwick-Evans et al. (2016)

Parameter	Empirical data	Baseline model output
Adult mortality (%)	0	0
Adult mass (kg)	3.3 \pm 0.23	3.3 \pm 0.21
Chick mortality (%)	0	0
Chick mass (kg)	3.7 \pm 0.28	3.7 \pm 0.24
Trip duration (hr)	24 \pm 9	24 \pm 5

pattern was also similar suggesting that the behaviour of the modelled birds was comparable to that of the natural population.

3.2 | Simulations

There was little evidence to suggest that the installation of the proposed wind farms would impact Alderney's population of Northern gannets. No differences were observed in the physiological state or mortality rate of the gannets between the baseline model and models where gannets

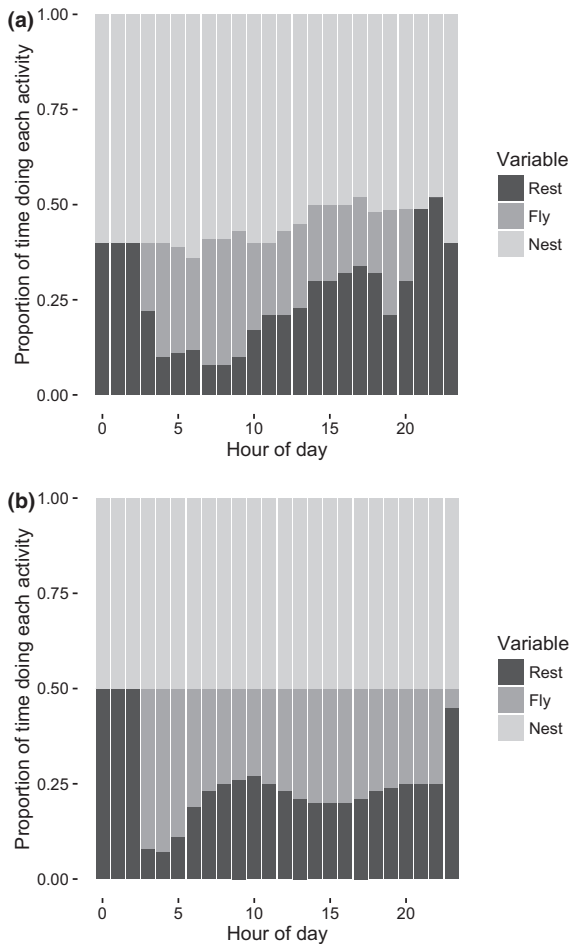


FIGURE 3 Behaviour budgets for (a) Accelerometer equipped Northern gannets, and (b) outputs from a baseline individual-based models (IBM) simulation for all years of data combined. Only the first second of diving behaviour was extracted from the accelerometer data, therefore there is no time budget for diving behaviour in the tracked gannets, thus flight and foraging behaviour are combined for both datasets

TABLE 4 Mean (\pm SD) state and mortality rates of birds under different model simulations: parameterized with data from all years combined

Parameter	Baseline	Avoidance	Collision	
			Best case	Worst case
Adult mortality (%)	0	0	0	0.02
Adult mass (kg)	3.3 \pm 0.21	3.3 \pm 0.28	3.3 \pm 0.23	3.3 \pm 0.24
Chick mortality (%)	0	0	0	0.04
Chick mass (kg)	3.7 \pm 0.24	3.7 \pm 0.28	3.7 \pm 0.24	3.7 \pm 0.25

showed avoidance behaviour either for all years combined (Table 4) or for individual years (Table 5). Simulations where the gannets entered the wind farm area and were exposed to collision risk showed minimal adult and chick mortality and no change in physiological state (Tables 4 and 5). There was some evidence of inter-annual variation in the baseline models, with a lower than normal fledging mass of chicks in 2015, yet no evidence of inter-annual variation in the impacts from wind farms (Table 5).

As the size of the proposed wind farm sites were increased both adult and chick mortality increased, with a much greater impact when avoidance behaviour was displayed, particularly when the size of the wind farms increased considerably (Figure 4a,b). Additionally when avoidance behaviour was displayed adult mass decreased (Figure 4c). These outcomes are a result of starvation, as displaced adults are forced to forage further from the colony and competition outside of the wind farm sites would be higher, as more birds are displaced. There was no impact on either adult or chick mass in the collision risk scenarios. As wind farms were placed in increasing numbers of highly used cells, both adult and chick mortality increased in the collision risk scenarios (Figure 5a,b) and adult mass decreased in avoidance scenarios (Figure 5c). As wind farms were placed in an increasing number of random cells, adult and chick mortality increased and adult mass decreased at a lower rate than when wind farms were placed in highly used cells (Figure 6). The placement of wind farms in small areas had little impact, however, once a critical size (c. 10 times the size of current sites or 5% of the most highly used cells) was reached, mortality increased dramatically.

3.3 | Sensitivity analysis

The model was fairly robust to changes in parameter values, with changes of <10% being recorded as a result of 10% changes in the parameter value in almost all cases (Figure 7). Both the adults and chicks in the model were most sensitive to changes in the energy density of fish. Even in the unlikely worst-case scenario that all model parameters were inaccurate, a change in c. 30% of the adult body mass is driven mostly by the energy density and size of fish, which can be justified biologically, and could easily be adjusted in the model based on more accurate data from a given study site.

4 | DISCUSSION

The use of individual based models to predict the effects of environmental change is a powerful tool that is widely used in many disciplines (Grimm, 1999). We have developed the most complex and

Year	Parameter	Baseline	Avoidance	Collision	
				Best case	Worst case
2013	Adult mortality (%)	0	0	0.02	0.04
	Adult mass (kg)	3.3 ± 0.23	3.3 ± 0.29	3.3 ± 0.23	3.3 ± 0.24
	Chick mortality (%)	0	0	0.02	0.06
	Chick mass (kg)	3.7 ± 0.24	3.9 ± 0.24	3.8 ± 0.23	3.8 ± 0.24
2014	Adult mortality (%)	0	0	0.01	0.08
	Adult mass (kg)	3.3 ± 0.23	3.3 ± 0.28	3.3 ± 0.23	3.3 ± 0.24
	Chick mortality (%)	0	0	0.02	0.08
	Chick mass (kg)	3.7 ± 0.24	3.7 ± 0.24	3.7 ± 0.23	3.7 ± 0.23
2015	Adult mortality (%)	0	0	0.02	0.03
	Adult mass (kg)	3.3 ± 0.23	3.3 ± 0.3	3.3 ± 0.23	3.3 ± 0.24
	Chick mortality (%)	0	0	0.04	0.08
	Chick mass (kg)	3.1 ± 0.29	3.1 ± 0.3	3.1 ± 0.29	3.1 ± 0.29

TABLE 5 Mean (±SD) state and mortality rates from model simulations parameterized individually for each year

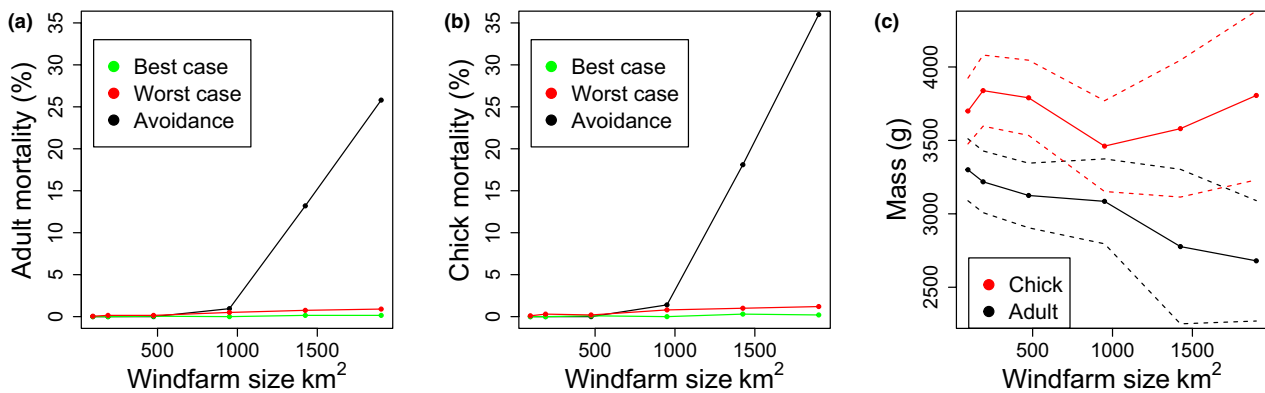


FIGURE 4 The impact of the size of proposed wind farms in the English Channel on (a) adult mortality, (b) chick mortality, (c) mass of adults and chicks (under the avoidance scenario, with SD) [Colour figure can be viewed at wileyonlinelibrary.com]

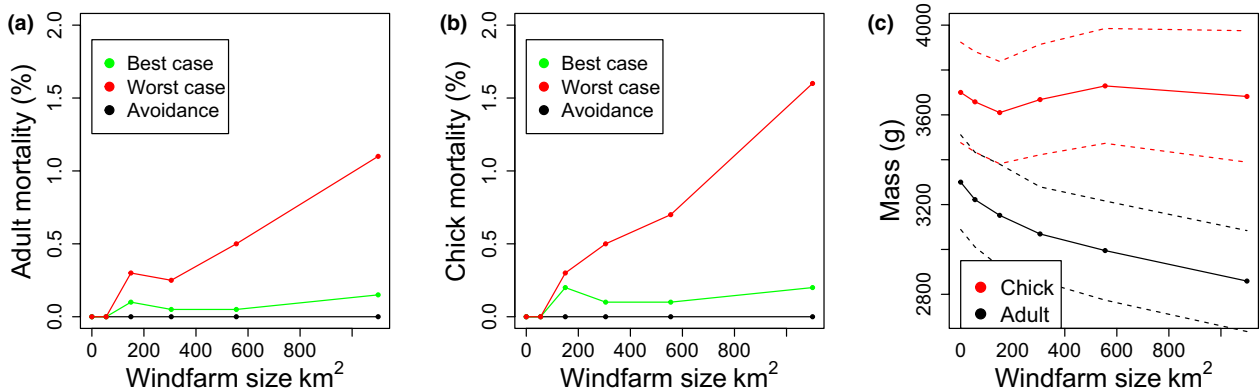


FIGURE 5 The effect of replacing the proposed wind farms in the English Channel with sites in the most highly used areas (i.e. the cells in which gannets spend 5%, 10%, 15%, 20%, 25% of their time) on (a) adult mortality, (b) chick mortality, (c) mass of adults and chicks (under the avoidance scenario, with SD) [Colour figure can be viewed at wileyonlinelibrary.com]

comprehensive model yet to predict the impacts of wind farms on seabirds; a spatially explicit model which incorporates direct interactions between birds and the environment, including the availability of prey and intraspecific competition. It can be used to predict the

cumulative impacts of changes in the environment on seabird populations. Baseline models accurately represented the behaviour and physiological state of Alderney's Northern gannets (Figure 3), and model simulations successfully explored the potential impacts from

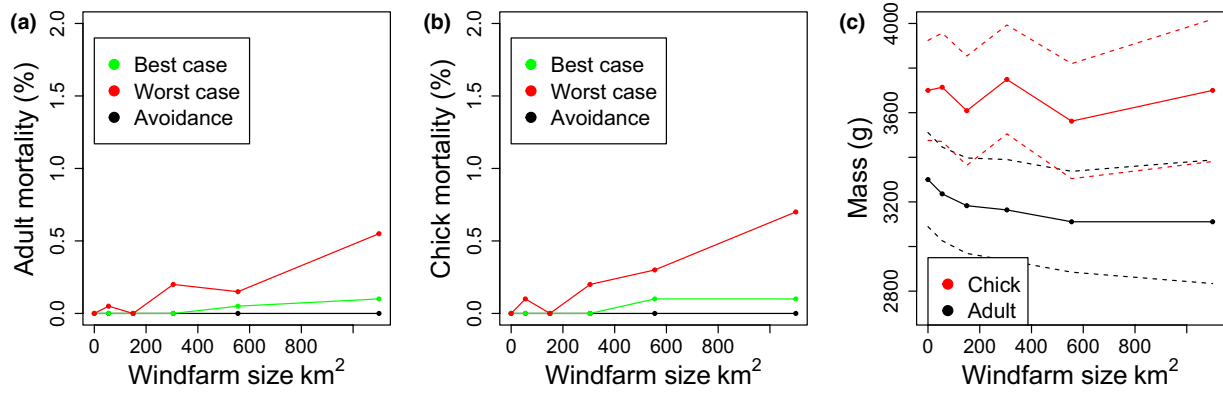


FIGURE 6 The effect of replacing proposed wind farms in the English Channel with random sites of size equivalent to those in Figure 6 (i.e. the same number of cells where adults spend 5%–25% of their time, but randomly assigned) on (a) adult mortality, (b) chick mortality, (c) mass of adults and chicks (under the avoidance scenario, with SD) [Colour figure can be viewed at wileyonlinelibrary.com]

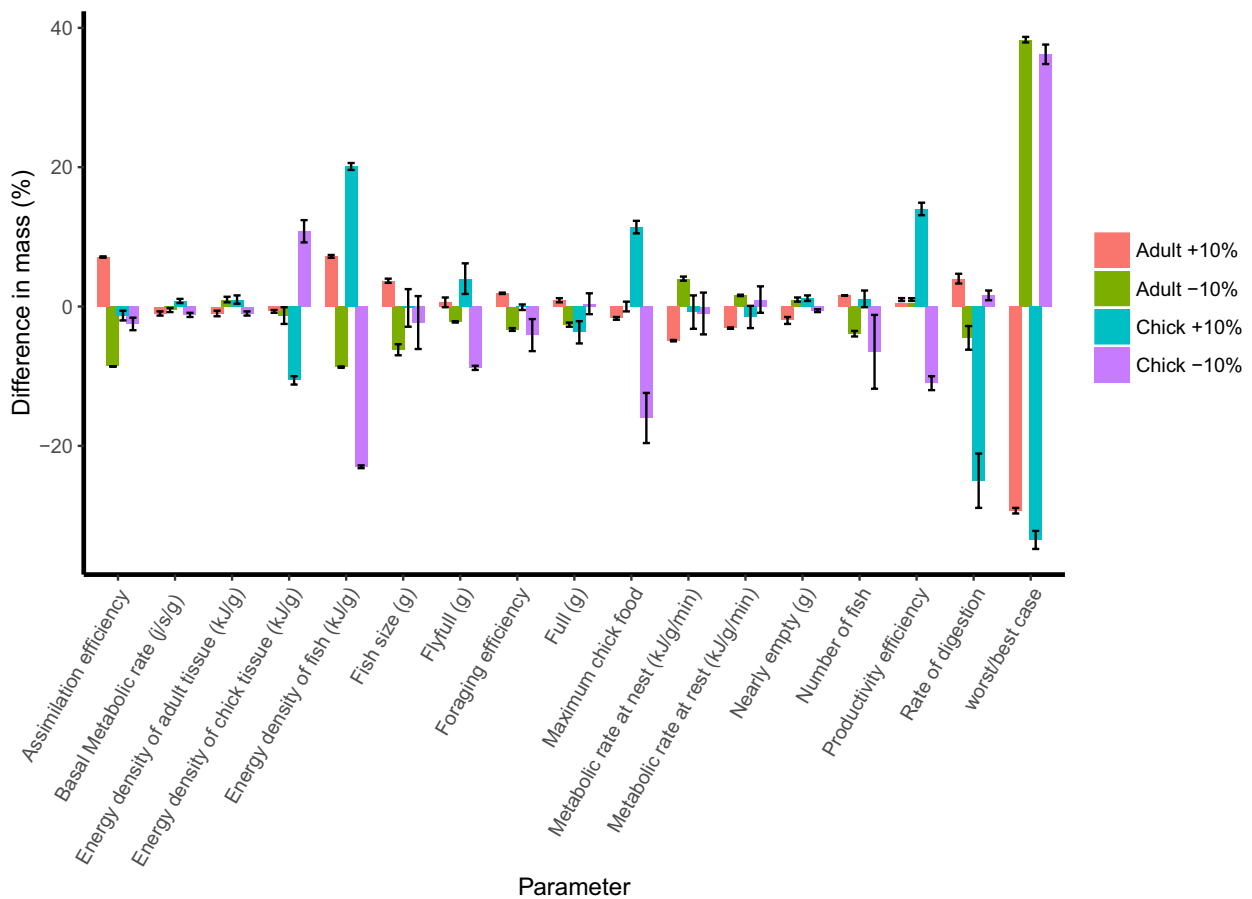


FIGURE 7 Sensitivity analysis of adult and chick body mass. Each of the model parameters were varied singly and sequentially by a standard variability of $\pm 10\%$ and their effect on adult and chick body mass calculated as a percentage of the baseline model [Colour figure can be viewed at wileyonlinelibrary.com]

environmental change. We found no impact of proposed wind farms on the mortality rate, productivity or physiological state of this population, although these risks may have been underestimated due to model assumptions discussed below. Our model indicated that there were no changes in mortality rate, productivity or physiological state if Northern gannets avoided the sites and negligible mortality and no

change in physiological state in the collision risk scenarios (Tables 4 and 5). Concerns that in years of poor prey availability, wind farms would have increased impact on gannets, were not supported by the model outcomes. For example, in 2015, when the chicks fledged at a lower mass than expected, impacts of wind farms were consistent with other years.

The home range of the gannets was large in comparison to the area proposed for wind farms, which represented only 4% of all of the 5 × 5 km cells which the gannets visited. Consequently, the proportion of foraging behaviour in these areas was low and, as the areas were relatively small, the displacement distances were small, resulting in negligible effects on birds' energy budgets. Other wind farm developments may pose greater threats to different colonies. For example, the areas of proposed wind farms in the North Sea are larger (4cOffshore, 2015), and they may be harder to avoid, thus posing a higher risk to gannet colonies nearby. Northern gannets avoidance rates to entire wind farm sites (macro-avoidance) is estimated to be 64% and the rate at which birds avoid individual turbines while inside the wind farm area (micro-avoidance) is 98.9%–99.5% (Cook et al., 2014). Industry standard data on the flight height of gannets indicates that only 11.3% of Northern gannets fly at a height with a risk of collision with a rotor (Cook, Johnston, Wright, & Burton, 2012) and when these data are combined in the extended Band model, used to calculate collision risk in this model, the probability of a gannet entering the wind farm and colliding with a rotating turbine is small. However, the strength of the IBM approach is that it allows cumulative impacts of collision risk across many individuals and foraging trips. Similarly alterations to energy budgets, which are low at an individual-level, are scaled up to allow prediction of population-level impacts that may be of more concern.

An increase in the size of proposed wind farms resulted in considerably higher mortality in avoidance simulations than collision risk simulations (Figure 4). This highlights the considerable changes in energy budgets and increased intraspecific competition in alternative sites if large-scale installations are created and birds are forced to avoid entering the wind farm sites. This supports previous conclusions that the impacts on the energy budgets of seabirds will be higher when wind farms are larger (Drewitt & Langston, 2006; Masden et al., 2010). This also goes some way to address concerns over the cumulative impacts of multiple wind farms within the range of a single population (Masden et al., 2010). The sudden increase in mortality when the size of the wind farms >1,000 km² is likely to be specific to the English Channel because of the location of proposed wind farms in highly used areas off the north coast of France and the south coast of the UK. When wind farms are increased to this scale they displace birds from a large proportion of the highly used foraging areas, forcing them into areas with fewer prey and increased competition (Burton, Rehfish, Clark, & Dodd, 2006). Additionally, wind farms of this scale would result in considerably increased energetic requirements as the gannets would be forced to leave the English Channel in order to forage, and potentially overlap with other populations. For gannets at least, populations appear to have segregated foraging areas (Wakefield et al., 2013) meaning colony-specific IBMs are sufficient to address the impacts of wind farms. However, in a scenario where gannets start to overlap and/or for other species which are likely to have overlapping foraging ranges between colonies (Ainley et al., 2004) then a multi-colony approach to impact assessment may be appropriate. In theory this could be developed within the IBM framework.

The size threshold at which the impact of wind farms would result in high seabird mortality is likely to vary between seabird colonies

depending on the size and quality of the remaining available habitat after wind farm development, and on the size of the seabird populations which require resources from these areas (Busch & Garthe, 2016). However, it is likely that for all populations there will be maximum size of wind farms, above which an increase in mortality would undoubtedly occur as a result of increased competition in remaining patches, leading to increased energy expenditure. The mass of adults decreased in all avoidance scenarios as wind farms increased in size, due to increased competition and altered energy budgets. However, the mass of chicks in the model was unaffected by these changes. This is because adults in the model do not stop feeding the chick when their own mass decreases (as they would in reality, Ponchon et al., 2014), and this should be addressed in future model iterations. Collision risk from these large sites is less important, presumably due to the high micro-avoidance rate of gannets to wind turbines. In contrast, when wind farms were placed in highly used areas (more patchily distributed) or random cells, collision risk scenarios resulted in greater mortality than avoidance scenarios, as wind farm sites were more easily avoided without large alterations to energy budgets (Figures 5 and 6). The highly used cells in the model are a result of both high intensity foraging, and important commuting paths. The placement of wind farms in areas which are highly used for either of these activities may have severe implications on seabird mortality (Drewitt & Langston, 2006). When wind farms were placed in highly used cells as opposed to random cells there was increased mortality from collision, as more birds were entering these areas to commute and to forage. These findings highlight the relationship between the size and location of proposed wind farms, and the impact that they may have on seabird populations. Planners should avoid highly used areas when identifying potential sites for wind farms, and take into account the scale of displacement when considering the size of proposed developments.

Both the adults and chicks in the model were highly sensitive to changes in the energy density of fish (Figure 7). This effect was much larger on the chicks, which were, in general, more sensitive to perturbations in model parameters than adults. The energy density of prey is directly related to the mass gain for both adults and chicks in the model, thus this result is not surprising. In natural populations the energy density of fish will vary widely, thus if dietary information specific to the focal colony is available it should be incorporated into the model. Additionally, the chicks in the model were very sensitive to the rate of digestion by adults. Indeed, this again is unsurprising, given that the rate of digestion is directly related to the amount of food available for the chicks. The rate used in the model was derived from experimental results by Jackson (1991), thus we are confident is a fairly accurate representation of the digestion rates of gannets. If this rate was faster, then impacts on chick mass would be greater in the scenarios where the adult was forced to travel further to forage in order to avoid wind farms, as less food would be available to feed the chick on the adults return from the foraging trip. However, this is unlikely to have major impacts on the outcome of the model given that the baseline model realistically represents chick growth, and thus the values used in the model are likely to be fairly accurate.

As with all modelling approaches, assumptions and simplifications to the behaviour and life history of modelled species were made, for example, that the prey type and size and the foraging efficiency of gannets breeding on Les Etacs was similar to that from the literature. Additionally, some behavioural characteristics were simplified, for example, no foraging occurs at night, adults are never at the nest together for more than one timestep and do not interact when on foraging trips. Consequently, birds cannot take visual cues from, or copy one another when on foraging trips (e.g. Boyd et al., 2016a,b). Additionally, the model uses tracking data to determine the probability of a bird moving from one of the cells to any of the adjacent cells, thus cells which were not visited by our sampled birds have a probability of zero for a modelled bird to enter. We know that our sample of tracked gannets did not represent the entire home range area for the population (Warwick-Evans et al., 2016), thus some cells may be under-represented in the model. However, this is unlikely to have severe implications on the model outputs, as these cells were likely to have very low usage, and thus even if they were available in the model, few birds would use them.

There is some debate surrounding the visual observation method to determine flight heights, and Cleasby et al. (2015) proposed that this method may underestimate collision risk. Thus, an alternative value of collision risk was calculated using empirical flight height data (extracted from Cleasby et al., 2015) and applied to the model for comparison (Appendix S9). In the worst-case scenarios, considerable differences in mortality rate were obtained as a result of these changes, thus the impacts of collision mortality from proposed turbines may be larger than these initial models suggest. However, as the flight height of gannets is very site specific (Cleasby et al., 2015), these new flight heights may not accurately represent the behaviour of gannets in the English Channel, thus, we present these data for comparison only and encourage further work to assess flight heights in other populations. In addition, there is the potential for wind turbines to attract schooling fish (Inger et al., 2009), which may attract gannets into the area, and potentially result in increased mortality.

Current approaches to assess the potential impacts on seabirds from proposed wind farms are based on observations within wind farm sites, making assumptions about the origins of these birds (Camphuysen, Fox, Leopold, & Petersen, 2004). However, legislation manages seabirds at the colony-level through the designation of SPAs (Wilson et al., 2009). Detecting change in the numbers of birds offshore is hard using this approach, as there is large spatial and temporal variation in seabird numbers at any given offshore location (Maclean, Rehfish, Skov, & Thaxter, 2013). Individual-based models are colony specific, thus, we propose that predictions from IBMs are superior to predictions based on observation data only, as they take into account the cumulative impact of disturbances within the foraging area of a colony. Although, the model was parameterized for breeding adults, with hatched chicks, it can be easily adapted for other individuals in the colony (e.g. non-breeders, incubating birds) and for other ganneries by maintaining the model structure and input parameters and simply changing the spatial environment.

In addition to a management tool, IBMs increase our understanding about the species' breeding ecology by mechanistically linking foraging

behaviour to physiological state and breeding success (Stillman, 2008; Zurell et al., 2015). The modelled inter-annual variation in breeding performance suggests that either the amount of prey or its distribution varied across the years. Modelled breeding performance was lowest in 2015, with a 16% reduction in mean fledging mass, coinciding with lower reproductive success in the gannets breeding on Alderney in 2015 (Warwick-Evans et al., 2016). The number of fish in the 2015 model was similar to that in 2014 (Appendix S5) when the chicks reached full fledging mass. Thus, it is likely that the distribution of prey in 2015 resulted in altered energy budgets, with increased foraging costs for the gannets. This is reflected in the tracking data as longer trips into the North Sea were recorded in 2015, and individuals had larger foraging areas with higher overlap than previous years (Warwick-Evans et al., 2016).

Despite the limitations discussed above, we believe that this model is a substantial improvement on previous models predicting the effects of environmental change on seabirds. This model could easily be adapted to predict the impacts from other examples of spatial change, such as oil spills (Montevocchi et al., 2012), fisheries depletion (Gremillet, Peron, Provost, & Lescroel, 2015), changes to fisheries bycatch policies (Votier et al., 2010) or comparing the likely success of proposed MPAs (Pichegru et al., 2012). Furthermore, it could be modified for other seabird species for which tracking data are available if the behaviour and physiology of the species is reasonably well understood, and the tracking data sufficiently represents the home range of the population (Soanes, Arnould, Dodd, Sumner, & Green, 2013). We demonstrate that this is a strong approach and should be implemented widely to predict the potential impacts from environmental change and assist policy makers when establishing management plans.

ACKNOWLEDGEMENTS

The project was funded by a CASE PhD studentship from the Natural Environment Research Council and the Alderney Commission for Renewable Energy. Permission for field work was granted by The States of Alderney. The Channel Island Bird Ringing Scheme gave permission to ring the gannets. We thank Tim Morley, Roland Gauvain and Jenni Godber for help in the field, and Jason Matthiopoulos for commenting on a draft of the manuscript. Three anonymous reviewers gave very helpful comments on previous iterations.

AUTHORS' CONTRIBUTIONS

V.W.-E., J.A.G. and P.W.A. conceived the ideas and designed methodology; I.W. assisted in software coding; V.W.-E. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

The data used in this study are available in the Movebank Data Repository: <https://doi.org/10.5441/001/1.30r98tb3> (Warwick-Evans, Atkinson, Walkington, & Green, 2017).

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REFERENCES

- 4cOffshore. (2015). 4cOffshore database. Retrieved from <http://www.4c offshore.com/> Accessed June 2015.
- Ainley, D. G., Ribic, C. A., Ballard, G., Heath, S., Gaffney, I., & Karl, B. J., ... Webb, S. (2004). Geographic structure of Adélie Penguin populations: Overlap in colony-specific foraging areas. *Ecological Monographs*, 74, 159–178.
- Band, W., & Band, B. (2012). Using a collision risk model to assess bird collision risks for offshore windfarms. Guidance document. SOSS Crown Estate.
- Birt-Friesen, V., Montevicchi, W., Cairns, D., & Macko, S. (1989). Activity-specific metabolic rates of free-living Northern gannets and other seabirds. *Ecology*, 70, 357–367.
- Botsford, L. W., Micheli, F., & Hastings, A. (2003). Principles for the design of marine reserves. *Ecological Applications*, 13, 25–31.
- Boyd, C., Grunbaum, D., Hunt, G. Jr, Punt, A. E., Weimerskirch, H., & Bertrand, S. (2016a). Effects of variation in the abundance and distribution of prey on the foraging success of central place foragers. *Journal of Applied Ecology*, <https://doi.org/10.1111/1365-2664.12832>
- Boyd, C., Grünbaum, D., Hunt, G. L. Jr, Punt, A. E., Weimerskirch, H., & Bertrand, S. (2016b). Effectiveness of social information used by seabirds searching for unpredictable and ephemeral prey. *Behavioral Ecology*, 27, 1223–1234.
- Burton, N. H. K., Rehfish, M. M., Clark, N. A., & Dodd, S. G. (2006). Impacts of sudden winter habitat loss on the body condition and survival of red-shank *Tringa totanus*. *Journal of Applied Ecology*, 43, 464–473.
- Busch, M., & Garthe, S. (2016). Approaching population thresholds in presence of uncertainty: Assessing displacement of seabirds from offshore wind farms. *Environmental Impact Assessment Review*, 56, 31–42.
- Calenge, C. (2006). The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197, 516–519.
- Camphuysen, C. J., Fox, A. D., Leopold, M. F., & Petersen, I. K. (2004). Towards standardised seabirds at sea census techniques in connection with environmental impact assessments for offshore wind farms in the UK: A comparison of ship and aerial sampling methods for marine birds, and their applicability to offshore wind farm assessments. Report commissioned by COWRIE. Texel, The Netherlands: Royal Netherland Institute for Sea Research.
- Cleasby, I. R., Wakefield, E. D., Bearhop, S., Bodey, T. W., Votier, S. C., & Hamer, K. C. (2015). Three-dimensional tracking of a wide-ranging marine predator: Flight heights and vulnerability to offshore wind farms. *Journal of Applied Ecology*, 52, 1474–1482.
- Cook, A. S. C. P., Humphreys, E. M., Masden, E. A., & Burton, N. H. K. (2014). The avoidance rates of collision between birds and offshore turbines. *Scottish Marine and Freshwater Science*, 5, 16.
- Cook, A. S. C. P., Johnston, A., Wright, L. J., & Burton, N. H. K. (2012). A review of flight heights and avoidance rates of birds in relation to offshore wind farms. *BTO Research Report*, 618, 1–61.
- Cooper, J. (1978). Energetic requirements for growth and maintenance of the Cape gannet (Aves: Sulidae). *Zoologica Africana*, 13, 305–317.
- Drewitt, A. L., & Langston, R. H. W. (2006). Assessing the impacts of wind farms on birds. *Ibis*, 148, 29–42.
- Fox, A. D., Desholm, M., Kahlert, J., Christensen, T. K., & Krag Petersen, I. B. (2006). Information needs to support environmental impact assessment of the effects of European marine offshore wind farms on birds. *Ibis*, 148, 129–144.
- Furness, R. W., Wade, H. M., & Masden, E. A. (2013). Assessing vulnerability of marine bird populations to offshore wind farms. *Journal of Environmental Management*, 119, 56–66.
- Garthe, S., Grémillet, D., & Furness, R. W. (1999). At-sea-activity and foraging efficiency in chick-rearing Northern gannets *Sula bassana*: A case study in Shetland. *Marine Ecology Progress Series*, 185, 93–99.
- Garthe, S., & Hupop, O. (2004). Scaling possible adverse effects of marine wind farms on seabirds: Developing and applying a vulnerability index. *Journal of Applied Ecology*, 41, 724–734.
- Garthe, S., Ludynia, K., Hüppop, O., Kubetzki, U., Meraz, J. F., & Furness, R. W. (2012). Energy budgets reveal equal benefits of varied migration strategies in Northern gannets. *Marine Biology*, 159, 1907–1915.
- Gill, A. B. (2005). Offshore renewable energy: Ecological implications of generating electricity in the coastal zone. *Journal of Applied Ecology*, 42, 605–615.
- Green, R. E., Langston, R. H., McCluskie, A., Sutherland, R., & Wilson, J. (2016). Lack of sound science in assessing wind farm impacts on seabirds. *Journal of Applied Ecology*, 53, 1635–1641.
- Gremillet, D., Peron, C., Provost, P., & Lescoel, A. (2015). Adult and juvenile European seabirds at risk from marine plundering off West Africa. *Biological Conservation*, 182, 143–147.
- Grimm, V. (1999). Ten years of individual-based modelling in ecology: What have we learned and what could we learn in the future? *Ecological Modelling*, 115, 129–148.
- Grimm, V., Berger, U., DeAngelis, D. L., Polhill, J. G., Giske, J., & Railsback, S. F. (2010). The ODD protocol: A review and first update. *Ecological Modelling*, 221, 2760–2768.
- Grimm, V., & Railsback, S. F. (2013). *Individual-based modeling and ecology*. Princeton, NJ: Princeton University Press.
- Halpern, B. S., Longo, C., Hardy, D., McLeod, K. L., Samhour, J. F., Katona, S. K., ... Ranelletti, M. (2012). An index to assess the health and benefits of the global ocean. *Nature*, 488, 615–620.
- Hamer, K. C., Phillips, R. A., Wanless, S., Harris, M. P., & Wood, A. G. (2000). Foraging ranges, diets and feeding locations of gannets *Morus bassanus* in the North Sea: Evidence from satellite telemetry. *Marine Ecology Progress Series*, 200, 257–264.
- Harwell, M. A., Gentile, J. H., Parker, K. R., Murphy, S. M., Day, R. H., Bence, A. E., ... Wiens, J. A. (2012). ‘Quantitative assessment of current risks to Harlequin Ducks in Prince William Sound, Alaska, from the Exxon Valdez oil spill. *Human and Ecological Risk Assessment: An International Journal*, 18, 261–328.
- Inger, R., Attrill, M. J., Bearhop, S., Broderick, A. C., James Grecian, W., Hodgson, D. J., ... Godley, B. J. (2009). Marine renewable energy: Potential benefits to biodiversity? An urgent call for research. *Journal of Applied Ecology*, 46, 1145–1153.
- Jackson, S. (1991). Do seabird gut sizes and mean retention times reflect adaptation to diet and foraging method. *Physiological Zoology*, 65, 674–697.
- Krijgsveld, K., Fijn, R., Japink, M., vanHorsen, P., Heunks, C., Collier, M., ... Dirksen, S. (2011). Effect studies offshore wind farm Egmond aan Zee: Final report on fluxes, flight altitudes, and behaviour of flying birds. Bureau Waardenburg report. Culemborg, the Netherlands.
- Langton, R., Davies, I., & Scott, B. (2014). A simulation model coupling the behaviour and energetics of a breeding central place forager to assess the impact of environmental changes. *Ecological Modelling*, 273, 31–43.
- Lewis, S., Sherratt, T. N., Hamer, K. C., Harris, M. P., & Wanless, S. (2003). Contrasting diet quality of Northern gannets *Morus bassanus* at two colonies. *Ardea*, 91, 167–176.
- Lindeboom, H., Kouwenhoven, H., Bergman, M., Bouma, S., Brasseur, S., Daan, R., ... Van Hal, R. (2011). Short-term ecological effects of an offshore wind farm in the Dutch coastal zone; a compilation. *Environmental Research Letters*, 6, 035101.
- Maclean, I., Rehfish, M. M., Skov, H., & Thaxter, C. B. (2013). Evaluating the statistical power of detecting changes in the abundance of seabirds at sea. *Ibis*, 155, 113–126.

- Masden, E. A., Fox, A. D., Furness, R. W., Bullman, R., & Haydon, D. T. (2010). Cumulative impact assessments and bird/wind farm interactions: Developing a conceptual framework. *Environmental Impact Assessment Review*, 30, 1–7.
- McDonald, C., Searle, K., Wanless, S., & Daunt, F. (2012). *Effects of displacement on marine renewable development on seabirds breeding at SPAs*. Edinburgh: Marine Scotland.
- Montevecchi, W., Hedd, A., Tranquilla, L. M., Fifield, D., Burke, C., Regular, P., ... Phillips, R. (2012). Tracking seabirds to identify ecologically important and high risk marine areas in the western North Atlantic. *Biological Conservation*, 156, 62–71.
- Montevecchi, W., Ricklefs, R., Kirkham, I., & Gabaldon, D. (1984). Growth energetics of nestling Northern gannets (*Sula bassanus*). *The Auk*, 101, 334–341.
- Pennyquick, C. J. (1998). *Bird flight performance 1.11*. Oxford: Oxford University Press.
- Petersen, I. K., Clausager, I., & Christensen, T. K. (2004). Bird numbers and distribution in the Horns Rev offshore wind farm area. Annual Status Report 2003: National Environmental Research Institute. NERI report, the Netherlands.
- Pettex, E., Bonadonna, F., Enstipp, M., Siorat, F., & Grémillet, D. (2010). Northern gannets anticipate the spatio-temporal occurrence of their prey. *The Journal of Experimental Biology*, 213, 2365–2371.
- Pichegru, L., Ryan, P. G., Van Eeden, R., Reid, T., Grémillet, D., & Wanless, R. (2012). Industrial fishing, no-take zones and endangered penguins. *Biological Conservation*, 156, 117–125.
- Ponchon, A., Grémillet, D., Christensen-Dalsgaard, S., Erikstad, K. E., Barrett, R. T., & Reiertsen, T. K., ... Boulinier, T. (2014). When things go wrong: Intra-season dynamics of breeding failure in a seabird. *Ecosphere*, 5, 1–19.
- Poot, M., vanHorssen, P., Collier, M., Lensink, R., & Dirksen, S. (2012). Cumulative effects of wind farms in the Dutch North Sea on bird populations. Bureau Waardenburg Research Report 11-026, Culemborg, the Netherlands.
- R Core Team (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. URL <https://www.R-project.org/>.
- Ropert-Coudert, Y., Grémillet, D., Kato, A., Ryan, P. G., Naito, Y., & Le Maho, Y. (2004). A fine-scale time budget of Cape gannets provides insights into the foraging strategies of coastal seabirds. *Animal Behaviour*, 67, 985–992.
- Sakamoto, K. Q., Sato, K., Ishizuka, M., Watanuki, Y., Takahashi, A., Daunt, F., & Wanless, S. (2009). Can ethograms be automatically generated using body acceleration data from free-ranging birds? *PLoS ONE*, 4, e5379.
- Soanes, L. M., Arnould, J. P. Y., Dodd, S. G., Sumner, M. D., & Green, J. A. (2013). How many seabirds do we need to track to define home-range area? *Journal of Applied Ecology*, 50, 671–679.
- Solesbury, W. (2001). *Evidence based policy: Whence it came and where it's going*. London, UK: ESRC UK Centre for Evidence Based Policy and Practice.
- Stillman, R. A. (2008). MORPH—An individual-based model to predict the effect of environmental change on foraging animal populations. *Ecological Modelling*, 216, 265–276.
- Stillman, R. A., West, A. D., Goss-Custard, J. D., Caldow, R. W., Mcgrorty, S., Durell, S. E. L. V., ... Bell, M. C. (2003). An individual behaviour-based model can predict shorebird mortality using routinely collected shellfishery data. *Journal of Applied Ecology*, 40, 1090–1101.
- Sumner, M. D. (2011). trip: Spatial analysis of animal track data. R package version 1.1-10.
- Sutherland, W. J. (1996). *From individual behaviour to population ecology*. Oxford series in ecology and evolution. Oxford, UK: Oxford University Press.
- Votier, S. C., Bearhop, S., Witt, M. J., Inger, R., Thompson, D., & Newton, J. (2010). Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. *Journal of Applied Ecology*, 47, 487–497.
- Wakefield, E. D., Bodey, T. W., Bearhop, S., Blackburn, J., Colhoun, K., Davies, R., ... Hamer, K. (2013). Space partitioning without territoriality in gannets. *Science*, 341, 68–70.
- Wanless, S., & Okill, J. (1994). Body measurements and flight performance of adult and juvenile gannets *Morus bassanus*. *Ringing & Migration*, 15, 101–103.
- Warwick-Evans, V., Atkinson, P. W., Arnould, J. P. Y., Gauvain, R. D., Soanes, L., Robinson, L. A., & Green, J. A. (2016). Changes in behaviour drive inter-annual variability in the at-sea distribution of northern gannets. *Marine Biology*, 163, 156.
- Warwick-Evans, V., Atkinson, P. W., Gauvain, R. D., Robinson, L. A., Arnould, J. P. Y., & Green, J. A. (2015). Time-in-area represents foraging activity in a wide-ranging pelagic forager. *Marine Ecology Progress Series*, 527, 233–246.
- Warwick-Evans, V., Atkinson, P. W., Walkington, I., & Green, J. A. (2017). Data from: Predicting the impacts of windfarms on seabirds: An individual based model. *Movebank Data Repository*, <https://doi.org/10.5441/001/1.30r98tb3>
- West, A. D., & Caldow, R. W. (2006). The development and use of individuals-based models to predict the effects of habitat loss and disturbance on waders and waterfowl. *Ibis*, 148, 158–168.
- Wilensky, U. (1999). *NetLogo*. Evanston, IL: Center for Connected Learning and Computer-Based Modeling, Northwestern University.
- Wilson, L. J., McSorley, C. A., Gray, C. M., Dean, B. J., Dunn, T. E., Webb, A., & Reid, J. B. (2009). Radio-telemetry as a tool to define protected areas for seabirds in the marine environment. *Biological Conservation*, 142, 1808–1817.
- Zurell, D., Eggers, U., Kaatz, M., Rotics, S., Sapir, N., Wikelski, M., ... Jeltsch, F. (2015). Individual-based modelling of resource competition to predict density-dependent population dynamics: A case study with white storks. *Oikos*, 124, 319–330.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Warwick-Evans V, Atkinson PW, Walkington I, Green JA. Predicting the impacts of wind farms on seabirds: An individual-based model. *J Appl Ecol*. 2018;55:503–515. <https://doi.org/10.1111/1365-2664.12996>