

1 Predicting demographic impacts from sublethal
2 cumulative effects of offshore renewable
3 developments on breeding seabirds
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32 **Author contributions**

33 Christopher J. Pollock, Kate. R. Searle and Adam Butler wrote the manuscript. Christopher J. Pollock,
34 Kate R. Searle, Adam Butler, Francis Daunt and Deena Mobbs conceptualised the study. Deena
35 Mobbs, Adam Butler, Francis Daunt, Kate R. Searle and Christopher J. Pollock created the model, and
36 Christopher J. Pollock simulated and analysed the data. All authors read and approved the final
37 manuscript.

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39 **Data availability statement**

40 Model code is provided in GitHub (https://github.com/NERC-CEH/seabORD_pkg) with guidelines
41 available at the following page: https://nerc-ceh.github.io/seabORD_pkg/index.html.

42

43 **Conflict of interest statement**

44 The authors declare no conflicts of interest which could impact on the findings of this work.

45

46 **Keywords:** agent-based model; barrier; displacement; seabirds; offshore wind farms

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54 **Abstract**

55 1. Offshore renewable developments (ORDs) are often located in habitat used by protected
56 seabird species and may cause sublethal effects by altering movement patterns and
57 displacing individuals from key resources. Predicting how these effects translate into
58 population-level impacts is challenging for long-lived species because demographic
59 consequences emerge from complex, state-dependent behavioural and energetic processes.
60 Individual-based models (IBM) provide a mechanistic framework to link behavioural
61 responses to fitness and demography.

62 2. We present an IBM, 'SeabORD', to estimate the demographic consequences of sublethal
63 displacement and barrier effects from ORDs. The model simulates time-energy budgets of
64 individual seabirds during the chick-rearing period under scenarios with and without wind
65 farms. From these simulations, we predict breeding success, adult mass change and year-
66 round survival, allowing assessment of cumulative effects from multiple developments. We
67 apply the model to black-legged kittiwakes *Rissa tridactyla* and common guillemots *Uria*
68 *aalge* breeding at a North Sea colony, examining how impacts scale with increasing number
69 of hypothetical ORDs. We also conduct a sensitivity analysis focussing on parameters with
70 limited empirical support.

71 3. Model predictions indicate that demographic impacts do not increase linearly with exposure
72 to ORDs. The strength and form of cumulative effects emerging from interaction between
73 behavioural decisions and energetic constraints differed between species, highlighting the
74 benefit of adopting a mechanistic approach in this context. The results of the sensitivity
75 analysis indicated high sensitivity to some parameters, such as an adult body condition
76 threshold below which adults abandon their breeding attempt. However, the emergent
77 properties of model outputs were biologically plausible, and serve to highlight areas for
78 future empirical work.

79 4. *Synthesis and applications.* SeabORD provides a transparent, mechanistic approach for
80 predicting population-level consequences of sublethal interactions with ORDs, with direct
81 relevance for environmental impact assessment and marine spatial planning. Our results
82 demonstrate that cumulative effects may be non-additive and species-specific, highlighting
83 limitations of current simplistic assessment approaches. Sublethal effects are the result of
84 complex, interacting state-related behavioural decisions, and IBMs provide a platform for
85 estimating stressor impacts and facilitating exploration into underpinning processes and key
86 areas for future research.

87 1. Introduction

88 Numerous countries around the world have invested extensively in offshore renewable
89 developments (ORDs) in the past two decades, with instalments in offshore wind capacity
90 amounting to around 83 GW in 2025, representing around 1% of global electricity generation (GWEC
91 2025). Such developments alter the environment, with potential consequences for protected
92 wildlife, including seabirds and marine mammals. Statutory regulations are in place that mandate
93 the prediction of potential effects for a proposed ORD, where the objective is to determine the
94 magnitude and range of effects on a population of interest and whether this exceeds specified
95 threshold levels. With expanding development across the globe, thresholds are likely to be exceeded
96 more regularly, causing cumulative impacts that may be sufficient to prevent consent or trigger the
97 application of compensatory measures and adaptive management to offset potential impacts.

98 Furthermore, with insufficient evidence concerning the impacts of offshore wind farms on seabirds
99 leading to high uncertainty, a precautionary approach may be adopted, as institutionalised in UK and
100 Europe legal frameworks (Horswill et al., 2017; Maclean et al., 2014).

101 The main effects of ORDs on seabirds can be classed into three categories; (i) collision mortality from
102 colliding with rapidly rotating rotors of a wind turbine, (ii) displacement, in which birds may be
103 displaced from key habitat resources such as profitable foraging areas inside ORDs, with potential to

104 experience higher competition in remaining areas devoid of ORDs, or (iii) barrier effects, wherein
105 movement patterns are altered as individuals are unwilling to enter ORD footprints, incurring
106 additional energetic costs by flying farther to and from foraging areas (Madsen et al., 2009). The
107 latter two effects are sublethal, as they may have energetic consequences through altered
108 behaviour, which may in turn influence vital rates, such as adult survival and breeding success,
109 resulting in population impacts. Such effects are likely to be exacerbated during the breeding season
110 when seabirds are obligate central place foragers (Lamb et al., 2024). Predicting how displacement
111 and barrier effects influence demographic impacts is challenging due to the underpinning set of
112 behavioural and energetic changes that may reduce body condition and increase the probability of
113 mortality in the affected individual, or if it is a breeding individual, result in reduced breeding success
114 (e.g., Ashbrook et al., 2008; Hamer et al., 1993). Consequently, understanding and empirical
115 evidence for the underlying mechanisms driving sublethal processes must be integrated into
116 predictive models and linked to population-level impacts.

117 Mechanistic or process-based models, such as individual based models (IBMs, also known as agent-
118 based models) simulate populations as being composed of discrete individuals, each having their
119 own state variables accounting for different attributes and behaviours. Through simulating
120 reproduction, growth and foraging of individuals, population-level dynamics emerge in a bottom-up
121 fashion from agents' interactions with their environment (Grimm & Railsback, 2013). IBMs provide a
122 way to model key biological processes explicitly, guided by empirical data and observed ecological
123 patterns. Through this method it is possible to establish a link between alterations to the
124 environment and demographic rates, translated through explicitly modelled behavioural changes
125 and energetic budgets, thus providing transparent predictions of the effects of altering a landscape
126 on population outcomes. Previous work has developed a limited range of seabird IBMs applied to
127 predict the impact of ORDs both for collision and sublethal effects (Warwick-Evans et al., 2018;
128 Langton et al. 2014; Searle et al. 2014, 2018; van Kooten et al. 2019; van Bemmelen et al. 2025;

129 Layton-Matthews et al. 2023), however their use remains limited in legislative processes guiding
130 impact assessment frameworks.

131 IBMs provide capacity for modelling discrete individuals across time, therefore it is possible to
132 simulate multiple interactions with ORDs for any given individual across a seasonal period or year. As
133 such, IBMs provide a natural framework for simulating cumulative effects of multiple developments
134 on a particular population (Green et al., 2016), likely to be critical for central place foragers due to
135 the possibility of interaction with numerous developments on successive occasions within foraging
136 range. Such cumulative effects are explicitly incorporated in assessment processes in many
137 countries, including those in Europe through the Environmental Impact Assessment (EIA) Directive
138 (EIA Directive 2014/52/EU). Efforts to assess cumulative effects have improved in the last decade
139 since a landmark review from Masden et al. (Masden et al., 2010) that highlighted shortcomings,
140 leading to updated regulatory guidance (Croll et al., 2022). However, a standardised quantitative
141 consideration for how cumulative displacement and barrier effects impact on marine bird
142 populations is still lacking, reducing confidence in the metrics adopted in population projections.

143 We have developed an IBM, SeabORD, which simulates pairs of central-place foraging adults
144 provisioning offspring during the chick-rearing season, each having separate simulations for their
145 behaviour and energy budgets thus allowing changes in body mass, survival and breeding success to
146 be predicted. By introducing ORD footprints through which adults may experience behavioural and
147 energetic consequences by way of interaction through barrier and/or displacement effects, we can
148 simulate a population of interest both with and without ORDs, with the resulting difference between
149 the two simulations being solely attributable to wind farm impacts. Here, we provide a description
150 of the model and its main components. We demonstrate use of the model using extensive
151 hypothetical ORD arrays to predict how increasing cumulative effects on populations of two example
152 seabird species, common guillemot *Uria aalge* and black-legged kittiwake *Rissa tridactyla* (hereafter
153 “guillemot” and “kittiwake”), breeding at the Isle of May NNR, in eastern Scotland, drive predicted

154 changes in breeding success and adult mass change and survival during the chick-rearing period. We
155 chose this location because the North Sea is undergoing a rapid expansion of offshore wind
156 development, with many projects potentially occurring within the foraging ranges of protected
157 breeding seabirds, such as the Isle of May. Finally, we present a sensitivity analysis of model
158 parameters focused on those parameters with the least empirical support.

159 [2. Methods](#)

160 [2.1 Model description](#)

161 A full description of the model following the ODD (Overview, Design concepts, Details) protocol
162 (Grimm et al., 2006, 2020) can be found in the appendix (Section 1). In brief, we constructed a model
163 to predict the demographic impacts of sublethal effects emanating from ORD interaction in seabirds
164 during the chick-rearing period (Figure 1). By simulating behaviour and time-energy budgets in the
165 presence (“scenario”) and absence (“baseline”) of ORDs, the difference between outputs for
166 breeding success and adult mass change and survival represents the demographic impacts of ORD(s).
167 The model is parameterised for four species: kittiwake, guillemot, razorbill *Alca torda* and Atlantic
168 puffin *Fratercula arctica*, but can be adapted to any central-place foraging seabird, data-permitting.
169 For our model application investigating cumulative effects we chose two of these four species,
170 kittiwake and guillemots, due to the species differing ecologies when foraging at sea. As such, they
171 are the focus here, but we expand on model details for puffins and razorbills in the appendix. The
172 model was parameterised from empirical values for time activity budgets, adult mass change during
173 chick-rearing, chick growth and chick survival from studies of these or closely related species from
174 UKCEH's long term study of foraging behaviour, energetics and demography of seabirds on the Isle
175 of May (Leedham et al., 2025; Newell et al., 2025) or from published studies elsewhere. In some
176 instances, it has been necessary to set parameter values based on expert opinion because relevant
177 empirical data do not exist (see Table 1 and Table S4 for details). The model was developed in R (R
178 Core Team, 2024) and is available here: https://github.com/NERC-CEH/seabORD_pkg.

SeabORD

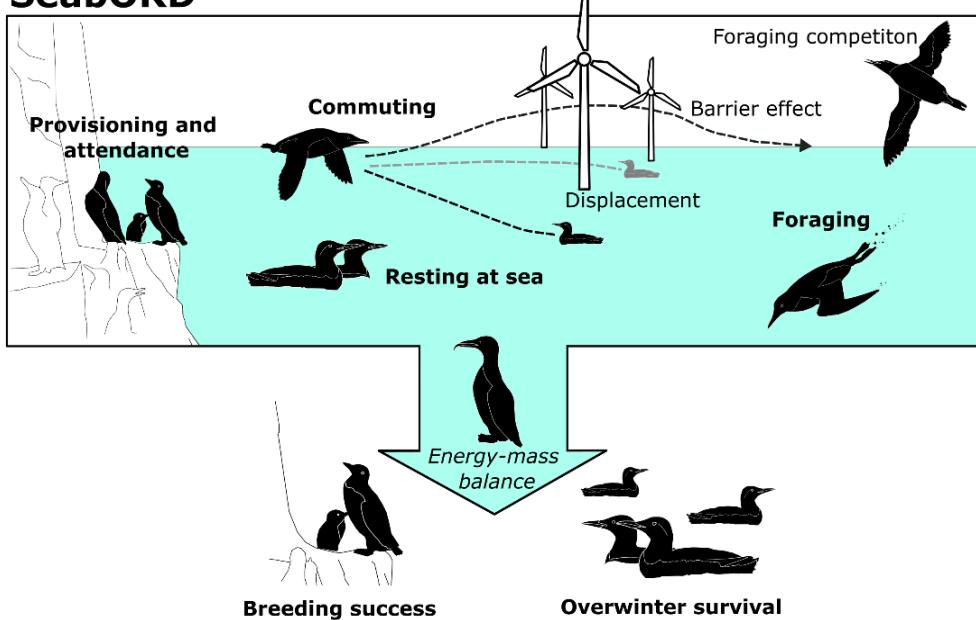


Figure 1: Conceptual diagram showing the different behavioural mechanisms represented within SeabORD

181 *Table 1: List of key SeabORD parameters with values for kittiwakes and guillemots. "IMLOTS" refers to data from the Isle of
182 May Long-Term Study.*

Parameter	kittiwake		guillemot	
	value	source	value	source
Initial adult body mass mean (g)	372.69	UKCEH unpubl. data	920.34	UKCEH unpubl. data
Initial adult body mass standard deviation (g)	33.62	UKCEH unpubl. data	57.44	UKCEH unpubl. data
Critical mass below which adult is assumed dead (proportion of mean mass)	0.6	Derived from Golovkin 1963	0.6	Derived from Golovkin 1963
Critical mass below which adult abandons chick (proportion of mean mass)	0.8	Expert judgement	0.8	Expert judgement
Critical mass below which adult favours itself over its chick when foraging (proportion of mean mass)	0.9	Expert judgement	0.9	Expert judgement
Initial chick body mass mean (g)	36	UKCEH unpubl. data	75.8	UKCEH unpubl. data
Initial chick body mass standard deviation (g)	2.2	UKCEH unpubl. data	1	UKCEH unpubl. data
Critical mass below which chick is dead (proportion of initial mass)	0.6	Derived from Golovkin 1963	0.6	Derived from Golovkin 1963
Number of hours per time step (hours)	36	-	24	-
Number of time steps per season	30 (45 days)	UKCEH unpubl. data	21 (21 days)	UKCEH unpubl. data
Critical time threshold for unattendance at nest above which a chick is assumed to die through exposure or predation (hours)	18	Expert judgement	18	Expert judgement
Adult daily energy expenditure mean (kJ)	802	Daunt et al. 2008 and refs therein	1489.1	Daunt et al. 2008 and refs therein
Adult daily energy expenditure standard deviation (kJ)	196	Daunt et al. 2008 and refs therein	169.9	Daunt et al. 2008 and refs therein
Chick energy requirement (kJ per day)	525.7	Enstipp et al. 2006	221.7	Thaxter et al. 2013

Maximum prey intake (g per minute)	4.369	UKCEH unpubl. data	2.95	UKCEH unpubl. data
Prey density intake rate is half its max/the rate of intake rate decrease with prey depletion (g per minute)	900	Calibrated in functional response	700	Calibrated in functional response
The effect of conspecific density on intake rate of individuals through assumed interference competition	0.02	Expert judgement in conjunction with Hassell & Varley 1969	0.02	Expert judgement in conjunction with Hassell & Varley 1969
Average speed in flight (m/sec)	13.1	Pennycuick 1997	19.1	Pennycuick 1997
Assimilation efficiency	0.74	Hilton et al. 2000	0.78	Hilton et al. 2000
Energy gained from prey (kJ per gram)	6.52	Leedham et al. 2025 and refs therein	9.26	Leedham et al. 2025 and refs therein
Energy cost of nesting at colony (kJ per day)	427.8	Leedham et al. 2025 and refs therein	780	Leedham et al. 2025 and refs therein
Energy cost of flight (kJ per day)	1400.7	Leedham et al. 2025 and refs therein	7266.2	Leedham et al. 2025 and refs therein
Energy cost of resting at seas (kJ per day)	400.6	Leedham et al. 2025 and refs therein	540.7	Enstipp et al. 2006
Energy cost of foraging (kJ per day)	1400.7	Leedham et al. 2025 and refs therein	1894.9	Enstipp et al. 2006
Energy cost of warming food (kJ per day)	26	Leedham et al. 2025 and refs therein	49.3	Leedham et al. 2025 and refs therein
Maximum chick mass gain per day (g)	11	UKCEH unpubl. data	9	UKCEH unpubl. data
Energy density of the bird's tissue (kJ g⁻¹)	38.5	Gabrielsen 1996	38.5	Gabrielsen 1996
Parameter for translation of adult mass change into year round survival	0.038	Oro & Furness 2002	1.03	Erikstad et al. 2009

183

184 Four entity types are represented: Adults, chicks (each belonging to a pair of adults), ORD footprints,
 185 and landscape grid cells. Adults are characterised by their sex, which pair they belong to and if their
 186 chick is alive, whether they are susceptible to ORD effects, body mass, Daily Energy Requirement
 187 (*DER*), Daily Energy Expenditure (*DEE*) relating to activity budgets, among others (see Table S1).
 188 Chicks are characterised by being alive or dead, their body mass, energy requirement, and hours
 189 unattended on each time step, the latter being a behaviour exhibited by parents when foraging
 190 conditions are suboptimal (e.g. Ashbrook et al., 2008). ORDs are represented as polygons within
 191 which all turbines in the development are contained, and a buffer and displacement zone, the
 192 widths of which are determined through user-set parameters. A buffer is the area around an ORD
 193 footprint from which birds are assumed to be displaced, and a displacement zone is the area around
 194 the footprint-plus-buffer into which displaced birds are assumed to disperse. The simulated
 195 landscape covers the North Sea and is composed of 1 x 1 km grid cells. Cells are classified as land or
 196 sea, and sea cells have prey value assigned following a calibration process (see below), which can
 197 either be uniform (i.e., all cells have the same prey value), or heterogenous, from simple distance

198 decay to being informed by empirical data. A bird distribution map modelled on GPS tracking data
199 determines the probability of foraging at a site (Figure S1 A). Time is represented in discrete time
200 steps of 24 hours for guillemot and 36 hours for kittiwake (due to empirical data indicating longer
201 foraging trips in this species), with the total number representing respective breeding season lengths
202 (kittiwake = 30 time steps = 45 days, guillemot = 21 time steps/days). Key model inputs include ORD
203 footprints, colony locations and population sizes, and maps for foraging density, conspecific density
204 for inferring competition (Figure S1 B), and prey density.

205 Simulation time steps proceed as follows (Figure S2): (1) adults conduct foraging trips and decide on
206 their behavioural strategy (e.g., prioritising themselves or their chick's needs) based on their current
207 condition (2) the consequences of these behaviours on the chick are determined, (3) adult energy-
208 mass balances are updated in light of this and daily energy requirements for the next day are
209 calculated, (4) at the end of the breeding season, adult survival over the subsequent winter period is
210 estimated.

211 Foraging and movement

212 The model simulates foraging decisions of individual seabirds under the assumption that they are
213 acting in accordance with optimal foraging theory (MacArthur & Pianka, 1966), minimising time
214 away from offspring whilst maximising energy gain. In each time step an individual selects a location
215 for feeding based on bird density maps, ideally derived from GPS data for the colony of interest via
216 spatial modelling (e.g. using a generalised additive model, GAM) but where such data are lacking a
217 simplified density decay option is advised (Appendix section 2). Subsequent behaviour of birds is
218 then simulated (Figure 1), incorporating realistic assumptions and constraints derived from observed
219 behaviour. Modelled foraging behaviour is driven by prey availability, travel costs, offspring
220 provisioning requirements, and conspecific density, together determining the number of trips to the
221 chosen foraging location in each time step. An individual's movement is directly to and from a

222 singular foraging location, each chosen independently for all time steps at the beginning of the
223 simulation meaning there is no adaptation in the selection of locations, and no site fidelity.

224 Intake rate and competition

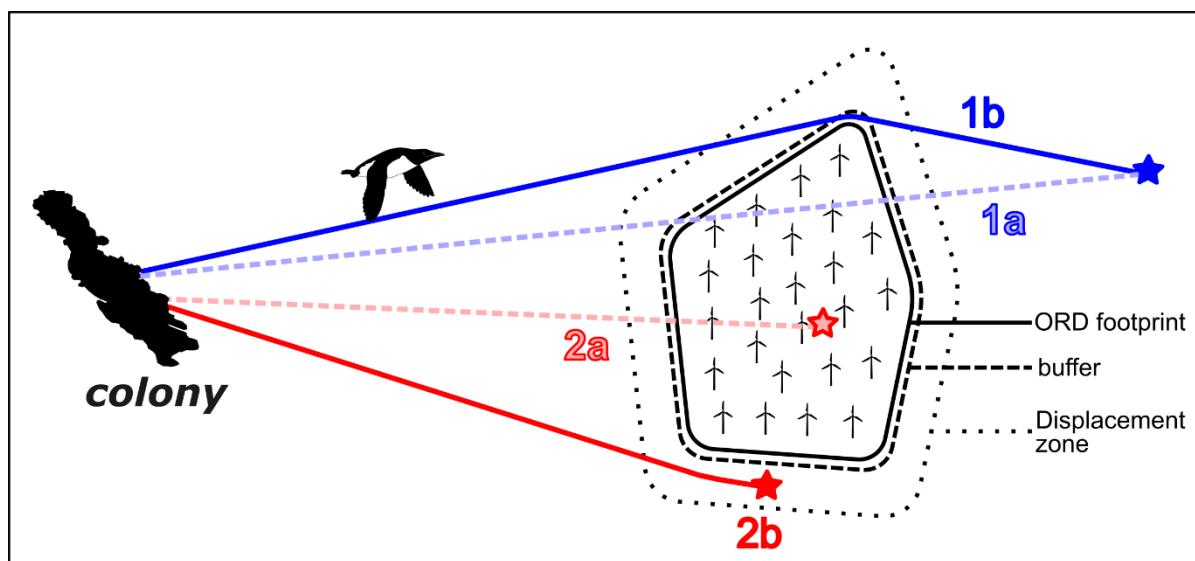
225 Intake rate by a bird at its foraging location is described by the Michaelis-Menten equation for Type
226 II function response (Holling, 1959), where the relationship between increasing density of prey and
227 instantaneous intake rate increases until reaching a maximum determined by handling time (Enstipp
228 et al., 2007). This relationship is used to simulate the decline in intake rate over time spent foraging
229 at a given location due to prey depletion, and to determine the amount of time an individual
230 requires to attain a certain cumulative intake. The total daily intake can then be calculated, given (i)
231 the number of foraging trips ($n = 1-6$) that the bird undertakes, and (ii) trip length.

232 We assume prey depletion at a location within a foraging bout but when the bird returns to a
233 location the amount of prey is reset to the original level on the basis of lacking evidence for long-
234 term prey depletion by seabirds (Birt et al., 1987), which instead may temporarily disturb prey (Lewis
235 et al., 2001). Another assumption dictates that intra-specific competition between individuals
236 foraging at the same location acts to reduce the intake rate multiplicatively, wherein competition is
237 experienced from conspecifics from the same colony in that simulated time step and estimated from
238 a competition map of the spatial abundance of birds from other colonies (Figure S1 B).

239 ORD interactions

240 The user specifies the spatial footprint of one or multiple ORDs and two main responses of
241 individuals to ORDs are simulated in the model: displacement and barrier effects. At the start of the
242 simulation birds are assigned as either both displacement and barrier susceptible, or unsusceptible.
243 A barrier event occurs when a susceptible bird has a foraging location that is obstructed by the ORD,
244 assuming birds travel directly to the foraging site (Figure 2, example 1). In this circumstance birds
245 take the shortest route to the foraging location whilst navigating around the edge of the ORD
246 footprint, with obstructed distance calculated using the R package 'gdistance' (van Etten, 2017).

247 Barrier effects may impact individuals negatively by increasing flight cost and time and reducing
 248 available foraging time and resulting in potential unattendance or lost adult condition.
 249 A displacement event occurs when a susceptible bird has a foraging location that falls within a
 250 footprint or surrounding buffer, they are displaced into the displacement zone (Figure 2, example 2)
 251 which extends beyond the footprint-plus-buffer (Figure 2). The foraging location in the displacement
 252 zone is selected with a probability proportional to the bird distribution map. Negative impacts may
 253 stem from increased flight cost (energetic or time) if displaced further from the location, and from
 254 increased competition in the displacement zone due to an increase in the abundance of birds using
 255 this area. Positive impacts may occur from decreased flight cost and/or flight time if an individual is
 256 displaced closer to the colony, or for non-displacement susceptible birds through reduced
 257 competition for birds that remain to forage within the ORD whilst others are displaced. If using a
 258 heterogenous prey map, there may be impacts stemming from being displaced to a foraging location
 259 with lower/higher prey density. Negative impacts from both barrier and displacement events
 260 manifest as increased DER for the following time step and positive effects as reduced DER at that
 261 time step.



262
 263 *Figure 2: Examples of potential interactions with offshore renewable devices (ORDs). Foraging trip 1b (blue) represents a*
 264 *barrier-susceptible bird, which has to fly the shortest distance around the ORD to get to its obstructed foraging site on the*

265 far side relative to the colony, where 1a (light blue) shows the track in absence of the ORD and what would be experienced
266 in baseline simulations. Foraging trip 2b (red) represents a displacement susceptible bird, which would have foraged within
267 the ORD footprint, as shown by 2a (light red), but is now foraging in the displacement zone. In all cases birds use the same
268 flightpath to both reach and return from their chosen foraging location.

269 Mass-energy and activity budgets

270 The daily mass change for each adult is calculated to be the difference between their current daily
271 energy gain and current *DER*, divided by the energy density of the bird's tissue (kJ/g)(Gabrielsen,
272 1996; Montevercchi et al., 1984). Daily mass change for chicks assumes a simple linear function in
273 relation to food provisioned by both parents. On the first time step of the simulation, adult *DEE* is
274 drawn from a normal distribution parameterised using the mean and standard deviation of empirical
275 data on the study species (Daunt et al., 2008). On all subsequent days, adult *DER* is matched to
276 energy expended in the previous time step, by dividing the *DEE* by assimilation efficiency (0.78,
277 Hilton et al., 2000). Chick *DEE* remains constant throughout the simulation, defined using species-
278 specific mean *DERs* are based on provisioning rates recorded from a sample of chicks of a range of
279 ages.

280 Adults divide their activities into four categories of behaviour – foraging, flight, time spent at the
281 colony, and time spent resting on the sea surface (Figure 1) following empirical activity budgets
282 (Daunt et al., 2002). The foraging model returns the simulated flight time spent travelling to the
283 foraging location, and the simulated foraging time required to meet *DER*. The remaining time is split
284 into time spent at the colony, where each bird attempts to spend half of each time step thereby
285 preventing the chick being left unattended at the nest, and a minimum of one hour spent resting at
286 sea (Daunt et al., 2002). Of the four listed, resting at sea is presumed to be the least constrained
287 activity, and therefore most likely to be used by birds to perform other activities when under stress.
288 The time spent carrying out each of these activities is then multiplied by species- and activity-specific
289 energy costs available from the literature, with the addition of the energy cost of warming food to

290 derive the total *DER* for each bird (Gremillet et al., 2003), that was converted into grams per day
291 assuming a mean energy density of prey (Harris et al., 2008).

292 The following set of decision rules were implemented based on a set of behavioural strategies which
293 determine adult behaviour in relation to its chick:

- 294 i. If an adult's body mass was greater than 90% of its starting body mass at the onset of chick-
295 rearing it would avoid leaving its chick unattended, even if it had not met its *DER*.
- 296 ii. If body mass was between 90% and 80% it would favour itself and leave its chick unattended
297 in order to attempt to achieve its required *DER* (for example see Figure S5).
- 298 iii. If body mass is less than 80%, they abandon the breeding attempt, and consequently their
299 partner also gives up, resulting in chick death.
- 300 iv. If an adult's body mass falls below 60% of their starting mass, the adult dies and is removed
301 from the simulation. This rarely happens in the model as an adult abandons its breeding
302 attempt and its mass tends to stabilise for the remainder of the simulation reflecting their
303 long-lived nature (see model processes in Figure 3).

304 A similar assumption is made for chicks, which die if their body mass falls below 60% of that of a
305 hypothetical chick that has received its *DER* on each model time step up to the current time. Chicks
306 can also die through exposure from lack of attendance by its parents (>18 hours), or increased risk of
307 predation if a chick was left unattended by both parents, modelled as a probability of death that
308 increased linearly with time left unattended.

309 Survival projections

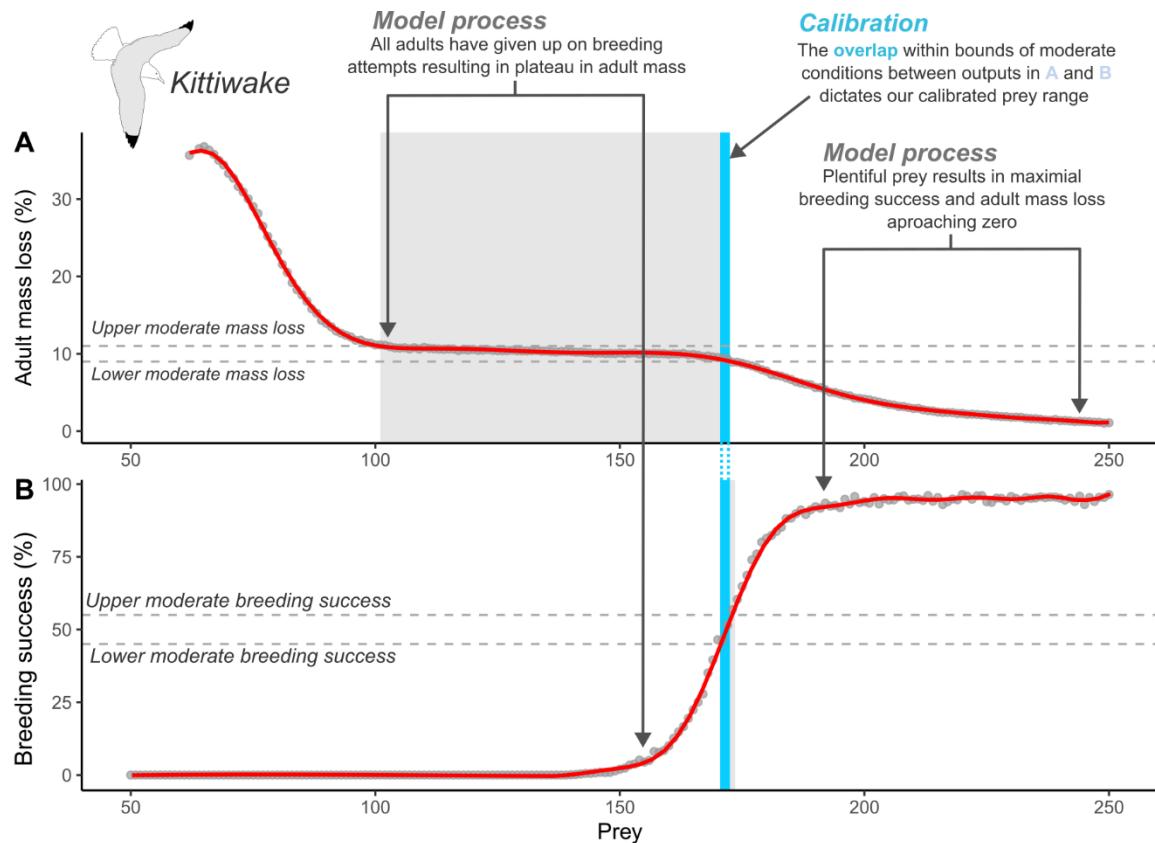
310 Past studies have shown a positive relationship between body mass at the end of the breeding
311 season and survival during the subsequent winter period in adults (Erikstad et al., 2009; Oro &
312 Furness, 2002). Accordingly, alongside the outputs of the status of chicks and adults as either bring
313 alive or dead, the model simulates adult survival during the subsequent winter period from mass at
314 the end of the breeding season, using the relationships in these studies (see Appendix section 1, 7.4

315 for more details). The overall survival rate for a simulation run is calculated by simulating survival of
316 each individual using a Bernoulli distribution, using individual-level survival probabilities based on
317 the published relationships, and then calculating the proportion of individuals that have survived.

318 [Model calibration](#)

319 As prey levels are a key source of uncertainty in practice, since empirical data on absolute quantities
320 of available prey at relevant spatial and temporal scales are rarely available, a prey calibration
321 process is a prerequisite step required to determine prey levels that correspond to the desired
322 conditions for this species/colony, which is typically set at “moderate” to align with the average
323 metrics seen for the population of interest. We achieve this by running baseline simulations (i.e., no
324 ORDs) across a range of prey values and assessing their outputs for adult mass loss over the chick-
325 rearing period and breeding success (proportion of chicks that fledge per nest) against upper and
326 lower boundaries of moderate conditions (Figure 3, details in Appendix section 1, 5.3). The prey
327 range captured by the overlap between the two outputs is then used in subsequent simulations
328 including ORDs to input a uniform arbitrary prey value for all cells (assuming standard uniform prey
329 distribution).

330



331

332 *Figure 3: Schematic plot of kittiwake adult mass loss (A) and breeding success (B) withdrawn from 300 baseline simulations*
 333 *(no ORD footprints) ranging from a prey value of 50 up to 250, to display a range of model dynamics. The red lines are for*
 334 *smoothed model outputs, which are overlaid on grey points indicating the individual estimates. For calibration we have*
 335 *upper and lower bound for each output (A & B) which are picked to reflect “moderate” conditions, i.e., what is observed in a*
 336 *typical year for kittiwakes at the Isle of May, and these are indicated by the dashed grey horizontal lines. The grey shaded*
 337 *blocks indicate where the respective outputs fall within these bounds, and the light blue shaded block indicates the prey*
 338 *values where there is overlap between the estimates, which is the prey range used in subsequent simulations with ORDs*
 339 *included.*

340 Key model outputs: metrics of ORD impact

341 Wind farm impacts on seabird populations can be assessed using the three primary SeabORD
 342 outputs; (i) adult mass change over the course of the chick-rearing season, (ii) year-round adult
 343 survival using published mass-survival relationships (Erikstad et al., 2009; Oro & Furness, 2002)
 344 translated from (i), and (iii) breeding success over the chick-rearing season. We evaluated the impact

345 of ORDs by comparing outputs of scenarios with ORDs against a “baseline” scenario with no ORDs,
346 so that:

347 (i) ORD effect on adult mass change = Simulated mean proportional adult mass change
348 over the chick rearing period with ORD(s) – Simulated mean proportional adult mass
349 change over the chick rearing period under the baseline

350 (ii) ORD effect on year-round adult survival = Simulated adult mortality rate with ORD(s) –
351 Simulated adult mortality rate under baseline

352 (iii) ORD effect on breeding success = Simulated fledged chicks per nest with ORD(s) –
353 Simulated fledged chicks per nest under baseline

354 Scenarios

355 SeabORD is run such that each model scenario contains a set of matched pairs of simulations for the
356 baseline (no ORDs present) and an impacted run (ORDs present), with the metrics of ORD impact
357 calculated for each matched pair of baseline and impacted model simulations (which we refer to as a
358 “replicate”). Matching ensures that the outcomes of stochastic events within the model that are
359 unrelated to wind farm impacts (e.g., in particular, initial body mass of each individual, and the
360 foraging locations selected at each timestep) are identical within the baseline and impacted
361 simulations.

362 Matched pairs have identical model parameters and other inputs, with exception that (a) each uses a
363 distinct random seed (so will have different outputs as a result of stochasticity) and (b) each uses a
364 different prey value (selected uniformly from within the range determined by model calibration).

365 [2.2 Modelling cumulative effects of multiple ORDs](#)

366 To investigate how cumulative impacts scale with increasing exposure to ORDs we ran simulations
367 on kittiwakes and guillemots at the Isle of May with hypothetical ORDs for each species (Figure 4A &
368 B), with buffer and displacement zones extents set at two and five km, respectively. We ran
369 simulations with all possible combinations of ORDs ranging from one up to the maximum of six,

370 resulting in $2^6 - 1 = 63$ different combinations for each species. ORDs were designed to result in
371 comparable exposure interactions for each species, which was achieved by calculating birds
372 displaced per time step (Figure 4C) using bird distribution utilisations for each species, and specifying
373 the size and location of ORD footprints for each species in such a way that the frequency of
374 interactions ranged from ~4% adults being displaced per time step for 1 ORD, up to ~25% adults for
375 the maximum number of ORD footprints (n=6), to capture a wide range of potential exposure.

376 Model calibration was conducted once for each species (Guillemot prey range = 172 – 174.5;
377 kittiwake prey range = 170.5 – 172.5). Displacement and barrier rate was set to 60% for both
378 species, following the NatureScot guidelines for auks (NatureScot 2023), and applying this rate to
379 kittiwakes (NS guidance suggests the lower value of 30%) to ensure outputs were comparable
380 between the two species. The number of breeding pairs was set to 10,906 for guillemots and 2,103
381 for kittiwakes, reflecting real population sizes.

382 We assessed the outputs of simulations against number of ORDs being simulated using the metrics
383 for adult mass change, adult survival and breeding success as a result of ORD effects detailed above
384 (Section 2.1).

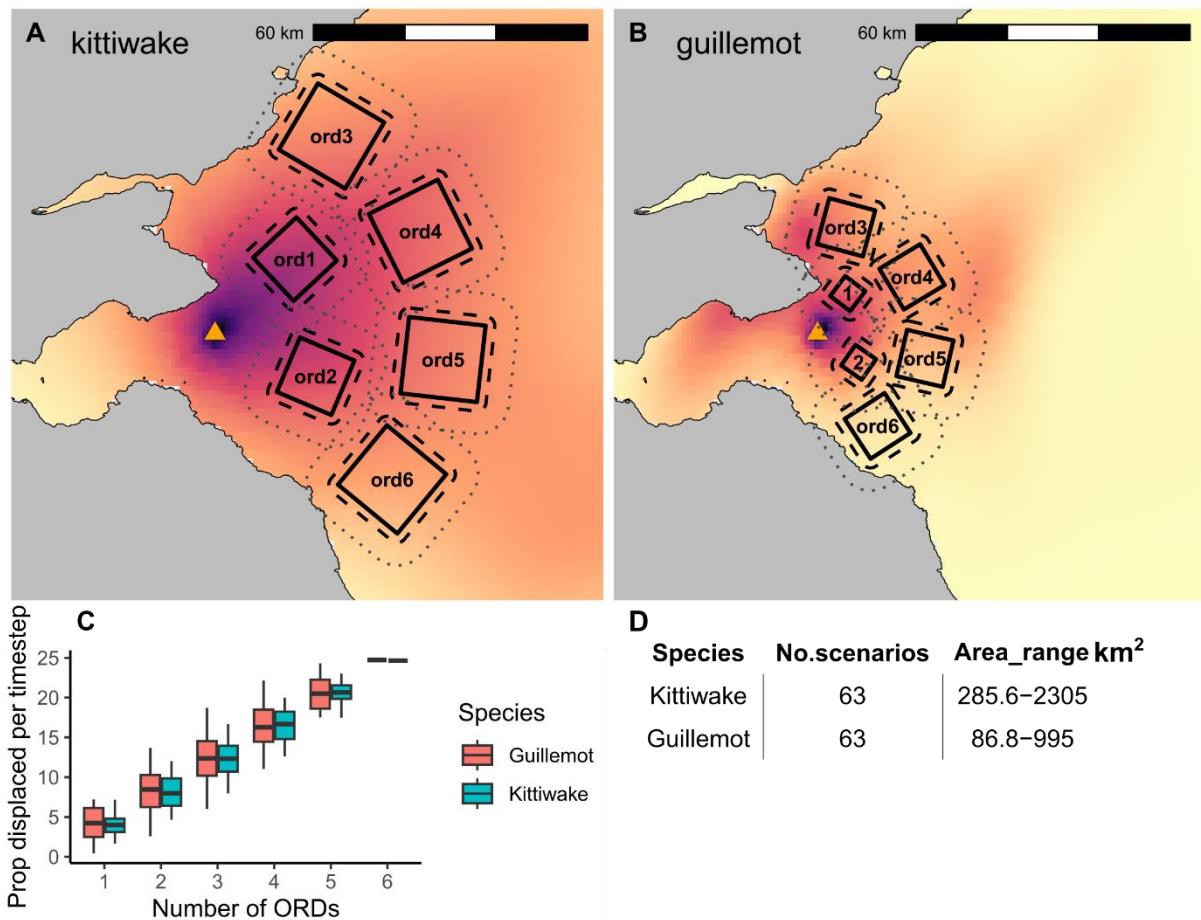


Figure 4: Hypothetical offshore renewable development (ORD) scenarios for (A) kittiwakes and (B) guillemots. Solid black lines indicate the footprint of the ORD, with the dashed black line indicating the 2 km buffer and the dotted grey line indicating the displacement zone a further 5 km beyond the footprint-plus-buffer. Panel C is a boxplot showing the estimated proportion of birds displaced per time step for both species for increasing number of ORDs in the respective 63 potential scenarios, and panel D shows a table of statistics relating to the ORD with the area range (km²) being the minimum (i.e., one small ORD) and maximum (all 6 ORDs).

385

386 [2.3 Sensitivity Analysis](#)

387 We conducted a local sensitivity analysis in which an individual parameter is perturbed separately to
 388 determine the model's sensitivity. We selected six parameters based on their relative lack of
 389 empirical support:

390 (i) **adult_mass_KG** - Energy density of the bird's tissue (kJ g⁻¹)

391 (ii) **BM_adult_abdn** - Critical mass below which adult abandons chick

392 (iii) **BM_Chick_mortf** - Critical mass below which chick is dead

393 (iv) **unattend_max_hrs** - Critical time threshold for unattendance at nest, which determines the
394 probability that an unattended chick dies through exposure or predation
395 (v) **IR_half_b** – A parameter controlling the influence of conspecific competition on intake rate
396 (vi) **Displacement zone extent** – How far the displacement zone extends beyond the ORD
397 footprint and buffer

398

399 Parameters were varied singly, with four levels of variations for each. Variations on (i) – (iv) were a
400 percentage change of the default value at +10%, +5%, -5%, and -10%. We lacked any empirical data
401 on parameter (v), so it was varied by quadrupling, doubling, dividing by two, and dividing by four.
402 For parameter (vi), which has a default value of 5km distance from the footprint border (Figure 3),
403 two extended buffers of 20 and 10 km and two smaller buffers at 2.5 and 1 km comprised the
404 parameter variations, based on empirical estimates of species responses to ORD footprints (Peschko
405 et al., 2020).

406 All sensitivity runs were conducted using the kittiwake population at Forth Islands SPA with 100
407 replicates, a representative population of 2,103 breeding pairs, and the inclusion of six hypothetical
408 ORDs (Figure 3 B). The buffer extending around ORD footprints was set at 2km, reflecting NatureScot
409 guidelines (NatureScot 2023), while the displacement zone extended 5km beyond the ORD footprint
410 and its buffer, based on expert judgement and knowledge of displacement in the two species (Searle
411 et al. 2014)(Peschko et al., 2020). For each variation for parameters relating to birds (i.e., not the
412 displacement zone width) the calibration process was repeated using baseline only simulations
413 (Section 2.1) to determine a suitable prey range aligning with moderate conditions for this species
414 (Table S4) where possible.

415 We calculated the mean, standard deviation and 95% confidence intervals of change in each of the
416 three key ORD-related outputs metrics (Section 2.1) between scenarios in which parameters had
417 been varied and the default parameter scenario, for each of the 100 replicates. If the 95%

418 confidence interval did not contain zero, we considered the output as significantly sensitive to that
419 parameter variation with distinguished sign of change.

420 **3. Results**

421 **3.1 Modelling cumulative effects**

422 The model revealed that decreases in kittiwake and guillemot adult mass change scaled positively
423 with increasing number of ORDs (Figure 5 A & B). Model predictions showed greater predicted
424 impacts on mass in adult guillemots compared to kittiwakes, corresponding to an additional 3.15g
425 lost in guillemots, and 0.81g additional lost in kittiwake with all 6 ORDs compared to the baseline
426 (Table S10). As anticipated, predicted decreases in mean adult survival were similar to adult mass
427 change in response to increasing exposure to ORDs, but variation was markedly larger across model
428 replicates, particularly in the kittiwake simulations (Figure 5 C & D). Decreases in breeding success
429 with increasing number of ORDs were more severe for kittiwakes (8%) than guillemots (3.9%; Figure
430 6 E & F). This corresponded to predicted breeding success dropping from 0.538 chicks per nest
431 (baseline) to 0.457 in kittiwakes, and from 0.830 to 0.79 in guillemots (Table S10).

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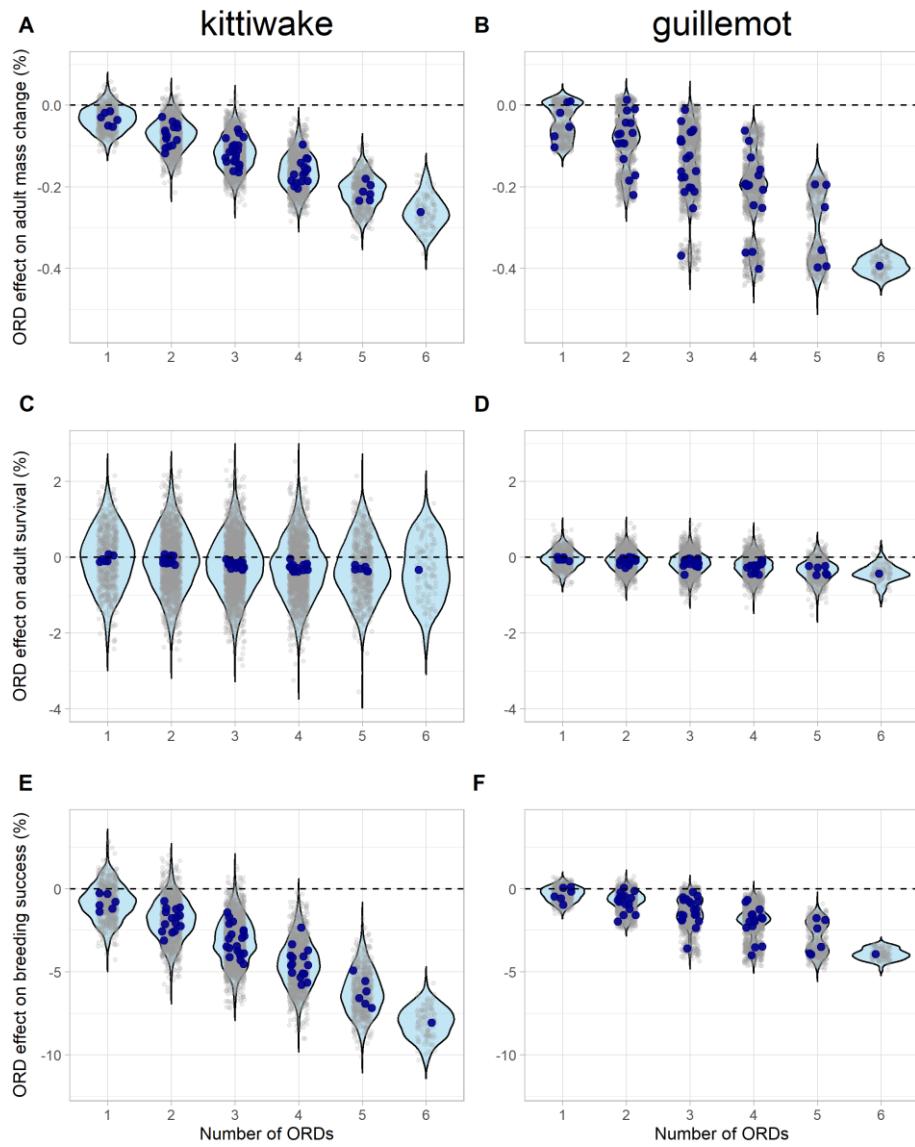


Figure 5: The effect of increasing number of hypothetical ORDs on adult mass change, adult year-round survival and breeding success in kittiwake (A, C, E) and guillemot (B, D, E), respectively. In each panel, dark blue points indicate the means of each hypothetical ORD combination ($n=63$), light grey points indicate all replicates, with violin plots illustrating their associated distribution.

433

434

435 [3.2 Sensitivity analysis](#)

436 Critical mass below which the chick suffers mortality (BM_chick_mortf), had very little bearing on
 437 the difference in percentage of adult mass loss between scenario and baseline simulations (Figure
 438 6), and had a small but significant reduction in breeding success impacts with ORDs at its lowest
 439 parameter variation (BM_chick_mortf [0.54] breeding success mean \pm sd = -0.213 ± 1.058 , upper &

440 lower CIs = -0.420, -0.006, Table 2). The critical time threshold for unattendance at the nest
441 (unattend_max_hrs) parameter showed similarly low levels of sensitivity, with small but significant
442 differences in adult mass loss for its highest and lowest variation (unattend_max_hrs = 18.9 & 16.2,
443 Table 2).

444 Energy density of the bird's tissue (kJ g⁻¹, adult_mass_KG) had small but significant effects for three
445 out of four parameter variations (adult_mass_KG = 40.425, 36.57, 34.65) for the difference in adult
446 mass loss between scenario and baseline simulations (Table 2), while there were no significant
447 differences between ORDs and baseline simulations for breeding success. The displacement zone
448 extent did not impact difference in adult mass loss significantly, except for when reduced to 1km
449 where adult mass loss increased relative to baseline simulations (Table 2, Figure 6). Significant
450 decreases in breeding success were seen with parameter reductions to 2.5km and 1km. The
451 parameter controlling the influence of competition on intake rate (IR_half_b) was the most sensitive
452 to the perturbations applied where all variations resulted in a significant difference in adult mass,
453 and three out of four parameter variations in breeding success (Table 2). Upon quadrupling this
454 parameter (IR_half_b = 0.08) adult mass decreased on average by 0.11% compared to the baseline,
455 with a reduction in breeding success of -1.46% (Table 2), comprising the largest effects on both
456 outputs across all parameter variations (Figure 6). We note that the higher relative magnitude of the
457 variations set in this parameter, owing to a lack of empirical data, are likely responsible for these
458 results and caveat direct comparisons with other parameters.

459 It was not possible to calibrate the model appropriately when the parameter for critical mass below
460 which the adult abandons chick was set to +10%, -5% & -10% of its original value in the model
461 (BM_adult_abdn = 0.88, 0.84, 0.72). This was because there were no overlapping prey values
462 resulting in corresponding model outputs for adult mass loss and breeding success within the
463 respective moderate ranges set using empirical data (Table S9, Figure S10). Upon increasing this
464 parameter by 5%/10% from its default value (BM_adult_abdn = 0.84 & 0.88), breeding success

465 dropped considerably, while adult mass loss also decreased, with the inverse occurring upon
466 decreasing the parameter value (BM_adult_abdn = 0.76 & 0.72). The magnitude of this divergence
467 between changes in adult mass and breeding success was such that it was not possible to identify
468 shared prey values corresponding to moderate conditions (Figure S10). This set of results highlights
469 it as a key parameter to which model outputs are particularly sensitive. Further support comes from
470 the parameter variation (-5% of default value) for which calibration was possible (BM_adult_abdn =
471 0.76), where assessing the differences between baseline and scenario of our two main outputs were
472 relatively large compared to other parameter variations (Figure 6), and confidence intervals for both
473 did not contain zero (Table 2).

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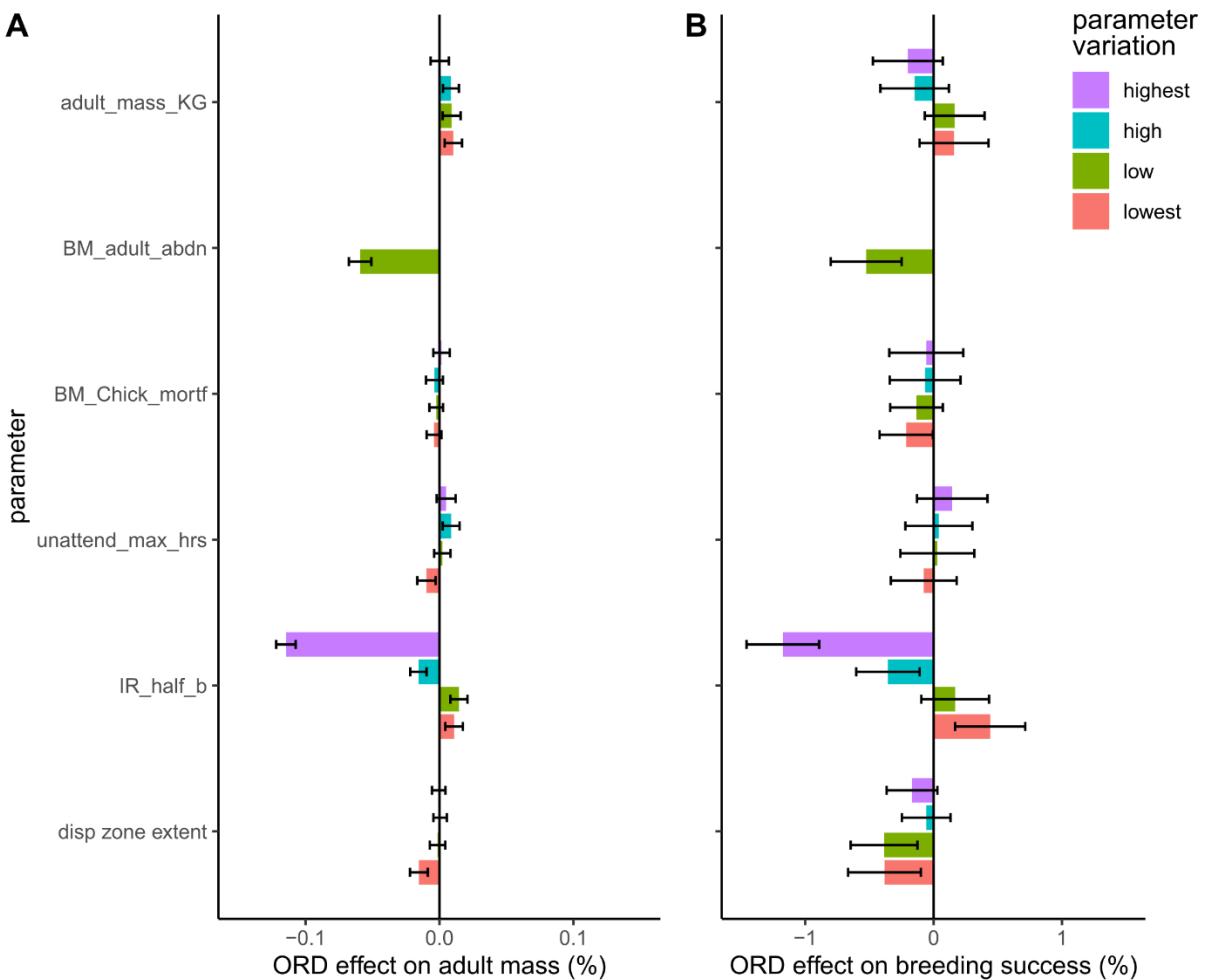
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484 Table 2: Sensitivity analysis results. 95% confidence intervals (CI) ranges shown in bold where they don't contain zero. Only
 485 one parameter is varied in each model. Differences are relative to the model run in which all parameters are fixed at their
 486 standard value (i.e. no parameters are varied).

Parameter (abbreviated name, standard value)	Variation	ORD effect on adult mass change (%)		ORD effect on breeding success (%)	
		Mean ± s.d.	Lower- upper 95% CI	Mean ± s.d.	Lower-upper 95% CI
Energy density of bird's tissue (adult_mass_KG, 38.5 kJ g⁻¹)	42.35 (+10%)	0.000 ± 0.035	-0.007, 0.007	-0.201 ± 1.388	-0.473, 0.0007
	40.425 (+5%)	0.009 ± 0.030	0.003, 0.015	-0.147 ± 1.362	-0.414, 0.119
	36.575 (-5%)	0.009 ± 0.034	0.002, 0.016	0.164 ± 1.188	-0.069, 0.397
	34.65 (-10%)	0.010 ± 0.033	0.004, 0.017	0.159 ± 1.368	-0.109, 0.428
Critical mass below which adult abandons chick (BM_adult_abdn, 0.8)	0.88 (+10%)	-	-	-	-
	0.84 (+5%)	-	-	-	-
	0.76 (-5%)	-0.059 ± 0.043	-0.068, -0.051	-0.525 ± 1.409	-0.801, -0.249
	0.72 (-10%)	-	-	-	-
Critical mass below which chick is dead (BM_chick_mortf, 0.6)	0.66 (+10%)	0.002 ± 0.031	-0.005, 0.008	-0.057 ± 1.469	-0.345, 0.231
	0.63 (+5%)	-0.004 ± 0.032	-0.010, 0.003	-0.066 ± 1.405	-0.342, 0.209
	(0.57) -5%	-0.002 ± 0.026	-0.008, 0.003	-0.133 ± 1.046	-0.338, 0.072
	0.54 (-10%)	-0.004 ± 0.028	-0.010, 0.001	-0.213 ± 1.058	-0.420, -0.006
Critical time threshold for unattendance at nest (unattend_max_hrs, 18 hrs)	19.8 (+10%)	0.005 ± 0.036	-0.002, 0.012	0.145 ± 1.401	-0.130, 0.420
	18.9 (+5%)	0.009 ± 0.032	0.002, 0.015	0.041 ± 1.332	-0.220, 0.302
	17.1 (-5%)	0.002 ± 0.031	-0.004, 0.008	0.029 ± 1.471	-0.259, 0.316
	16.2 (-10%)	-0.010 ± 0.035	-0.017, -0.003	-0.077 ± 1.308	-0.333, 0.180
Influence of conspecific competition on intake rate (IR_half_b, 0.02)	0.08 (*4)	-0.115 ± 0.037	-0.122, -0.107	-1.174 ± 1.442	-1.457, -0.891
	0.04 (*2)	-0.016 ± 0.031	-0.022, -0.010	-0.356 ± 1.260	-0.603, -0.109
	0.01 (/2)	0.015 ± 0.032	0.008, 0.021	0.168 ± 1.347	-0.096, 0.432
	0.005 (/4)	0.011 ± 0.034	0.004, 0.017	0.441 ± 1.394	0.168, 0.714
Displacement zone extent (5 km)	20km	-0.001 ± 0.026	-0.006, 0.004	-0.168 ± 1.008	-0.365, 0.030
	10km	0.000 ± 0.026	-0.005, 0.005	-0.058 ± 0.967	-0.247, 0.132
	2.5km	-0.001 ± 0.029	-0.007, 0.004	-0.386 ± 1.326	-0.646, -0.126
	1km	-0.015 ± 0.034	-0.022, -0.009	-0.382 ± 1.446	-0.666, -0.099

487



488

489 *Figure 6: Sensitivity analysis results for variations of six parameters showing the difference between effects due to ORDs*
 490 *(baseline output – scenario output) for a particular parameter variation and a standard baseline run (where parameters are*
 491 *not varied) for the following two primary model outputs: (A) percentage of adult mass, and (B) breeding success. The legend*
 492 *refers to the four levels of parameter variation which varied for different parameters: IR_half_b was varied by dividing by*
 493 *four (lowest) and by two (low), and by multiplying by two (high) and by four (highest), while displacement zone extent*
 494 *variations were 1 km (lowest), 2.5 km (low), 10 km (high), and 20 km (highest). All other parameters were varied at the*
 495 *standardised rate of -10% (lowest), -5% (low), +5% (high), and + 10% (highest). Bars indicate 95% confidence intervals.*

496 4. Discussion

497 We have developed a process-based model that represents the relevant mechanisms pertaining to
 498 time-energy budgets and behaviour of protected seabird species during the chick-rearing season and
 499 demonstrate that it captures realistic system dynamics in line with empirical evidence for time-
 500 activity budgets, adult condition, breeding success and survival in the absence of ORDs. With the

501 inclusion of ORDs, and assumptions relating to how seabirds interact with developments, we have
502 produced a transparent means of predicting sublethal impacts of renewable developments on the
503 demographic rates of protected seabird populations, informed by the full breadth of available
504 literature available. We demonstrate the IBM's ability to predict the demographic impacts resulting
505 from sublethal individual interactions with cumulative ORDs, where demographic impacts scale
506 positively with increasing exposure to ORDs in kittiwakes and guillemots. Critically, we provide a
507 transparent method for predicting how the cumulative interactions of breeding seabirds with
508 multiple ORDs permits estimation of a policy relevant set of population-level outputs that can readily
509 be used as inputs for population viability analysis, thus increasing confidence in seabird population
510 projections used in environmental management decisions concerning planned ORDs.

511 [4.2 Modelling cumulative effects](#)

512 Our results indicate that demographic impacts of sublethal interactions scale positively with
513 cumulative exposure to ORDs, and that despite the model simulations having similar exposure across
514 the two species, the outcomes varied in both form and extent. Guillemots experienced a larger
515 effect on adult mass change than kittiwakes but increasing numbers of ORDs had comparatively
516 lower impact on their breeding success. This result is likely attributable to respective parameters
517 sets capturing behavioural and energetic dynamics for each species, thus highlighting the
518 importance of using mechanistic models that are capable of including such nuanced processes. We
519 also conducted a more in-depth analysis into how different metrics relating to proxies for barrier
520 effects, displacement, and competition were associated with changes in adult condition and
521 demography (Appendix Section 2, 4). Here, we demonstrate that such impacts do not always scale in
522 a linear fashion with increasing ORD exposure, with predicted impacts of ORDs becoming more
523 severe with increasing magnitude of interactions. This violates the simplifying assumption currently
524 used in cumulative impact assessments, where the impacts from different developments are
525 assumed to be additive (Madsen et al., 2010). This divergence may be driven by behavioural
526 buffering where the model captures threshold behaviour across a range of mechanisms, for example

527 when adults favour their own survival over that of their chick. The ability of IBMs to represent such
528 dynamics in a transparent way reinforces the advantage in using such models over other, more
529 simplistic methods.

530 It is difficult to disentangle how such nonlinear relationships between model output metrics for
531 condition and demography and ORD interactions arise. Due to high flight costs in some seabird
532 species, modelled individuals may experience larger energetic costs for barrier effects than for
533 displacement effects, particularly when displacement does not incur an additional travel cost when
534 compared to the foraging location chosen in the baseline. Flight is a costly activity, particularly for
535 guillemots, so barrier effects incurring longer distances flown tend to result in greater energetic
536 consequences than those incurred via increased foraging competition. Building such mechanisms
537 into IBMs provides a transparent and flexible modelling platform to explore the consequences of
538 such mechanisms on the demography of seabirds, revealing key areas for future research that will
539 lead to an improved evidence base and will reduce uncertainty in impact assessments, facilitating
540 the transition to renewable energy

541 [4.1 Sensitivity analysis](#)

542 The results of the sensitivity analysis show that model outputs are relatively robust to realistic
543 variation in key model parameters lacking in empirical support. However, the parameter variations
544 in one of the behavioural parameters – determining the mass below which adults abandon their
545 chick (*BM_adult_abdn*) – resulted in model calibration not being possible, due to divergence in the
546 set of model outputs upon which calibration is based (adult mass loss and breeding success).
547 Nevertheless, model outputs demonstrated that the model mechanisms relating to behaviour and
548 consequent impact on breeding success have been captured in a way consistent with ecological
549 understanding, where the directionality of changes in impacts that arose from parameter variation
550 demonstrated that the model is successfully capturing the underpinning biological processes known
551 to exist in breeding seabirds. The strong sensitivity of this model parameter highlights the priority for

552 further empirical investigation in understanding the condition-related causes of breeding attempt
553 abandonment in these species.

554 A previous model predicting the effects of ORDs on northern gannets *Morus bassanus* (Warwick-
555 Evans et al., 2018) was particularly sensitive to parameters relating to prey, intake and assimilation.
556 Our model has analogous parameters, but a considerable amount of its sensitivity to them is likely
557 absorbed by adopting the calibration procedure, which acts to stabilise the model to produce
558 empirically consistent model outputs before the introduction of ORDs and prediction of their
559 influence on demographic rates. This process is essential in ensuring the model's transferability, as
560 ultimately it is designed to be applied to any breeding colony for the four parameterised species
561 (kittiwake, guillemot, razorbill, puffin) with potential for wider application (Section 4.4).

562 Reducing the displacement zone extent to below 5 km negatively influenced breeding success more
563 than adult mass change, which is likely a result of mechanisms within the model whereby adults
564 prioritise their own condition over that of their chicks in response to increased competition for prey
565 resources when displacement is confined to a smaller area. The precise value of this key model
566 parameter is likely to depend on ecological and environmental factors such as population size,
567 foraging range, prey selection, prey availability and social foraging patterns. Seabird responses to
568 ORDs vary considerably between species, with some being completely avoidant such as red-throated
569 diver *Gavia stellata* (Heinänen et al., 2020), and other species attracted to the areas around turbines
570 such as some large gulls *Larus* spp. and cormorants *Phalacrocorax carbo* (Dierschke et al., 2016;
571 Johnston et al., 2022). For our focal species, kittiwakes and guillemots, analysis of response radii to
572 ORDs indicates behavioural reactions at ~20 km and ~9km respectively (Peschko et al., 2020). The
573 same study also reported reduced density inside the footprint during the breeding season of 45% for
574 kittiwakes, and 44% for guillemots. Variation in responses has also been seen within species, where
575 individuals may show differing responses as in gannets (Peschko et al., 2021), or populations may
576 respond differently to ORDs depending on the season (Peschko et al., 2020), the latter likely being a

577 consequence of the differing constraints experienced throughout the year. Variation in responses
578 both between and within species could be linked to factors such as turbine density or prey
579 availability (Thaxter et al., 2024; van Bemmelen et al., 2024), and the shape of these responses will
580 often depend on the spatial scale of data and analyses. For example, kittiwakes display attraction to
581 ORD footprints on the macro-scale (0-4 km away from the ORD footprint), but avoidance when
582 considering response at the turbine level (Pollock et al., 2024). IBMs provide a flexible platform to
583 include such variation in responses as evidence emerges.

584 [4.3 Future development](#)

585 A key area for IBM development is the incorporation of more realistic foraging tracks(e.g.,
586 Chudzinska et al., 2021) to accommodate nuanced responses to ORDs as evidence emerges for how
587 foraging birds alter movement patterns in and around offshore wind farms. The development of
588 tracks to include further behavioural mechanisms, such as active choice in foraging site during trips
589 and adaptive decisions based on previous successful foraging areas, would facilitate the inclusion of
590 heterogenous prey distributions informed from empirical data, such as the lesser sandeel
591 *Ammodytes marinus* (Langton et al., 2021). Furthermore, the indirect effects of renewable
592 developments on prey redistribution, for which evidence is accumulating (e.g., Bicknell et al., 2025),
593 could also be accounted for by including mechanisms linking seabird movement and space use to
594 prey density. By using a pattern-orientated modelling approach (Gallagher et al., 2021; Wiegand et
595 al., 2003), simulation experiments with foraging mechanisms invoking various forms of memory
596 and/or social interaction to guide adaptation to profitable foraging sites could help underpin which
597 mechanisms drive foraging site fidelity. Such an approach has already been used in gannets (Pollock
598 et al. *in review*), where model outputs were compared against empirical levels of foraging site
599 fidelity that have recently been quantified in SeabORD's focal species (Regan et al., 2024). Several
600 other avenues for development include extending SeabORD to cover the incubation period when
601 reduced constraints will influence behaviour, or updating the mass-survival equations used to
602 predict year-round adult survival in light of new evidence (Daunt et al. 2020).

603 [4.4 Wider applications](#)

604 We have developed an open source, transparent, evidence-based IBM for predicting demographic
605 impacts of sub-lethal effects arising from breeding seabird interactions with ORDs. We demonstrate
606 the model using empirical information for two species of key consent risk, however we also provide
607 parameter sets for a further two species thereby expanding the potential use of the model. Our
608 Appendix contains extensive information on the inputs (Table S3) and parameters (Table S4)
609 required to run the model, providing a platform for others to further develop and apply the model to
610 other species in new contexts. We also provide alternative model options for accommodating
611 varying complexity dependent on the level of information available, for example the use of bird
612 distribution maps derived from GPS data when available, or alternatively, provision of a distance
613 decay function with a minimum requirement of a species' typical foraging distance. With
614 development of renewables continuing apace across the globe, our approach is likely to be useful for
615 practitioners elsewhere, either in scoping exercises or in EIA equivalents relating to specific
616 developments.

617 [4.5 Conclusion](#)

618 We provide a novel analytical tool for estimating the population level consequences of displacement
619 and barrier effects for breeding seabirds. By simulating the individual interactions of seabirds with
620 their environment, including one or more ORDs, and then scaling up to the population-level, we
621 provide policy-relevant metrics that emerge from the interaction of key ecological processes,
622 generating predictions based on the best available evidence. We apply the model to demonstrate
623 that increasing exposure to cumulative ORDs may result in higher demographic impacts in two
624 seabird species, highlighting the need for models that can incorporate mechanistic processes and
625 allow for increased confidence in predictions of anthropogenic alterations to the environment. The
626 use of IBMs in contexts such as this, especially when underpinned by strong empirical data (e.g.,
627 Leedham et al., 2025), should form a central role in legislative frameworks for understanding and

628 predicting anthropogenic impacts on species for which complex behavioural pathways shape
629 emergent demographic rates and population change.

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Supplementary material: Predicting demographic impacts from sublethal cumulative effects of offshore renewable developments on breeding seabirds

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Supplementary material section 1: SeabORD ODD

Introduction

This document comprises a description of the SeabORD individual-based model (IBM), that was developed in R (R Core Team, 2024). The code is provided in GitHub (https://github.com/NERC-CEH/seabORD_pkg with guidelines available at the following page: https://nerc-ceh.github.io/seabORD_pkg/index.html). We follow the ODD (Objectives, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm et al., 2006, 2020).

ODD

1. Purpose and patterns

The purpose of the model is to predict the demographic impacts on seabirds of sub-lethal displacement and barrier effects resulting from interactions with ORDs, evaluated through predicted changes to adult mass, adult survival and breeding success. Demographic impacts are derived by estimating alterations to behaviour and time-energy budgets of four different seabird species during the chick-rearing period, when exposed to ORDs within their foraging ranges. To estimate the impacts of ORDs, baseline scenarios (no ORD footprints included) are compared with scenarios containing one or more ORDs, providing estimates of potential changes to adult mass, adult survival, and breeding success under alternative scenarios of ORD exposure.

To evaluate if our model represents these key behavioural and energetic processes in line with empirical data, we parameterised and evaluated the model against the following patterns obtained from empirical data or available literature or, where information from these sources was not available, expert opinion: time activity budgets, adult mass change during chick-rearing, chick growth and chick survival, distribution of foraging birds, and the form and frequency of interactions with ORDs. Body condition and behavioural data comes from the Isle of May long-term study (“IMLOTS”, Leedham et al., 2025; Newell et al., 2025) and expert opinion. The spatial distribution of foraging birds is another key pattern which we derive from GPS data.

2. Entities, state variables and scales

The model is composed of four kinds of entities: adults, chicks, landscape grid cells, and ORD footprints (Table S1). The adults and chicks may belong to one of four species for which the model has been parameterised: common guillemot (*Uria aalge*), razorbill (*Alca torda*), Atlantic puffin (*Fratercula arctica*), and black-legged kittiwake (*Rissa tridactyla*). One simulation of the model involves selecting one of these species and one breeding population to simulate. Adults in these species form breeding pairs, which between them have a viable chick(s) at the beginning of the breeding season. In the case of kittiwakes, which often have two chicks in a brood, the energy requirements are modelled as such, but we will hereafter refer to chick as singular for consistency.

The population being investigated is partitioned into different categories of individuals relating to susceptibility to ORD interactions, where they can be either unsusceptible, and thus flying around ORDs does not change their behaviour, or susceptible to both displacement and barrier effects. All parameters used in simulations can be found in Table S4.

Table S1: Model entities and the state variables they are characterised by

Entity	Name of state variable	Unit/option	Type	Description and associated submodel(s)
adults	Species	Kittiwake/ puffin/ guillemot/ razorbill	Static	Which seabird species is being modelled
	Colony	e.g. Isle of May	Static	Which colony/SPA is being modelled
	Bird ID	Integer	Static	A unique ID for the individual
	Pair ID	Integer	Static	A unique ID for the pair which two individuals will share
	Sex	Male/female	Static	
	Displacement susceptible	Boolean	Static	If true, the bird will experience displacement effects
	Barrier susceptible	Boolean	Static	If true, the bird will experience barrier effects
	Body mass, $T = 0$	Grams	Static	Body mass of adult at the beginning of the time step
	Body mass	Grams	Dynamic	Body mass of adult in the current time step
	BM_condition	proportion	Dynamic	Relative condition at any point during the simulation to initial body mass
	Energy requirement total	Kilojoules	Dynamic	Total daily energy requirement for adult bird plus its share of the chick
	Energy requirement adult	Kilojoules	Dynamic	The energy requirement for the adult in this timestep
	Energy requirement chick	Kilojoules	Dynamic	The energy requirement for the adult's chick in this timestep
	Energy caught	Kilojoules	Dynamic	The energetic content of prey caught by the bird
	Ereq_intakef_a	Proportion	Dynamic	Fraction of the food intake that goes to the adult bird
	Energy gain adult	Kilojoules	Dynamic	Energy gain by the adult
	Energy gain chick	Kilojoules	Dynamic	Energy gain by the chick
	Req_gram	Grams	Dynamic	Quantity of food required in this timestep (to cover previous step's activity)
chicks	Number of trips per timestep	Integer (1-6)	Dynamic	The maximum number of potential trips to choose from is six for all species
	Time flying	Hours	Dynamic	Time spent flying in this time step
	Time foraging	Hours	Dynamic	Time spent foraging in this time step
	Time at colony	Hours	Dynamic	Time spent at the colony in this time step
	Time spent resting at sea	Hours	Dynamic	Time spent resting at sea in this time step
	Feeding mode	Integer (1-4)	Dynamic	Dictate's the adults foraging strategy: 1 = Provisioning optimally, 2 = Nest is unattended, 3 = Nest abandoned, 4 = Adult is dead

chicks	Is chick alive?	Boolean	Dynamic	Is this adult's chick alive in this time step?
	Destination	Integer	Dynamic	Grid cell number of the foraging destination
	Displaced?	Boolean	Dynamic	Did this adult experience displacement in this time step?
	Barriered?	Boolean	Dynamic	Was this adult barriered in this time step?
	Extra Km flown	Kilometres	Dynamic	Extra km flown in this timestep due to barrier/displacement effects
	Cause of death	none/starved	Dynamic	The adult's cause of death
	Pair ID	Integer	Static	Indicates which adult Pair ID this chick belongs to
	Body mass, T = 0	Grams	Static	Body mass at the beginning of the simulation
	Body mass	Grams		Chick body mass in this time step
	Alive?	Boolean		Is this chick alive or dead
patches	Cause of death	none/Starved/ killed/ unattended/ other		If the chick died, what was its cause of death?
	Energy requirement	Kilojoules	Dynamic	Energy required in this time step
	Unattended hours	H	Dynamic	How many hours was this chick unattended in the current time step
	Prey0	g/area	Static	Prey available at the foraging site
Offshore renewable developments (ORDs)	Bird density	Proportion	Static	Probability of foraging in a particular area each time step
	Competition from other colonies	Individuals per grid cell	Static	Derived from a map of the modelled distribution of birds from nearby colonies
	Name	e.g. "ORD1"	Static	A unique ID for each of the ORDs in the scenario run
	Location, size and shape		Static	A polygon provided in a shapefile to indicate the extent of the ORD footprint
	Buffer	Km from footprint edge	Static	The area around an ORD footprint from which birds are assumed to be displaced
	Displacement zone	Km from buffer edge	Static	When a bird is displaced from inside the ORD footprint-plus-buffer, its alternative foraging area is located in the displacement zone.

Space is represented as two-dimensional, where cells in the landscape are 1 x 1 km in dimension and can represent anywhere in the UK. The extent of the grid of foraging locations is dictated by the bird distribution maps which are an input to the model alongside a distribution map of conspecifics from surrounding colonies, used to infer competition, and they set the model domain. For example, the guillemot bird distribution map (Fig S1) has an extent of 201 x 275 km.

Cells are designated as land or sea, and if they are sea cells, they have a prey value assigned to them that is determined in the prey calibration process (section 2.1.5), which dictates the amount of prey an adult encounters if it visits the location. Selection of foraging locations is based on probabilities from the bird distribution map (Figure S1 A), typically a utilisation distribution specifying the proportion of time birds from the focal population spend in each habitat grid cell. All adults are assumed to fly directly over sea (i.e., if straight line path to foraging site is obstructed by land, they will take the shortest path possible) to and from the colony to foraging patches unless they are obstructed by an ORD due to barrier effects.

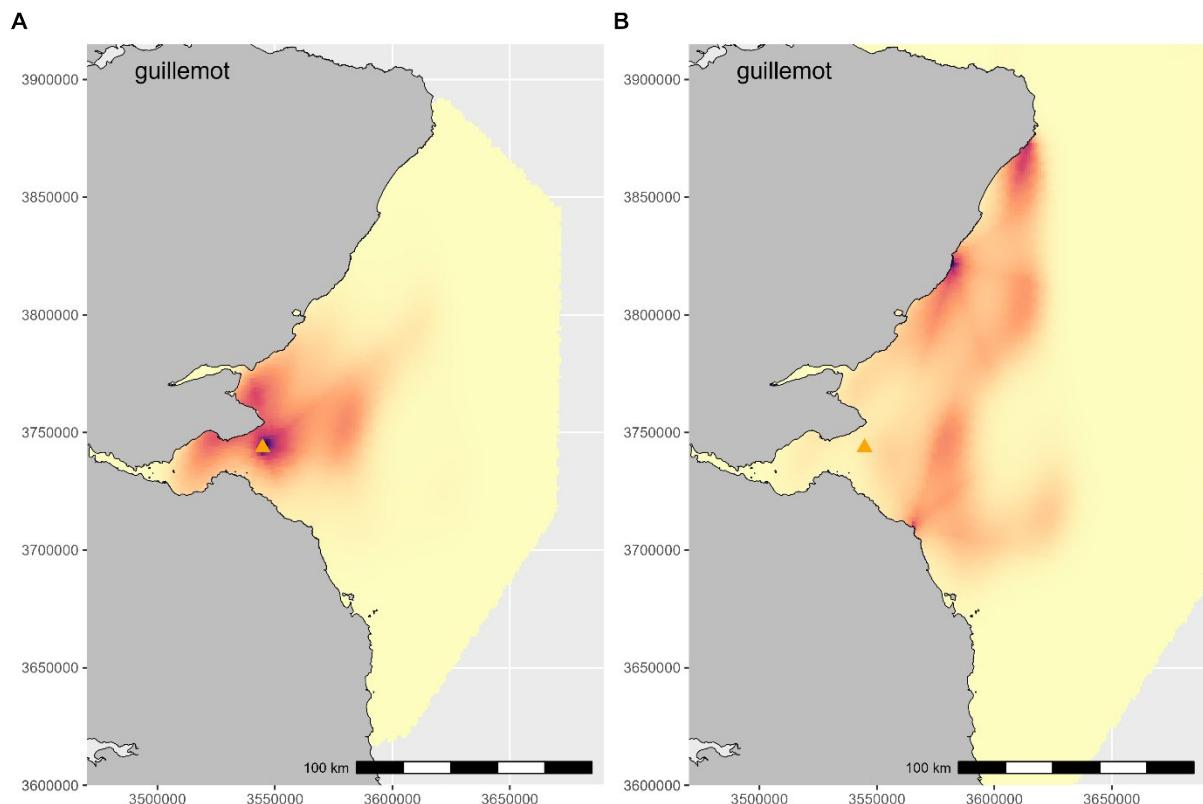


Figure S1: Landscape example using the guillemot (A) bird distribution map from the Isle of May and (B) map of competition from conspecifics with colony location indicated by the orange triangle. Darker areas within the bird distribution extent indicate a higher probability of picking these locations as foraging areas each time step for A.

ORD footprints are static objects in the landscape that have a buffer around the footprint, in which displaced and barriered adults will be excluded from, and a wider displacement zone into which birds that choose a foraging site in the footprint-plus-buffer will be displaced. These two parameters may be varied within the model and were set at 2km (buffer), in line with current UK guidance from NatureScot (NatureScot 2023), and 5km (displacement zone) for the purposes of the cumulative effects modelling presented here. Adults may enter ORDs if they are not barrier/displacement susceptible, but if they are they will need to negotiate depending on the wind farm impact they are experiencing (further described in section 7.5).

Time is represented in discrete time steps, during which multiple foraging trips can take place, and are 24 hours for all species apart from kittiwakes, which have 36-hour long time steps to accommodate longer foraging trips in this species according to empirical data. The number of time steps in each simulation varies with species, allowing the model to be representative of their respective breeding season lengths (kittiwake = 45 days, guillemot = 21 days, razorbill = 21 days, puffin = 40 days).

3. Process overview and scheduling

The model is developed to represent the chick-rearing season of four different seabird species found in UK waters with each time step being structured into three main procedures. The scheduling of the procedures is iterated on each individual in the same order in each sub model. Therefore, there are no interactions between individuals simulated at sea which could be influenced by the scheduling of processes, and thus no unintentional advantages are imparted on the adults, nor consequently on the chicks in the model.

The model can be separated into the set-up process and main model, which has a nested structure (Figure S2). Within each time step the adults make foraging decisions and then based on the outcomes of those decisions, a pair's chick's condition is updated depending on whether its parents managed to catch enough prey to feed themselves and their chick, with prioritisation of themselves occurring when constraints imposed by foraging conditions and/or experienced body condition are sufficiently bad. Names in bold refer to the submodels within these processes which are elaborated on in the submodels section.

- i) *Foraging and adult behaviour* - At the beginning of a time step, each adult is stochastically assigned a location for feeding during each foraging trip from the colony based on bird density maps. The prey available in this foraging location is used to calculate the time taken to forage their required amount in this time step (**calc_foragecapture**) using an intake rate based on a Type II functional response (Holling, 1959), with an adjustment to account for the effect of competition from conspecifics on individual instantaneous intake rate. Using this information in conjunction with knowledge of associated activities such as flying to and from the foraging site (including barrier effects of flying around the ORD), plus a knowledge of their own condition and whether or not their chick is alive, each adult then chooses the optimal foraging strategy for this time step (**calc_strategy**), which is based upon attempting to acquire their required energy intake for the day, whilst minimising time spent away from their chick to avoid unattendance. This determines how many trips the adult will undertake in this time step and what behavioural strategy the adults exhibit with respect to their chick

("feeding mode", Table S1), such as potentially leaving them unattended or abandoning the breeding attempt due to constraints.

- ii) *Consequences for chicks* – The amount of food captured by each adult during the time step is then converted to energy shared between themselves and the chick and summed to estimate the energy provided to the chick. The resulting increase in chick body mass, based upon food provided by both its parent, is calculated and compared to a corresponding optimum body mass for a chick at the given stage of the season (**calc_chickcare**). If this value falls below a defined threshold the chick starves and suffers mortality. At this point the consequences of the adults' behaviour towards the chick determine whether the chick remains alive, or if it dies through abandonment, a parent dying, which is followed by several stochastic processes relating to other potential causes of death: unattendance by the parents (**calc_unattendance**), other mortality from causes like storms (**calc_othermortality**), or in the case of puffins, mortality from predation via hunger driving them to the entrance of the burrow (**calc_puffinmortality**).
- iii) *Update adults* – Each adult's state variables are then updated with the chick's status, which can result in a change in the feeding mode if their chick dies, having consequences for their foraging strategy in the next time step. Adult body masses are then updated based on the energy gained and expended foraging and in other activities (**calc_adultbmchange**). Daily energy requirement (*DER*) for the following time step is then calculated (**calc_adultdee**).
- iv) *Adult survival* – Upon completion of all time steps for each season (baseline/scenario) within each replicate, adult survival over the subsequent winter period is estimated using the mass of each adult which survived to the final time step, representing the end of the chick-rearing season. Survival is estimated using relationships from previously published studies (Erikstad et al., 2009; Oro & Furness, 2002), by converting the mass of each adult into a probability of survival via mass-survival relationships (**calc_pSurvival**). This probability is then passed to a stochastic process which dictates which individuals survive according to their relative probabilities.

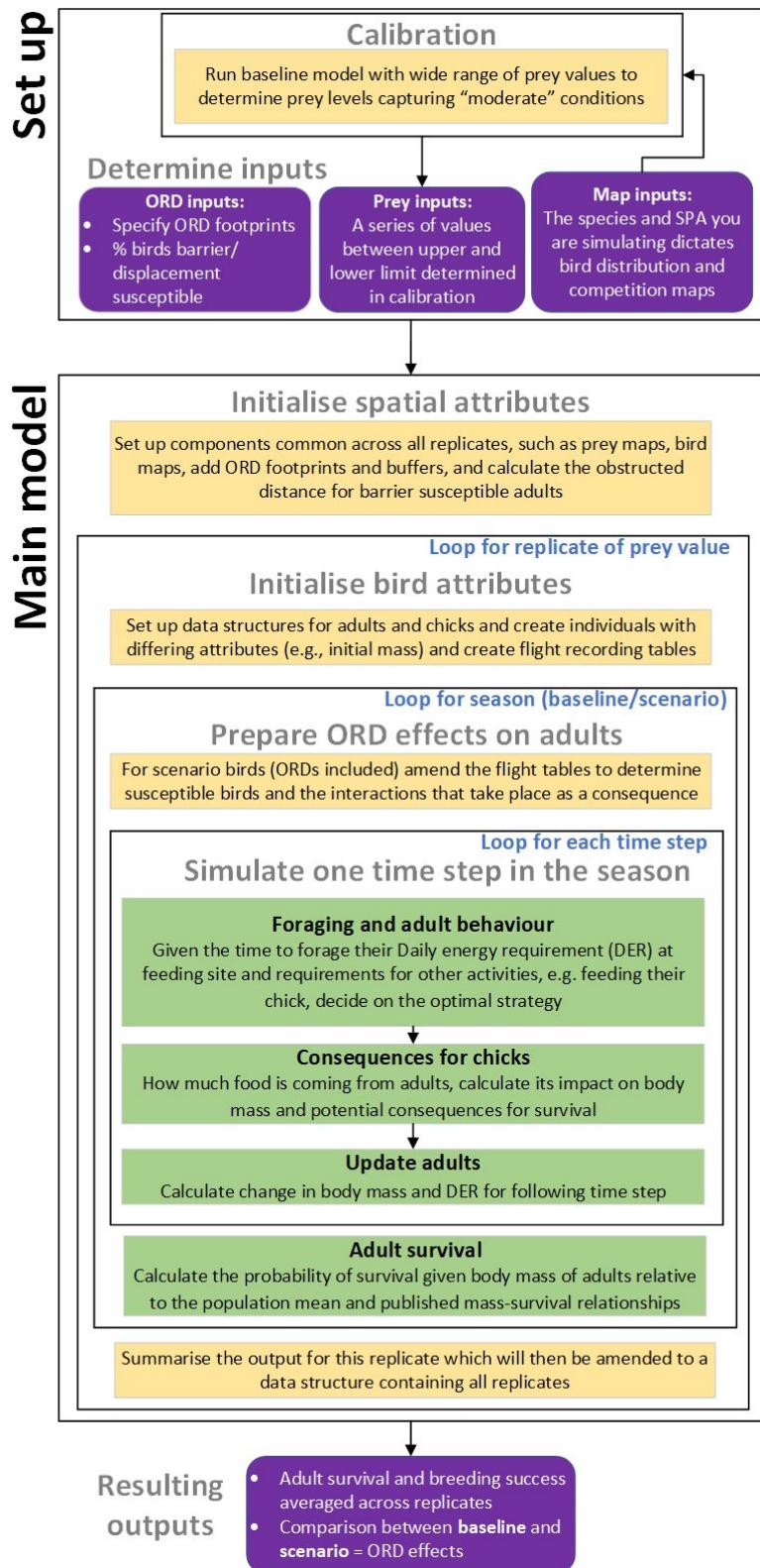


Figure S2: Schematic of SeabORD model, divided into two parts with the set up including calibration at the top and the main model below, with nested structure shown by black boxes with looping indicated in blue text where relevant. Purple rounded boxes indicate inputs and outputs of the model, yellow boxes indicate initialisation and housekeeping, with the green boxes corresponding to the main processes elaborated on in Section 2.1.3.

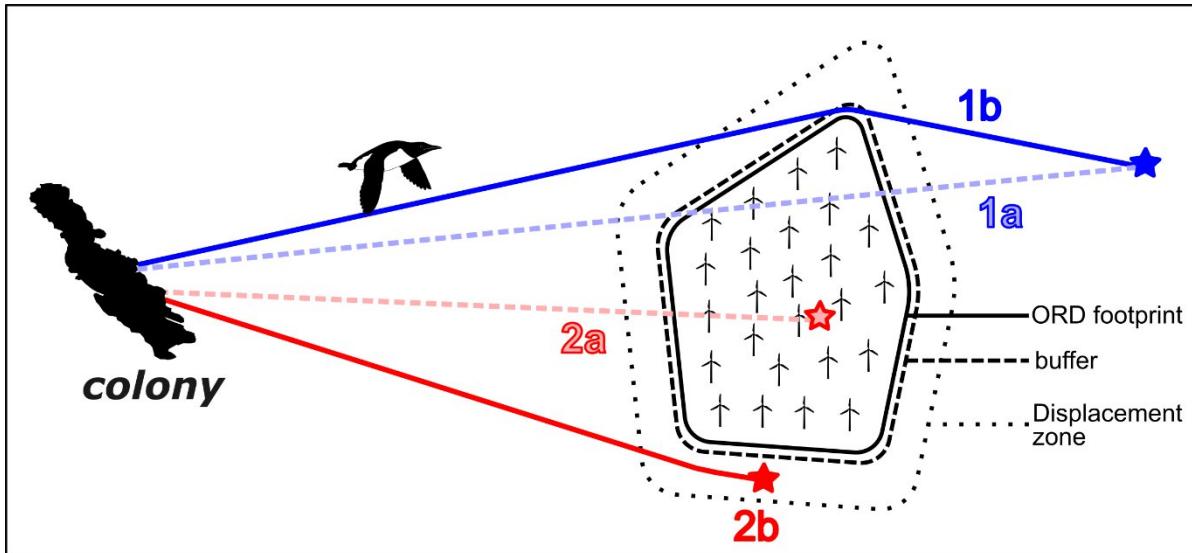


Figure S3: Examples of potential interactions with offshore renewable devices (ORDs). Foraging trip 1b (blue) represents a barrier-susceptible bird, which has to fly the shortest distance around the ORD to get to its obstructed foraging site on the far side relative to the colony, where 1a (light blue) shows the track in absence of the ORD and what would be experienced in baseline simulations. Foraging trip 2b (red) represents a displacement susceptible bird, which would have foraged within the ORD footprint, as shown by 2a (light red), but is now foraging in the displacement zone. In all cases birds use the same flightpath to both reach and return from their chosen foraging location.

4. Design concepts

4.1 Basic principles

The model simulates foraging decisions of individual seabirds under the assumption that they are acting in accordance with optimal foraging theory, minimising time away from offspring whilst maximising energy gain. The model assumes that the foraging behaviour of individual seabirds is driven by prey availability, travel costs, provisioning requirements for offspring, and behaviour of conspecifics with all assumptions and constraints derived from observed behaviour to the fullest extent possible.

Adult behaviour concerning sublethal interactions with ORDs is split into two widely accepted potential impacts, barrier and displacement effects. A barrier effect is thought to occur when a bird is attempting to access a foraging site from the colony where the most direct path is obstructed, such that avoiding the ORD results in increased travelling distance with potential energetic consequences (Masden et al., 2009). Barrier effects operate within the model by adjusting baseline flight paths (when no ORDs are present) using the shortest path directly around the ORD in the scenario run (Figure S3, example 1). A displacement effect occurs when an individual is excluded from foraging in a potentially productive area within an ORD footprint. The model represents this by displacing a bird from its previously chosen foraging location inside an ORD footprint into a new location in the displacement zone, with new foraging locations chosen proportional to the probability of bird usage within the displacement zone (Figure S3, example 2).

The three key model outputs are adult mass change over a season, from which we estimate adult overwinter survival, and productivity. By providing individual and population level estimates for change in adult mass and productivity, we provide a direct link for observed or estimated foraging patterns of breeding seabirds in the presence or absence of ORDs, through to metrics important for assessing demographic effects on populations, the unit of interest in many statutory assessments and conservation efforts.

4.2 Emergence

The key outputs of the model, adult mass change throughout the breeding season and breeding productivity, vary in a non-linear fashion with variation in prey availability. The emergence of these patterns is driven by the behavioural mechanisms of adults in response to the amount of prey they can obtain and what their current body condition and constraints are. One example of this is how decreasing availability of prey from the point at which both adult mass change and chicks per nest outputs are representative of moderate conditions causes chicks per nest to reach zero, at which point adult mass loss levels off and plateaus for a considerable range (Fig S4). This indicates that when adult kittiwakes prioritise their own survival over chicks, they can sustain themselves in relatively poor prey conditions. In our model, general adult survival is much more robust to changes in conditions than chicks, which require relatively good conditions to experience a productive year, which is similar to what is observed in reality given that many seabird species are long-lived and thus parents prioritise their own survival over that of their chicks.

Another of the model's emergent properties regards the effects of ORD interactions on adult mass loss and chick survival. Barrier effects, which cause the adults to fly further longer distances around the footprint that they would in the baseline, seem to have a larger impact on model outputs than displacement effects. When an adult is displaced, it picks another foraging site within the 5 km buffer around the ORD footprint it has been displaced from, and since this alternative site is chosen through the bird distribution map which shows a general trend of decreasing with distance from the colony (Fig S1A), it will more often than not be closer to the colony than the site it was displaced from. The consequence of this is shorter flying time to reach the foraging site, which results in less energy expenditure for that trip. This may be offset by increased competition with conspecifics within the buffer zone where this individual and others are displaced into, resulting in a higher density of birds than seen in the landscape beyond ORDs and their buffers. As yet, there is a lack of empirical evidence to corroborate this emergent pattern although there is some evidence of aggregations of seabirds around the outside of ORD footprints which aligns with our model (Johnston et al., 2022; Pollock et al., 2024; Vanermen et al., 2020).

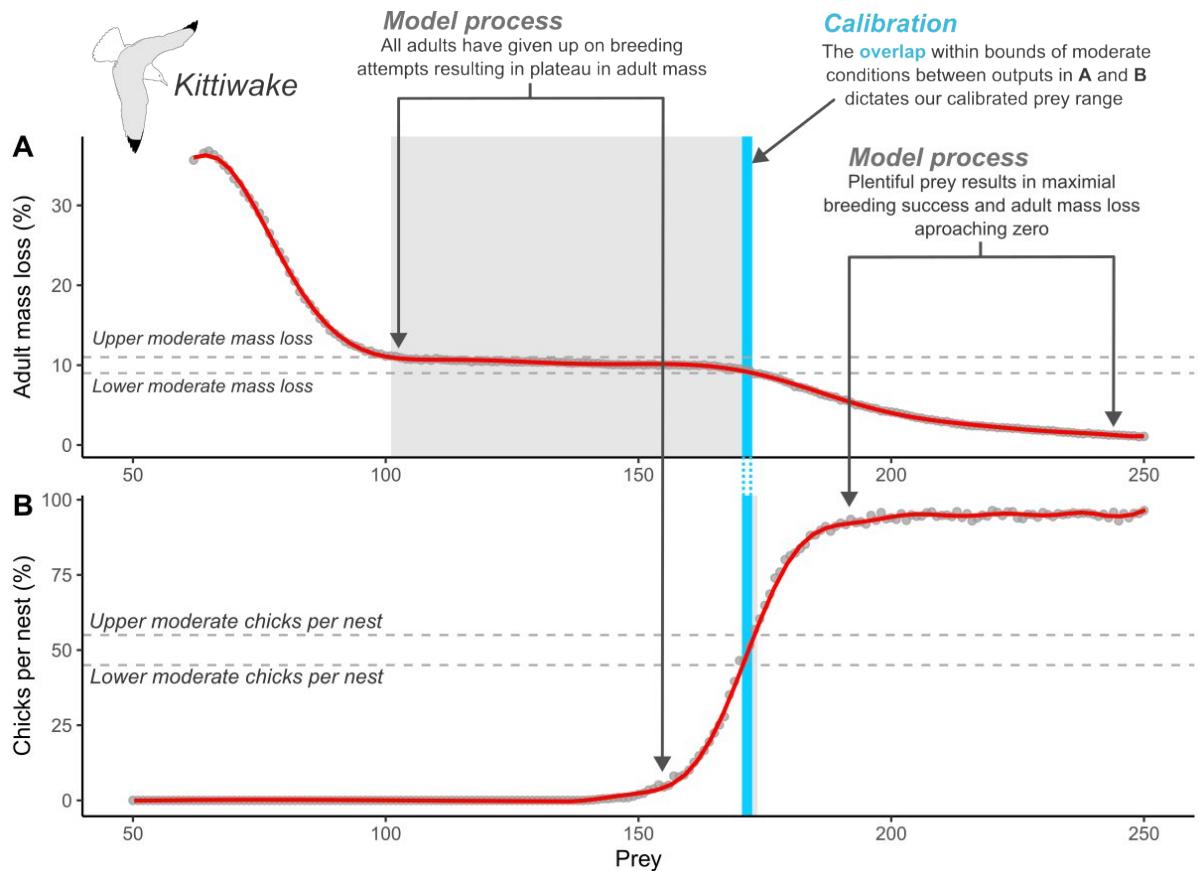


Figure S4: Schematic plot of kittiwake adult mass loss (A) and chicks per nest (B) withdrawn from 300 baseline simulations (no ORD footprints) ranging from a prey value of 50 up to 250, to display a range of model dynamics. The red lines are for smoothed model outputs, which are overlaid on grey points indicating the individual estimates. For calibration we have upper and lower bound for each output (A & B) which are picked to reflect “moderate” conditions, i.e., what is observed in a typical year for kittiwakes at the Isle of May, and these are indicated by the dashed grey horizontal lines. The grey shaded blocks indicate where the respective outputs fall within these bounds, and the light blue shaded block indicates the prey values where there is overlap between the estimates, which is the prey range used in subsequent simulations with ORDs included. We also highlight some patterns which emerge in the outputs driven by model processes of adult behaviour and how it relates to chick survival.

4.3 Adaptation

Adults decide how many trips are optimal in a given time step, based on how far away the foraging destination is from the colony, what condition they are in, provisioning requirements for the offspring, and behaviour of conspecifics. Adults also adapt their behaviour towards their chick depending on their own condition and depending on whether they are still rearing a chick or have abandoned the attempt. Adults also attempt to compensate for higher energy output in previous days by acquiring more energy on subsequent days. It is important to note that adults are not adaptive in trying to compensate for their partner’s behaviour e.g., by feeding the chick more or making up any attendance deficit.

Foraging decisions are modelled implicitly as individuals have a higher probability of selecting foraging sites from areas which have a higher density on the normalised bird distribution map (which is preferably derived from GPS data). This means that there is no adaptation in movement and space use for choosing profitable foraging sites based on prior experience in the model, and as such no foraging site fidelity between time steps.

4.4 Objectives

The objective of adult birds is to optimise their foraging strategy to maximise energy gain while minimising time away from the nest depending on the condition of the adult. If conditions become suboptimal it is possible for adults to adopt a strategy which favours their own survival over that of the chick.

4.5 Learning

There are no adaptive behaviours of agents that are modelled in a way which includes learning.

4.6 Prediction

There is no estimation of the future consequences of decisions, beyond that of the current time step which has already been described.

4.7 Sensing

Adults can sense their own body condition, which is their mass at the current timestep, t , relative to their mass at the beginning of the simulation (mass, t_0). They can also sense what their energy requirement is for the current time step, the condition of their chick, and whether their chick will be left unattended due to their own actions.

Adults can sense the relative prey availability of the patch they are foraging on in the current time step (t). They are aware of the coastline and the location of their breeding colony, as well as the location of ORDs, and choose the shortest path available to avoid obstructions on the way to and from their foraging site. This extends to birds which are susceptible to ORD interactions. When the path to their foraging site is obstructed by an ORD birds may choose the shortest path around it to their intended foraging site (Figure S3), constituting a barrier event. If they were planning on foraging within a wind farm footprint and choose a location within the surrounding displacement zone, this is a displacement event.

4.8 Interaction

Competition does not arise from direct interaction, but indirectly through the sum of all other individuals using the same grid cell during the same time step which influences the intake rate. Included in this calculation are other individuals from the colony of interest, and conspecifics from other colonies.

4.9 Stochasticity

The key stochastic processes are listed in Table S2. Stochasticity is used to (i) capture variability in the characteristics in individuals, such as initial body mass, to (ii) represent the stochastic processes occurring during foraging, such as choosing foraging area, and to infer competition, and finally (iii) in processes to decide the fate of adults at the end of the breeding season and chicks in different context-dependent situations.

Table S2: List of key stochastic processes and a brief description with and the associated procedure (section 3)

Stochastic process	Description	Associated procedure
Inter-individual variability in the initial values of body mass in adults and chicks	Adult/chick body mass (g) withdrawn from respective normal distributions characterised by initial body mass mean and standard deviation withdrawn from empirical data.	Initialisation
Initial Daily Energy Expenditure (DEE)	On first time step adult DEE drawn from a normal distribution parameterised using the mean and standard deviation of adult DEE from empirical data.	
Susceptibility to wind farm impacts	In the model set up, adults are randomly assigned displacement susceptibility (Boolean) based on the displacement rate input, and then the subset of displacement susceptible birds are randomly assigned as barrier susceptible or not based on the equivalent barrier input.	
Choice of foraging location	Adults choose a random foraging location in proportion to the expected intensity of usage in bird maps.	Foraging and adult behaviour
Foraging location following displacement	If an adult's chosen foraging location is within a wind farm footprint and the bird is displacement susceptible it will choose another foraging location based on expected intensity of usage in the subset of cells which are within the displacement zone surrounding the given wind farm.	
Simulating other birds for competition	A stochastic process is used to simulate the number of birds in each grid cell per time step, which is used to infer competition in the foraging effort. This is conducted separately for baseline and scenario runs, where in the scenario the displacement rate used to assign displacement susceptibility of each adult in initialisation is also used in a stochastic process to simulate the number of birds being displaced into the displacement zone of each wind farm.	
Chick death	There are several potential ways for a chick	Consequences for

	to die which all have a stochastic element, including through: (i) unattendance, where probability of death increases with time unattended; (ii) “other” mortality from other causes such as flooding or storms, which occurs randomly with a fixed probability and is not dependent on other variables, and (iii) puffin chick mortality from predation due to hunger, which is dependent on chick condition dropping below a threshold in which a chick might take the risk of venturing to the burrow entrance.	chicks
Adult survival	Probability of survival, which is calculated by converting each adult’s mass at the end of the breeding season and using published mass-survival rates, is used to decide, through simulation from a Bernoulli distribution, whether each adult survives the upcoming winter period or not.	Adult survival

4.10 Collectives

For competition calculations the aggregated number of individual conspecifics in the current cell is calculated from the number of individuals from the simulated colony currently at this location and an estimate of conspecific competition from the supplied competition map (Figure S1B). Aside from this there are no other aggregations of individuals or direct interaction between adults at sea or at the colony.

4.11 Observation

The key outputs of the model are population-level estimates of breeding success and adult survival, the latter being inferred from estimates of adult mass at the end of the breeding season and published adult mass-over winter survival relationships for the respective species. To determine ORD effects, baseline scenarios are compared with scenarios containing one or more ORDs. More detailed outputs are available, such as records of each individual’s state variables at the end of each timestep, thus permitting further inspection of changes in state and characteristics of a particular pair of adults and their chick throughout a simulation (Figure S5).

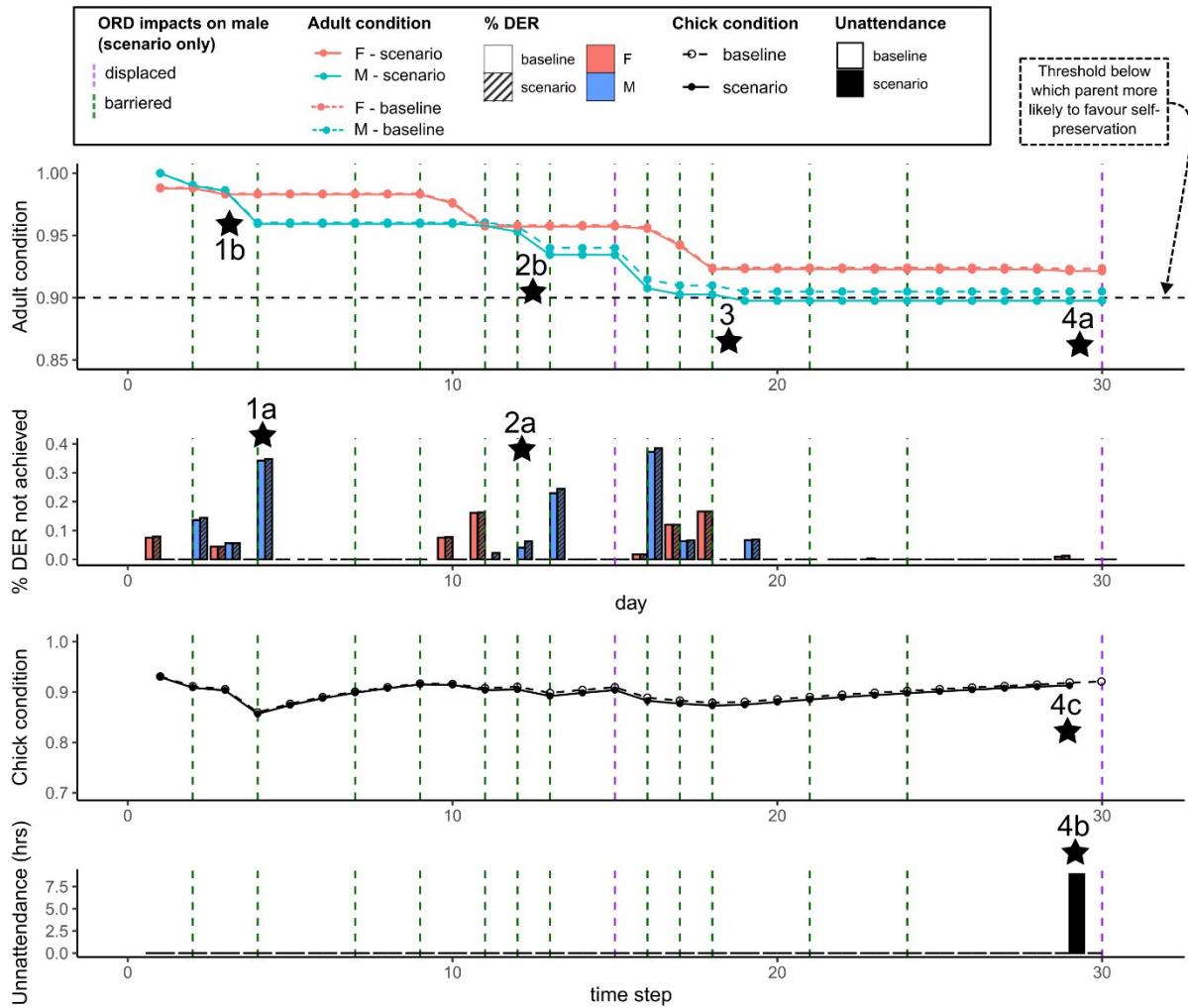


Figure S5: An individual-level plot tracking a pair of kittiwake adults and their chick through one full season in matched baseline and scenario simulations plotted using the individual outputs from a SeabORD simulation run. All plots run from time step 1 to 30, which is the duration of a kittiwake simulation. The top row tracks adult condition with red lines indicating the female, and blue for the male, where the dashed line represents baseline (no ORDs) adults, and the solid line for scenario (including ORDs). Vertical dashed lines throughout plots indicate male interactions with an ORD (female not susceptible), with green representing barrier effects and purple showing displacement. The second row from the top is the percentage of daily energy requirement (DER) not achieved on that particular day, where red and blue bars represent female and male respectively, and the hashed bars indicate the scenario runs, with no hash indicating the baseline individual. The third row from the top tracks the chick condition, where the solid points and line represent the scenario chick, and the dashed line and hollow points represent the baseline. The bottom row indicates the number of hours a particular chick was unattended during that day where black bars indicate the scenario chick being unattended and white for the baseline chick. The numbered stars indicate key events that we wish to highlight: Males from both seasons (baseline and scenario) have not achieved ~30% of their DER on time step 4 (1a), resulting in a drop in their condition (1b). On time step 11, 12 and 13 the males of both seasons are increasing in % of DER not achieved (2a), with the scenario male having slightly exaggerated impacts from experiencing barrier effect, which results in the scenario and baseline males' conditions diverging (2b). As their condition continues to drop, at time step 19 the scenario male falls below the threshold which results in this individual being more likely to prioritise their own upkeep (3) which means the possibility for unattendance of their chick. At time step 29 the scenario male remains below this threshold, while the baseline bird remains above it (4a), which results in the scenario chick being unattended for ~8 hours (4b), which results in its death (4c), while the baseline chick survives to the end of the simulation.

ORD related individual metrics

The effects of ORDs are summarized by calculating the relative difference in mortality with and without an ORD, via

$$\frac{(\text{Number of birds simulated to die when the ORD is present} - \text{Number of birds simulated to die when the ORD is absent})}{\text{Population size}}$$

This relative difference is calculated for the entire population (we term this metric P1). A range of metrics (I1-I6) are also derived by calculating this relative difference for subsets of the population determined by the frequency with which individuals interact with the ORD and the nature of these interactions (barrier or displacement effects):

- i. birds that never interact with the ORD at any point during the breeding season, via either displacement or barrier effects (I1);
- ii. birds that ever (at least once) interact with the ORD at any point during the breeding season, via either displacement or barrier effects (I2);
- iii. birds that are displaced by the ORD at least once during the breeding season, but are never barrier affected (I3);
- iv. birds that are barrier affected by the ORD at least once during the breeding season, but are never displaced (I4);
- v. birds that are displaced and barrier affected by the ORD at least once during the breeding season (I5);
- vi. birds that are displaced on exactly d time steps, and barrier affected on exactly b time steps (I6).

Quantifying uncertainty

Outputs are generated for each of R model runs. For each metric we calculate the mean m across runs to provide our “best estimate” for this quantity. We quantify uncertainty by calculating the standard deviation across runs, s , and the 95% prediction interval $m \pm T_{R-1}s\sqrt{1 + 1/R}$ (where T_{R-1} represents the 2.5% quantile of a t-distribution with $R - 1$ degrees of freedom). The prediction interval, which is derived under an assumption of normality, represents the uncertainty associated with using outputs from the R simulated populations to predict the output that we would have obtained for the true but unobserved “real” population.

The standard errors and prediction interval represent the uncertainties that arise from both inherent stochastic variability between populations and the uncertainty associated with determining the overall level of prey. It is crucial to note that the standard errors and prediction intervals do not account for any other sources of uncertainty: e.g., for the uncertainty associated with estimating model parameters, for the uncertainty associated with the underlying structure of the model, or the uncertainty associated with the spatial distribution of birds. Since a number of these other sources

of uncertainty – particularly the uncertainty in the adult mass-survival relationship – are likely to be large, the prediction intervals that we present should be treated with caution and regarded as lower bounds on the actual level of uncertainty.

5. Initialisation

5.1 Inputs

SeabORD is applicable to multiple sites/species/ORD set ups. The user must define the form of simulation being conducted through a range of inputs which are listed in Table S3. A key component of the seabORD model is the need to calibrate the prey level inputs used for each new species and colony combination. This currently involves running the model without ORDs (baseline simulations) with a range of prey levels to ascertain the range of values that returns adult mass and chick mortality rates that are consistent with pre-defined values representing “moderate” conditions based on empirical data (Figure S4). This is to allow simulation of the range of outcomes expected under these conditions, as the model is highly sensitive to the prey density parameter.

We do this as empirical data on absolute quantities of available prey at relevant spatial and temporal scales are rarely available, so the intake rate function has been parameterised to unitless prey to produce time-activity budgets that match with those observed in empirical data. This means that the prey value used in calibration (determining prey values in all cells) has to be adjusted for each new bird density map to ensure that the outputs from the model are consistent with empirical data.

Table S3: List of key user inputs for determining the type of SeabORD run

Associated entity/process	Input	Options
General setup	Model mode	“calibration” (baseline runs over a wide range of prey densities to determine prey range used in scenario runs, Section 5.2) or “scenario” (runs with ORDs included once prey level has been calibrated)
	Model environment	Options for running the model replicates in “serial” (i.e., for capabilities of running on a local computer) or “parallel” (for the capabilities of high-performance computing clusters to reduce runtime and increase replicate capacity)
	Number of replicates	The number of replicates to run for this simulation
Bird population	Initial seed	Set the value of a seed to ensure reproducibility
	Species	Kittiwake/Guillemot/Puffin/Razorbill – this will dictate what species parameters are used (Table S4)
	Colony/SPA	Choose the Special Protected Area (SPA) you wish to model. It’s possible to override this and model just one colony which you specify yourself but may require additional inputs (e.g., colony coordinates, distance by

		sea to colony map).
	Number of pairs	Specify the population size you wish to simulate
	Scale factor	Here you can specify if you want to run only a proportion of individuals in the population which reduces runtime.
Landscape	Prey	The prey value which is withdrawn according to the replicate number from the range determined in the calibration stage.
	Bird distribution map	Map specifying the density of birds which determines foraging locations
	Competition map	Map specifying the density of birds from surrounding colonies of conspecifics, used to infer competition
ORD	ORDs to include	List of ORD names corresponding to shapefiles for wind farms footprints around the UK, otherwise the user can provide their own polygons.
	ORD buffer size	Specify the extent of the buffer around the wind farm which birds will avoid if barriered or be displaced from in the simulation. Typically set to 2 km.
	ORD displacement zone size	Specify how far beyond the buffer you want the displacement zone to extend, where will be displaced in to for respective wind farms.
	Displacement rate	Determines the proportion of birds of the population that will be susceptible to displacement effects for the duration of the simulation.
	Barrier rate	Determines the proportion of barrier susceptible birds from the subset of birds already defined as displacement susceptible.

Table S4: Parameters and their sources

Parameter	kittiwake		guillemot		razorbill		puffin		
Name	Description (units)	value	source	value	source	value	source	value	source
BM_adult_mn	Initial adult body mass mean (g)	372.69	UKCEH unpubl. data	920.34	UKCEH unpubl. data	582.9	UKCEH unpubl. data	392.8	UKCEH unpubl. data
BM_adult_sd	Initial adult body mass standard deviation (g)	33.62	UKCEH unpubl. data	57.44	UKCEH unpubl. data	26	UKCEH unpubl. data	21.95	UKCEH unpubl. data
BM_adult_mortf	Critical mass below which adult is assumed dead (proportion of mean mass)	0.6	Derived from Golovkin 1963						
BM_adult_abdn	Critical mass below which adult abandons chick (proportion of mean mass)	0.8	Expert judgement						
BM_adult_hlthy	Critical mass below which adult favours itself over its chick when foraging (proportion of mean mass)	0.9	Expert judgement						
BM_chick_mn	Initial chick body mass mean (g)	36	UKCEH unpubl. data	75.8	UKCEH unpubl. data	64.9	UKCEH unpubl. data	42.2	UKCEH unpubl. data
BM_chick_sd	Initial chick body mass standard deviation (g)	2.2	UKCEH unpubl. data	1	UKCEH unpubl. data	6.3	UKCEH unpubl. data	3.7	UKCEH unpubl. data
BM_chick_mortf	Critical mass below which chick is dead (proportion of initial mass)	0.6	Derived from Golovkin 1963						
daylength	Number of hours per time step (hours)	36	-	24	-	24	-	24	-
seasonlength	Number of time steps per season	30 (45 days)	UKCEH unpubl. data	21 (21 days)	UKCEH unpubl. data	21 (21 days)	UKCEH unpubl. data	40 (40 days)	UKCEH unpubl. data
unattend_max_hrs	Critical time threshold for unattendance at nest above which a chick is assumed to die through exposure or predation (hours)	18	Expert judgement	18	Expert judgement	18	Expert judgement	NA	-
adult_DEE_mn	Adult daily energy expenditure mean (kJ)	802	Daunt et al. 2008 and refs therein	1489.1	Daunt et al. 2008 and refs therein	1231.89	Daunt et al. 2008 and refs therein	871.5	Daunt et al. 2008 and refs therein
adult_DEE_sd	Adult daily energy expenditure standard deviation (kJ)	196	Daunt et al. 2008 and refs therein	169.9	Daunt et al. 2008 and refs therein	95.3	Daunt et al. 2008 and refs therein	80	Daunt et al. 2008 and refs therein
chick_DER	Chick energy requirement (kJ per day)	525.7	Enstipp et al. 2006	221.7	Thaxter et al. 2013	195.67	Thaxter et al. 2013	325	Harris & Wanless 2011

IR_max	Maximum prey intake (g per minute)	4.369	UKCEH unpubl. data	2.95	UKCEH unpubl. data	3.066	UKCEH unpubl. data	3.293	UKCEH unpubl. data
IIR_half_a	Prey density intake rate is half its max/the rate of intake rate decrease with prey depletion (g)	900	Calibrated in functional response	700	Calibrated in functional response	600	Calibrated in functional response	1000	Calibrated in functional response
IR_half_b	The effect of conspecific density on intake rate of individuals through assumed interference competition	0.02	Expert judgement in conjunction with Hassell & Varley 1969	0.02	Expert judgement in conjunction with Hassell & Varley 1969	0.02	Expert judgement in conjunction with Hassell & Varley 1969	0.02	Expert judgement in conjunction with Hassell & Varley 1969
flight_msec	Average speed in flight (m/sec)	13.1	Pennycuick 1997	19.1	Pennycuick 1997	16	Pennycuick 1997	17.6	Pennycuick 1997
assim_eff	Assimilation efficiency	0.74	Hilton et al. 2000a	0.78	Hilton et al. 2000a	0.79	Hilton et al. 2000a	0.78	Hilton et al. 2000a
energy_prey	Energy gained from prey (kJ per gram)	6.52	Leedham et al. 2025 and refs therein	9.26	Leedham et al. 2025 and refs therein	6.1	Harris et al. 2008	6.1	Harris et al. 2008
energy_nest	Energy cost of nesting at colony (kJ per day)	427.8	Leedham et al. 2025 and refs therein	780	Leedham et al. 2025 and refs therein	932.17	Hilton et al. 2000b	665.41	Hilton et al. 2000b
energy_flight	Energy cost of flight (kJ per day)	1400.7	Leedham et al. 2025 and refs therein	7266.2	Leedham et al. 2025 and refs therein	3581.34	Pennycuick 1989	3113.9	Pennycuick 1989
energy_searest	Energy cost of resting at sea (kJ per day)	400.6	Leedham et al. 2025 and refs therein	540.7	Enstipp et al. 2006	646.15	Enstipp et al. 2006	461.24	Enstipp et al. 2006
energy_forage	Energy cost of foraging (kJ per day)	1400.7	Leedham et al. 2025 and refs therein	1894.9	Enstipp et al. 2006	1421.45	Birt-Friesen et al. 1989	974.97	Birt-Friesen et al. 1989
energy_warming	Energy cost of warming food (kJ per day)	26	Leedham et al. 2025 and refs therein	49.3	Leedham et al. 2025 and refs therein	47.317	Gremillet et al. 2003	35.84	Gremillet et al. 2003
chick_mass_a	Maximum chick mass gain per day (g)	11	UKCEH unpubl. data	9	UKCEH unpubl. data	7	UKCEH unpubl. data	6	Harris & Wanless 2011
adult_mass_kg	Energy density of the bird's tissue (kJ g ⁻¹)	38.5	Gabrielsen 1996	38.5	Gabrielsen 1996	38	Gabrielsen 1996	38	Gabrielsen 1996
beta	Parameter for translation of adult mass change into year round survival	0.038	Oro & Furness 2002	1.03	Erikstad et al. 2009	1.03	Erikstad et al. 2009	1.03	Erikstad et al. 2009

Once inputs have been decided, the way the model agents and landscapes are initialised is largely similar for calibration (baseline only) and scenario (ORDs included). Data structures which contain all individuals are created, summing to the specified number of pairs (inputs, Table S3), including the stochastic process of setting initial body mass of adults and chicks (Table S2), with parameters sourced for chosen species (Table S4). The landscape, coastline and how the bird and competition maps are included are the same for calibration and scenario runs. They diverge in how they treat ORDs, where there is no inclusion of ORDs in the calibration runs and there is only a baseline set of runs, while the scenario runs will have the same baseline runs and a set of matched runs with the specified ORD footprints included. This provides a counterfactual to allow assessment of the wind farm impacts.

5.2 Scenarios

SeabORD is run such that each model scenario contains a set of matched pairs of simulations for the baseline (no ORDs present) and an impacted run (ORDs present), with the metrics of ORD impact calculated for each matched pair of baseline and impacted model simulations (which we refer to as a “replicate”). Each pair of baseline and impacted simulations is “matched” in the sense that the outcomes of stochastic events within the model that are unrelated to wind farm impacts (e.g., in particular, initial body mass of each individual, and the foraging locations selected at each timestep) are assumed to be exactly identical within the baseline and impacted simulations. Matching is used in order to isolate, and thereby provide more precise estimates of, the ORD impacts, by ensuring that unnecessary stochastic differences between the impacted and baseline run do not arise.

Replicates (matched pairs of impacted and baseline simulations) have identical model parameters and other inputs to each other, with exception that (a) each replicate uses a distinct random seed (so will have different outputs as a result of stochasticity) and (b) each replicate uses a different prey value (selected uniformly from within the range determined by model calibration).

5.3 Prey calibration process

Calibration entails conducting a series of baseline runs (i.e., no ORD footprint) across a range of prey values attempting to encompass a wide range of conditions in the model, from poor to good. These conditions are assessed by plotting mean adult percentage mass loss and nest survival outputs obtained at the end of each run against the range of prey values which we have simulated and identifying the range of prey values which correspond with the range of values for both outputs we consider “moderate”, or representative of a standard year, for the species/population being modelled (Table S5). In the case where there is no overlap between the set of prey values that yield plausible values for mass loss and nest survival, it is not possible for the model to be calibrated, and

you should not continue. In this case, we advise that you go back and reassess the plausibility of input parameter values.

For example, in Figure S4 we show outputs from 300 baseline simulations ranging over prey values of 50 up to 250 in a population of kittiwakes. In Figure S4A we can see that there is a wide range of prey values (103 – 172) within the range of mass loss (9 – 11%, Table S4) indicating moderate conditions. However, for nest survival (Fig S4B) we can see the range of prey values (170 – 173) corresponding with moderate conditions in nest survival (45 – 55%, Table S4) is much narrower owing to the steeper slope. In this case we select only the shared prey values across the two outputs, 170 – 172, indicated by the blue area in Figure S4, which is the prey range used for any subsequent scenario runs conducted.

We note that it is important to do a sufficiently high resolution of prey ranges to allow for characterisation of the nonlinear relationships often present which thus permits precision in finding the (potentially small) overlapping shared prey values for both outputs. It is possible that this will require a staged approach, where a very wide range of prey values with lower resolution is assessed to find the general range indicating moderate conditions, before targeting a narrower range with a higher resolution to pinpoint the best values for the given conditions.

Table S5: Example of output ranges indicating moderate conditions for each species. Please note that you will need to source your own site- and species-specific ranges for moderate conditions if conducting your own simulations.

Species	Adult mass loss and range (%)	Nest survival (%)
Kittiwake	10 (9 – 11)	50 (45 – 55)
Guillemot	6 (5 – 7)	72.5 (65.3 – 79.8)
Razorbill	6 (5 – 7)	75 (67.5 – 82.5)
Puffin	6 (5 – 7)	75 (67.5 – 82.5)

5.4 Bird and competition maps

Other key inputs are the bird distribution and competition maps. The maps used will depend on the amount of GPS data available for the species, colony and surrounding colonies of conspecifics in question. Here, we consider a suite of methods classed within two standard alternatives:

1. If reasonable amounts of GPS data are available for this species at the focal and surrounding colonies then those data can be modelled (e.g., using a GAM, similar to the methods used in Searle et al. (2014);
2. If GPS data are unavailable or very limited for a species, then the foraging distribution can be specified more simply by assuming a simple relationship between the distance from the

focal colony and the foraging density (e.g., that the density decays exponentially as distance increases).

We expand on this further in the dedicated section “Bird distribution and competition maps” in Supplementary Information 2.

5.5 Selecting the number and size of the simulations

The size of each simulated population and the number of simulated populations are features of the model simulations, and as such can be specified by the user. Ideally, we recommend using simulated populations which are specified to have the same size as the actual population and for replicates of this population simulation to be carried out. In practice, it will often only be computationally feasible to run the model for simulated populations that are smaller than the population of interest, especially when running on a machine locally. SeabORD does, in this situation, adjust the levels of competition to account for the fact that only a subset of individuals have been simulated. However, this approach will increase the width of the prediction intervals and reduce the reliability of estimates of the mean and standard deviations calculated from aggregated outputs.

It is possible to run SeabORD in parallel, using a high-performance computer system such as JASMIN, which is available to environmental researchers in the UK. The model lends itself well to this environment, as each replicate containing a population can be sent of independently to run in parallel, as long as the initial seed and prey value for that replicate are supplied in the initiation. We provide an example of a parallelised script on the GitHub hosted website (https://nerc-ceh.github.io/seabORD_pkg/index.html).

6. Input data

There is no input to represent processes that change over time throughout the duration of the model.

7. Submodels

Submodels perform the behaviour of adults on each foraging trip and consequent decisions relating to daily energy requirement (DER), the mass-energy consequences for chicks and adults, and survival projections as listed in section 3. Here we elaborate further on these submodels, while initialisation and housekeeping submodels which are listed in Table S6 are covered adequately in the description column.

Table S6: List of the different functions used in SeabORD and which model process they are used in.

Process	Function	Description
Initialisation	set_seedvalues	Sets the seeds needed for reproducibility.
	set_medianprey	Set the median prey value across the region – if not using

		uniform prey levels the median value is used to scale the prey availability.
	set_initialbirdtype	Create a table object (tibble) which holds one row per individual seabird describing characteristics that remain constant like species, sex and colony.
	set_initialbirdstate	Set initial values for adult birds in the simulation such as body mass at $t=0$ and initial daily energy expenditure (DEE) used to calculate DER on the first time step of the simulation.
	set_initialchickstate	Set initial values for individual chicks including body mass at $t=0$.
	make_fldist_scen	Knowing the choice of colonies and ORDs, we can generate the obstructed distance by sea to all sea cells.
	select_destinations	Used to create a list of default foraging locations for each adult (FlightListA), based on the bird distribution map, and a list of alternative locations if a bird is displaced in the displacement zone, given the ORD footprints (FlightListB).
	sim_nbirds_wwf_perimestep	Simulate the number of birds in each grid cell at each time step in the baseline and with one or more ORDs present, under a specific displacement rate for use in the calculation of how competition affects intake rate.
Foraging and adult behaviour	calc_foragecapture	Estimate how long it would take for a given adult to acquire the food it needs given the starting prey density and competition for food.
	calc_strategy	Given the information about one flight and the time available, determine the foraging strategy and update the feeding mode (1-4) chosen by an individual bird.
Consequences for chicks	calc_chickcare	Tally the food received by the chick from both parents and update the chicks body mass.
	calc_unattendance	Chick mortality as a function of the duration of time they have been unattended by their parent(s).
	calc_othermortality	Chick mortality from other causes such as flooding or storms.
	calc_puffinmortality	Calculates puffin chick mortality from predation from emerging from the burrow due to hunger.
Update adults	calc_adultbmchange	Update adult body mass at the end of each day based on the energy they gain and expend foraging and in other activities.
	calc_adultdee	Calculate adults' daily energy expenditure based on the activities carried out.
Adult survival	calc_pSurvival	Calculate year-round survival based on the body mass of the individual relative to the population mean, species expected survival and parameters.

This function simulates one time step in the season. Given the flight pattern, potential displacement or collision risk, and the foraging strategy calculate the activities in the time step for each adult bird and the chicks.

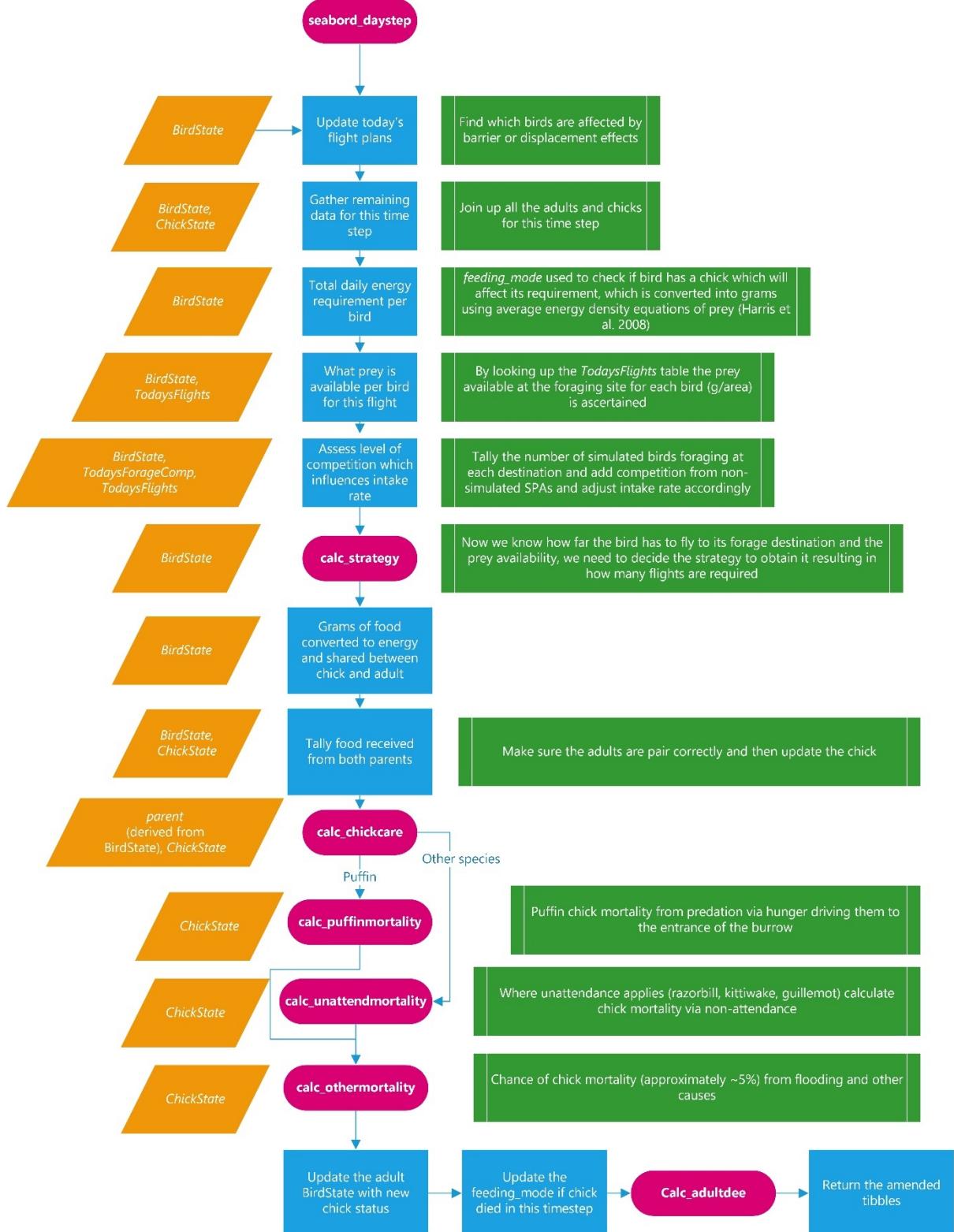


Figure S6: Schematic of the code structure within a time step (seabord_daystep). Blue boxes are main actions, green boxes are explanatory notes of these actions, orange parallelograms are data inputs with their name in the code, and pink ovals represent functions called from within a time step.

7.1 Foraging and adult behaviour submodels

Intake rate and conspecific competition

In the submodel `calc_foragecapture` an individual must calculate the time taken to forage their required amount in this time step, given the prey density and competition for food. This intake rate is achieved with a Michaelis-Menten equation for a Type II functional response (Holling, 1959), which describes the relationship between the density of prey and instantaneous intake rate for an individual. Despite some studies suggesting that piscivorous marine predators exhibit a Type III response (Enstipp et al., 2007; Middlemas et al., 2006), wherein the response of predators to prey is depressed at low prey density, we have adopted the more widely used Type II response here to minimise the number of unknown parameters being incorporated. The Type II form, which has a stronger theoretical underpinning, assumes that intake rate increases asymptotically with the density of prey:

$$\text{Intake rate at time } t = IR_MAX * \text{Prey at time } t / (IR_HALF + \text{Prey at time } t)$$

Where IR_MAX is a parameter denoting the maximum possible intake rate, which we estimated from empirical data (see following section), and IR_HALF is a parameter noting the prey level that is associated with the intake rate reaching half of the maximum possible value. The value of IR_HALF was determined as part of the model calibration process and is specific to each species.

We use this relationship to simulate the decline in intake rate over time spent foraging at a location due to prey depletion, and to determine the amount of time an individual requires at a location to attain a certain cumulative intake of prey. This form of the functional response implies that the prey quantity remaining at the foraging location at time t is equal to:

$$x(t) = \{x: (x - x_0 + IR_{MAX} + IR_{HALF} \log(x) - IR_{HALF} \log(x_0)) = 0\} \# (1)$$

where x_0 denotes the prey quantity at time 0.

This in turn implies that the total prey consumed by foraging up to time t is equal to:

$$y(t, x_0) = x_0 - x(t, x_0) \# (2)$$

and this formula is used to calculate the total daily prey intake for a bird given a) the number of foraging trips that a bird undertakes, and b) the length of each trip. Note that "time" is assumed to return to zero at the start of each new foraging trip – we assume prey depletion at a location within a foraging bout or trip, but when the bird returns to a location for a subsequent foraging bout the amount of prey in that location is reset to the original level. The solution to Equation 2 cannot be written down analytically, but it can be calculated numerically using a non-linear solver. Using

numerical methods, we pre-calculate the total prey consumed for a grid of times t and initial prey quantities x_0 at a foraging location.

For example, when $x_0 = 300$, $IR_MAX = 900$, $IR_HALF = 4.369$, and $MAXT = 2160$, where $MAXT$ is the maximum number of minutes available in one kittiwake time step (equivalent to 36 hours), providing the grid of times to pass to the nonlinear solver from the 'nleqslv' package (Hasselman, 2023). Which would return a look up table which has been plotted below (Figure S7).

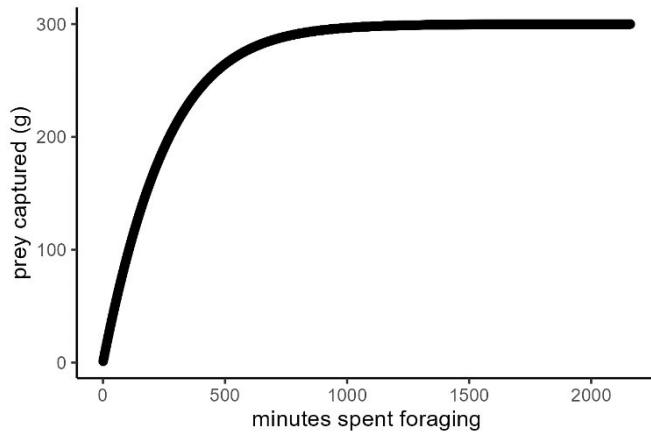


Figure S7: Plot of look up table output from *calc_foragecapture*

Derivation of intake rate parameters

Empirical data on the relationship between prey availability and intake rate is not available for these species of seabirds. Therefore, we parameterised the functional response using data from time-activity budgets of individuals from each species for the average number of foraging trips per day and the average amount of time spent foraging (Table S7). We implemented the widely used Michaelis-Menton form of the Type II functional response formula to simulate intake rates over a range of values for the model parameter, IR_HALF_a , with parameter IR_MAX derived from empirical data) across hypothetical variation in prey levels. The value of IR_HALF_a was then set so as to match the desired number of trips and time spent foraging to reach the individual's DER based on the summaries of empirical data (Table S7: 'parameters set to achieve:'), with the minimum and maximum time spent foraging constrained to be within those observed from empirical data (Table S7). No interference competition was assumed when calibrating the functional response.

The value for parameter IR_HALF_b (which controls the effect of conspecifics at the same foraging location on intake rate) was set to 0.02 for all species based on expert judgement.

Table S7: Empirical data from time-activity budgets used to parameterise the functional response curve for each species, relating the intake rate of individuals to prey availability at the chosen foraging location.

	Black-legged kittiwake	Common guillemot	Razorbill	Atlantic puffin
Mean number of trips per 24 hours	1.9	2.0	2.35	3.3
Foraging hours per day (24 hours)	3.2	5.6	5.1	6.5
Flying hours per day (24 hours)	4.9	0.8	1.9	2.4
Parameters set to achieve:	3 foraging trips over model time step (36 hours) lasting in total 4.8 hours	2 foraging trips over model time step (24 hours) lasting in total 5.0 hours	2 foraging trips over model time step (24 hours) lasting in total 5.0 hours	3 foraging trips over model time step (24 hours) lasting in total 6.0 hours

Effect of competition on intake rate

We assume that intra-specific competition between individuals foraging at the same location acts to reduce the intake rate. More specifically, the intra-specific competition effect is assumed to be a power-law model of the form:

Intraspecific competition effect

$$= (\text{Total number of birds within the grid cell, summed across all colonies})^m$$

in which the unknown parameter m controls the magnitude of the intra-specific competition effect. The value of this parameter must, in terms of the biology, lie between zero and one. A value of zero corresponds to the special case in which there is no competition (i.e., the intake rate for each bird is unaffected by the number of other birds present), while a value of one corresponds to the special case in which competition is linearly related to the number of birds present.

Within the model we apply the intra-specific competition function to the *IR_half* parameter in the functional response (which controls the shape of the curve relating intake rate to prey density). We assume that:

$$\text{IR_half with competition} = \text{IR_half without competition} * \text{Intraspecific competition effect}$$

The approach to simulation the total number of birds within the grid cell, summed across all colonies, is detailed in Appendix 2, Section 2.

Calculation of levels of competition

The level of competition that is used in calculating the intake rate for a particular individual at a particular timestep is based on summing all of the other individuals (of the species of interest) that are using the same grid cell as the individual being simulated within the same time step. The “other individuals” involved in this calculation arise from two different sources: (a) other individuals from the colony of interest, and (b) individuals from other colonies.

The location of other individuals from the colony of interest is already being simulated as part of the SeabORD run, so we can simply sum up the number of such individuals using the grid cell at this time step. Note, however, that if only a proportion of the population is being simulated in SeabORD, for computational reasons, this will be divided by proportion in order to scale the number of individuals up to the entire population.

To calculate the level of competition arising from other colonies we assume that each population of interest has a “competition map” (e.g. Fig S1 B), in addition to the “bird distribution map” (e.g. Fig S1 A) that was already associated with each population. This competition map specifies the total (combined) expected number of birds in each grid cell that arise from all colonies other than the colony of interest – it does not separate which colony these birds arose from, just that they were from colonies other than the colony of interest.

The competition map is constructed in the same way as the bird distribution map: so if the user provides a bird map derived from GPS tracking data then they also need to provide a competition map, and if the bird map is derived using distance-decay maps then the competition map is constructed using distance-decay maps (with the same foraging range and decay parameter).

Within the baseline (i.e. without windfarms) the number of competing individuals in each grid cell at each time point, from all colonies other than the colony of interest, is simulated from the competition map by simulating independently from a multinomial distribution at each time point. The sample size for the multinomial distribution is the sum of the competition map (i.e. the total abundance from colonies other than the colony of interest) and the multinomial probabilities are given by the normalized competition map (rescaled to sum to one across grid cells). The corresponding simulated number of competing individuals once windfarms are present is then calculated by adjusting the number of competing individuals in the baseline by the number of birds that are net number of birds that displaced into the grid cell by the windfarm. The net number of displaced birds is simulated via applying a binomial distribution (to determine the probability of being displaced away from each grid cell) followed by a multinomial distribution (to determine the

probabilities associated with the destination of a displaced birds). Full mathematical details are given in Supplementary Information 2.

`calc_strategy`

The look up table produced from `calc_foragecapture` is used in conjunction with a key adult state variable, *bm_condition*, which is an index indicating the condition of the adult and is derived from of the mass of the bird in the current time step t , relative to its starting mass at $t = 0$. Using this information in conjunction with knowledge of associated activities such as flying to and from the foraging site (barrier effects of flying around the ORD are incorporated here), plus a knowledge of their own condition and whether or not their chick is alive, each adult then chooses the optimal behavioural strategy for this time step (`calc_strategy`). This dictates how many trips the adult will undertake in this time step and what behaviour the adults exhibit with respect to their chick (“feeding mode”, Table S1) such as leaving them unattended or abandoning due to constraints the adult is facing (Figure S8).

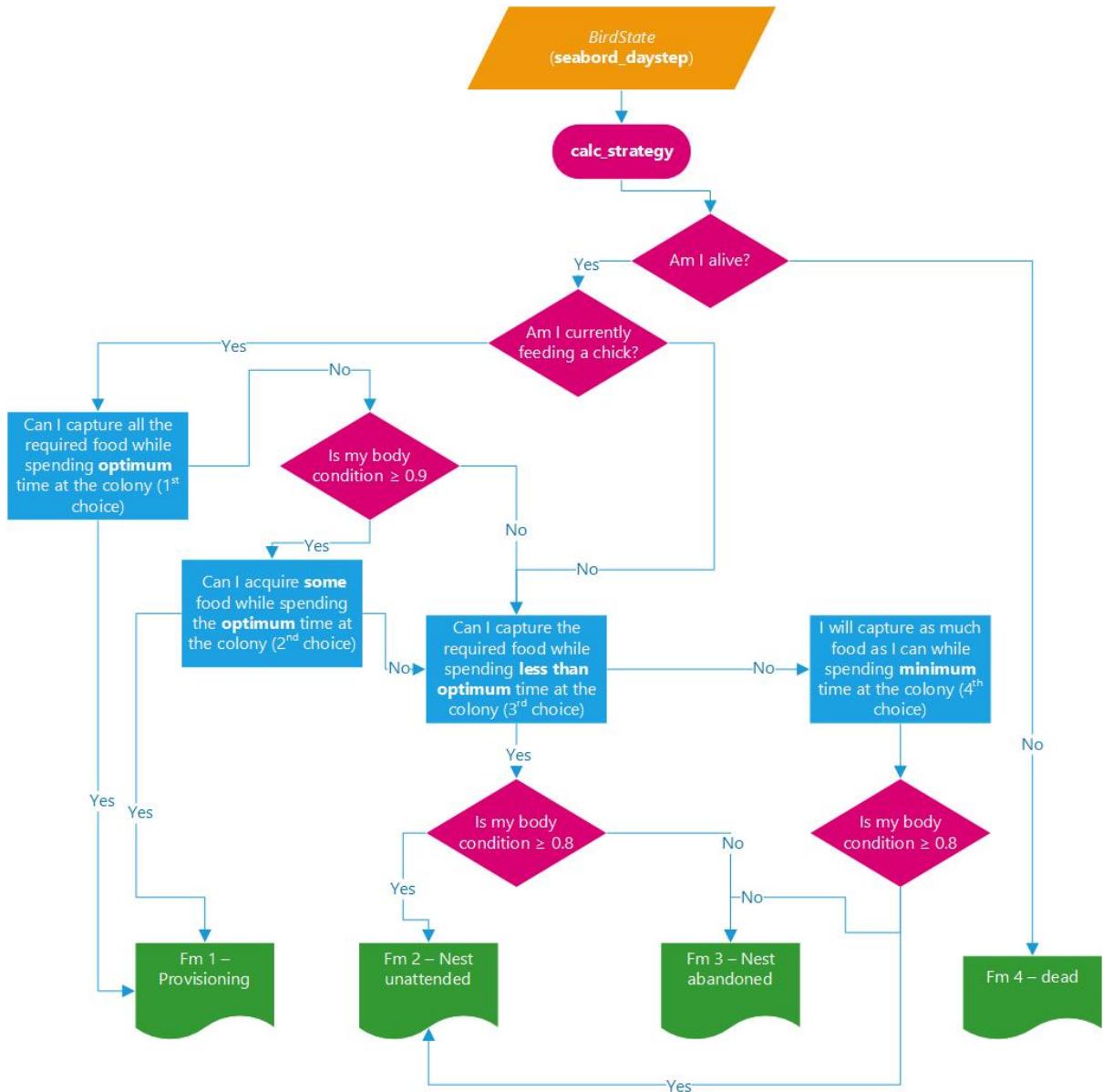


Figure S8: Schematic of `calc_strategy` function. Blue boxes are main actions, pink ovals represent function names, orange parallelograms indicate data inputs, pink diamonds indicate decisions, and green boxes represent the final behavioural strategy outcome of the function.

Behavioural (feeding) modes for adults were determined by a critical mass threshold below which the adult is assumed to defend its own survival over that of its chick, based on expert judgement because the lack of empirical data on these thresholds. Therefore, when an adult's body mass was greater than 90% of its starting body mass at the onset of chick-rearing it would avoid leaving its chick unattended, even if it had not met its DER. However, if its body mass was between 90% and 80% of its initial mass it would favour itself, and leave its chick unattended in order to attempt to achieve its required DER. There are no precise empirical data available to set these thresholds, therefore, in the model the thresholds were set based on similar logic to that used by Langton et al. (2014). Using guillemot as an example, the 90% threshold represents an average mass of around 820

g, which is well above the starvation mass (Golovkin, 1963) and about 2/3 of the difference in mean initial mass (920g) and the minimum mass recorded in UK ringing data (770g; Robinson 2005), the majority of which probably came from birds at breeding colonies (Langton et al. 2014). The 80% threshold corresponds to around 735 g in guillemots, which is below the minimum mass recorded in UK ringing data for this species, and, therefore, likely to represent a reasonable mass at which individuals give up the breeding attempt to minimise further mass loss and safeguard their own survival. Therefore, for all species, we set behavioural models to switch using the 90% and 80% thresholds of the individuals starting mass.

Adults with a body mass of less than 80% of their starting mass abandon the breeding attempt. This necessarily means that their partner also gives up the breeding attempt, resulting in chick death. Golovkin (1963) found that unfed guillemot adults had lost approximately 40% of their body mass at death, therefore, should an adult's body mass fall below that deemed critical for survival (60% of the average pre-breeding season adult body mass for each species; Golovkin 1963), the adult is assumed to have died and is removed from the simulation. This causes its partner to abandon the breeding attempt for the remainder of the simulation. A similar assumption is made for chicks, which are assumed to have died if their body mass falls below 60% of that for a hypothetical chick that has received its DER on each model time step up to the current time.

Number of trips

We select the number of trips per time step (for each species the chick-rearing period is divided into biologically relevant time steps - 24 hours for all species in this report except black-legged kittiwakes where the time step was 36 hours) that a bird undertakes by considering the possible outcomes that occur for each possible number of trips from one to six. An upper limit of six trips per time step was selected because the vast majority of empirical data on these species suggest that most individuals complete between two and four foraging trips per time step. Specifically, for each potential number of trips, r , we divide the daily energy requirements (DER; of both chick and adult) by r , and the numerically invert Equation 2 to determine the total amount of foraging time required to achieve this energy intake. We then calculate the total time required to be

$$\begin{aligned} & \text{Total time required for all } r \text{ trips on a day} \\ &= \text{Foraging time required to achieve } DER_r + \text{flying time required per trip} * r \end{aligned}$$

where the 'Foraging time required to achieve DER_r ' is dependent upon the number of trips (r) because of the link between foraging time at a location and decline in intake rate whilst foraging. We do this for all possible values of r . We then select the number of trips in one of two ways depending upon whether the bird is able to acquire its DER within the time available for foraging:

1. If the total time requirement is less than the total time available, for at least one possible value of r , then we select the number of trips to be the value that minimises the total time requirement required to achieve the DER;
2. If the total time requirement exceeds the total time available for all possible values of r then it is impossible for the bird to achieve their DER on this day. In this situation we select the value of r that leads to the greatest total prey intake by the bird (i.e., which minimises their shortfall in intake relative to the DER).

7.2 Consequences for chicks submodels

calc_chickcare

This function calculates the chick-mass growth rate according to how much food has been provided by both of its parents. Chick growth in relation to food provisioning has not been well estimated under field conditions. Therefore, we assume a simple linear function for daily mass change of chicks in relation to food provisioned by its parents. One of the parameters for this function ('P', below) is derived from an energetics study on the growth and physiology of kittiwake chicks (Gabrielsen et al., 1992). Given the lack of empirical data on the other study species, we used the value of P obtained from kittiwakes, and it is challenging to judge the implications of this decision. The second parameter ('G', below) is estimated from observations of chick mass change from hatching to fledging for each species (CEH unpublished data; Harris & Wanless, 2011). More specifically, we assume that

$$\text{Mass change} = G * (((\text{intake} / \text{DER}) - P) / (1 - P))$$

Where 'intake' is the actual amount of food provided to the chick, the parameter "G" represents the maximum possible mass gain (g) per day if the chick receives 100% of its DER, and the parameter "P" represents the proportion of the daily energy requirement (DER) for the chick that corresponds to zero mass change: i.e., to neither an increase nor a decrease in mass.

The resulting increase in body mass is calculated and compared to a corresponding optimum body mass for a chick at the given stage of the season (calc_chickcare), and if this falls below a defined threshold the chick starves (Figure S9).

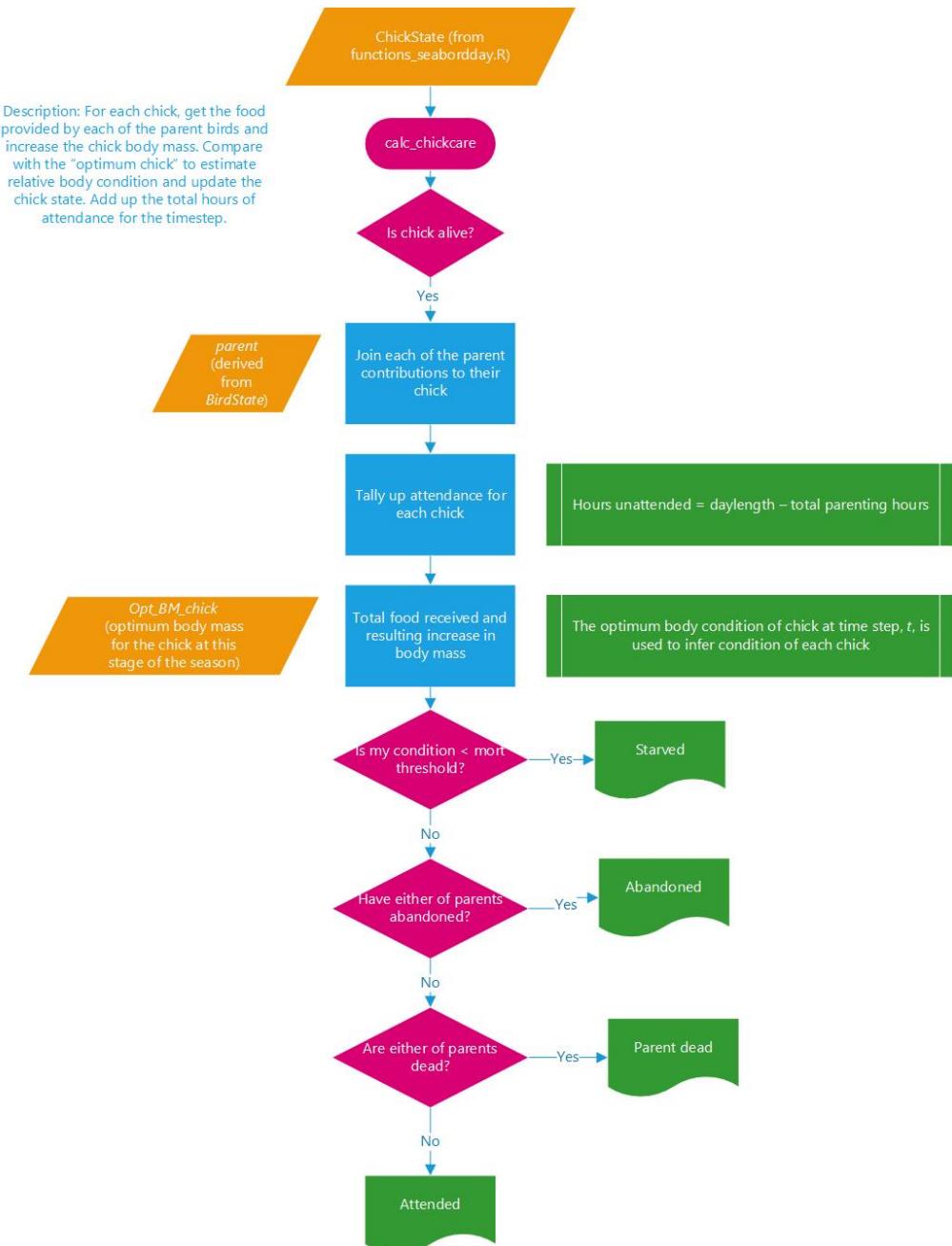


Figure S9: Schematic of calc_chickcare function. Blue boxes are main actions, green rectangles accompanying blue boxes are explanatory notes of these actions, pink ovals represent function names, orange parallelograms indicate data inputs, pink diamonds indicate decisions, and green boxes with a wavy bottom line represent the final outcome of the function for the chick in any given time step.

calc_unattendance

If the time a chick's parents spend attending the nest falls below a critical threshold the chick is assumed to die through exposure. This parameter ('unattendance_hrs') could not be set using

empirical data, therefore, we set it to be 18 hours for all species (except Atlantic puffins – see *calc_puffinmortality* below and Figure S6) based on expert judgement. If a chick suffers mortality its parents switch to ‘nest abandonment’ mode. We also incorporated an increased risk of predation if a chick was left unattended by both parents for an amount of time less than that which would result in its death through exposure. This was modelled as a probability of death that increased linearly with time left unattended, up until the time threshold was reached at which point the chick was assumed to have died from exposure or predation (*‘unattendance_hours’*).

calc_puffinmortality

For burrow-nesting puffins, once the chick reached a certain energy deficit (80% of the body mass of a chick that has been provisioned with all its requirements at every previous time step, using the same threshold employed for adults abandoning young, given the absence of empirical data) it was assumed the chick ventured to the entrance of the burrow and suffered a linearly increasing predation risk with its body mass deficit as a consequence (between 60% and 80%). Above the threshold body mass value of 80% there was no risk to the chick from being left unattended by parents. Below the lower threshold of 60% the chick was assumed to have died.

calc_othermortality

As chicks can be lost from other causes such as flooding, storms etc. this function takes that into account and calculates the probability of death per time step. This amounts to around ~5% of chicks dying in a run when conditions are optimal, and no other mortality is taking place from unattendance or starvation. This can be seen for higher prey values (>200) in Figure S4B where chick survival never reaches 100%.

7.3 Update adults submodels

calc_adultbmchange

In the model all adult birds update their body mass at the end of each day based on the energy they gained and expended in foraging and other activities. We used the published equation from Langton et al. (2014) to calculate the body mass of all adults at the end of each time step:

$$Mass_{t+1} = Mass_t + \frac{Energy_gained_t - DER_t}{K_G}$$

where $Mass_{t+1}$ is the body mass at the start of the next time step, $Mass_t$ is the body mass in the current time step, $Energy_gained_t$ is the energy the individual acquired during the current time step, DER_t is the daily energy requirement for the adult for the current time step, and K_G is the energy density of the bird’s tissue (kJ/g). Published values for the energy density of bird’s tissue are available for guillemots (Gabrielsen, 1996) and gannets (Montevecchi et al., 1984), both of which are close to 38.5 kJ/g; therefore for all species in the model we use this value.

calc_adultdee

This submodel calculates the energy expenditure in time step t for adult birds, based on the proportion of activities carried out during the time step multiplied by activity-specific energy costs available from the literature (see Table S4) and the cost of warming food derived from (Leedham et al., 2025) and (Gremillet et al., 2003).

Adult DEE

$$\begin{aligned} &= \text{energy}_{\text{nest}} * \text{propday}_{\text{colony}} + \text{energy}_{\text{flight}} * \text{propday}_{\text{flying}} + \text{energy}_{\text{forage}} * \text{propday}_{\text{forage}} \\ &+ \text{energy}_{\text{searest}} * \text{propday}_{\text{restingsea}} + \text{energy}_{\text{warming}} * (\text{daylength}/24) \end{aligned}$$

This is then converted to the energy requirement for the following time step, $t+1$ with the following equation:

$$\text{Energy required by adult} = \frac{\text{Adult DEE}}{\text{Assimilation efficiency}}$$

Activity costs

Foraging cost for each bird is defined by the energetic costs of foraging and the amount of time an individual is required to spend foraging to meet both its own DER and 50% of the DER of its offspring. On the first time step of the simulation, adult Daily Energy Expenditure (DER) was drawn from a normal distribution parameterised using the mean and standard deviation of adult DEE from empirical data on the study species ((Daunt et al., 2008) and references therein) divided by an assimilation efficiency (0.78, (Hilton et al., 2000a)). On all subsequent days adult DER was set to match the energy expended by each bird in the previous time step divided by assimilation efficiency. Chick DER (Table S4) remained constant throughout the simulation. We chose not to model increases in chick DER with growth in order to constrain model processing time to reasonable limits, but species-specific mean daily energy requirement of chicks was based on provisioning rates recorded at colonies for each species, from a sample of chicks of a range of ages, so we do not think this simplification in the model would have had a large bearing on the results. This calculation implies both parents share the costs of provisioning equally.

Empirical daily time budgets of birds during chick-rearing demonstrate that adults divide their activities into four categories of behaviour - foraging, flight, time spent at the colony, and time spent resting on the sea surface (Daunt et al., 2002). For each bird, the foraging model returns the simulated flight time for each bird spent travelling to its chosen foraging location, and the simulated foraging time required to meet its required DER. The remaining time during each model time period is split into time spent at the colony and time spent resting at sea. A minimum of one hour spent resting at sea was required for each bird (Daunt et al., 2002), and each bird attempted to spend half

of each time step at the colony thereby preventing the chick being left unattended at the nest. Any remaining time was split evenly between time at the colony and time resting at sea. If a bird could not meet its DER in the time available without leaving its nest unattended, a set of decision rules were implemented based on the energy state of the adult (Figure S8).

We derived the flight cost incurred by each bird by calculating the time taken to travel the distance both to and from the chosen foraging location assuming a mean flight speed for each species (Pennycuick, 1997), upscaled to match the chosen number of trips per time step.

We then multiplied the time spent carrying out each of these activities by species- and activity-specific energy costs available from the literature (i.e. cost of flight, foraging, resting at and time at colony). In addition, we incorporated the energy cost of warming food to derive the total DER for each bird (Gremillet et al., 2003). These DER were converted into grams per day assuming a mean energy density of 6.1 kJg⁻¹ (Harris et al., 2008).

7.4 Adult survival submodel

Calc_pSurvival

The mass of each leaving adult (g) at the end of the breeding season provides an indirect way of quantifying the adult survival rate during the subsequent winter period. We used published relationships between adult mass and annual survival rates in order to convert simulated adult mass values into estimated survival rates. This is done in the same way for baseline simulations and for simulations that have been generated in the presence of ORDs such that we may assess the impact of the ORD upon the adult survival rate by contrasting the paired model runs.

The procedure for converting individual adult mass values into an overall estimate of adult survival for each simulation run is summarised here. Our approach is essentially based previously published studies (Erikstad et al., 2009; Oro & Furness, 2002) where the general assumption is that mass and survival are linked via a logistic regression – i.e. through the equation:

$$\log\left(\frac{p_i}{1-p_i}\right) = \log\left(\frac{s_0}{1-s_0}\right) + bm_i$$

where m_i denotes the standardized mass of individual i and p_i denotes the (annual winter) survival probability of this individual. The value of b quantifies the strength of the relationship between mass and survival, and the value of s_0 denotes the ‘baseline’ survival (i.e., the survival rate that would be associated with a bird of average mass in the absence of an ORD). The overall survival rate for a simulation run, P is simply assumed to be the average (mean) of the survival probabilities for all of the individuals within it, so that

$$P = \frac{1}{n} \sum_{i=1}^n p_i$$

(where n denotes the total number of individuals).

The validity of this approach will depend primarily upon the validity of the values that are selected for b and s_0 . It is worth noting that the approach also makes one substantive assumption - that the relationship between mass and survival is linear, on a logit-transformed scale - but it would be impossible in practice to check the validity of this assumption using currently available information.

The value of the baseline survival, s_0 , is assumed to vary between species - the specific values are based upon the results of the population modelling performed by CEH for Marine Scotland (Freeman et al. 2014).

Table S8: Baseline survival probabilities for birds under baseline conditions (no ORDs present) with poor, moderate and good prey availability (Freeman et al. 2014). The level of prey availability is determined by the percentage mass loss of adults birds over the chick-rearing season.

	Poor	Moderate	Good
Kittiwake	0.65	0.80	0.90
Puffin	0.85	0.90	0.95
Guillemot	0.82	0.92	0.94
Razorbill	0.80	0.90	0.95

The strength of the relationship between mass and survival, b , is determined using values given in the published literature. For kittiwakes the value of b is based on the value given in Oro & Furness (Oro & Furness, 2002), and for all other species it is based on the value given in Erikstad et al. (Erikstad et al., 2009), published values do not exist for razorbill or guillemot, so we assume that they have the same value as that estimated for puffin in the Erikstad et al. (Erikstad et al., 2009) paper. The kittiwake study was undertaken on a population in Shetland experiencing low food abundance, and the puffin study was based on a population in northern Norway. Both populations may have differed in terms of adult body mass and relationships between condition and survival from populations in the Forth/Tay region. Furthermore, mass/survival relationships in guillemots and razorbills may differ from puffins. The actual estimated values for b are 1.03 (Erikstad et al., 2009) and 0.038 (Oro & Furness, 2002), but it is important to note that these values cannot be directly compared because they relate to mass values that are expressed on direct scales: for kittiwakes the mass is standardised solely by deducting the mean mass under the baseline scenario (because the paper by Oro & Furness 2002 expresses b in grams), whereas for other species the standardisation

also involves dividing by the standard deviation under the baseline scenario (because Erikstad et al., 2009, expresses mass as a unit-free quantity).

7.5 ORD effects on individuals

Two main behavioural responses to ORDs are simulated in the model: displacement and barrier effects (Figure S3).

At the start of each simulation run, individuals can be assigned as either birds that would be displaced if their foraging location fell within the ORD footprint ('displacement-susceptible birds'), and/or as birds that would choose to fly around the ORD footprint ('barrier-susceptible birds') if their chosen foraging location lay on the far side of a wind farm. These values were fixed for the lifetime of each bird meaning that no habituation to wind farms occurred. The proportion of birds that were assigned by the user to be displacement-susceptible and barrier-susceptible depended upon the species and scenario.

In the model the user specifies the width of an exclusion 'buffer' zone to be added to the ORD footprint supplied by the user as a shapefile. This buffer zone represents the area around an ORD footprint into which displacement or barrier susceptible birds will not enter due to assumed disturbance effects. If a displacement-susceptible bird chooses a foraging location within the ORD footprint plus the exclusion 'buffer' area (solid & dashed line, Figure S3) then it instead chooses a new foraging location within a 5 km displacement zone (dotted line, Figure S3) of the ORD footprint plus the selected buffer zone. This distance was chosen by the steering group of the previous project (Searle et al. 2014) based on expert judgement and carried forward into this project. The precise foraging location in the 5 km buffer is selected with a probability proportional to the prey availability in the buffer zone. Displacement-susceptible birds only incur an additional travel cost if their new foraging location in the buffer zone lies on the far side of the ORD from their source colony. Should their new foraging location lie on the nearside of the ORD in relation to the source colony, it is assumed that no additional travel cost is incurred as a result of displacement and that the bird flies directly to the new location using the shortest route. We did not impose an additional travel cost for these birds because we assume that over the course of the breeding season birds will have determined the location of the ORD and, therefore, fly directly to the location displaced to.

Additional travel costs are incurred as a result of barrier effects if its chosen foraging location lies on the far side of the ORD relative to the colony. The barrier affected bird takes the shortest route to the new foraging location whilst navigating around the edge of the ORD footprint-plus-buffer. This is calculated using the R package 'gdistance' (van Etten, 2017). We chose this flight path as it corresponds to the assumption that birds know the location of the ORD and adjust their flight path

to minimise travel costs. This implies that birds have spatial memory for the position of the ORD as well as spatial memory for a pre-determined foraging location selected before leaving the colony. All birds that navigate around a coastline use this pathfinding routine to identify the shortest route around land.

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Supplementary material section 2

1. Method for deriving maps from GPS tracking data

Where possible, we recommend using GPS tracking data to create colony-specific bird distribution maps, in order to account for the effects of environmental heterogeneity and competition. Spatial models can be used to estimate spatial distributions from tracking data.

Within the SeabORD runs used in this paper we use the maps generated as part of the SEANSE project (Searle et al., 2020) by modelling GPS tracking data from 2010 to 2018 for colonies in the Forth-Tay region – further context and details can be found within that report.

Wakefield et al. (2017) fitted habitat association models to a large multi-colony GPS tracking dataset, collected within the FAME and STAR projects, by using a Binomial Generalized Linear Model (GLM) to model “cases” (GPS tracking point) versus “controls” (points on a regular grid) in relation to a range of potential explanatory variables relating to accessibility (e.g. distance to colony), parapatric (inter-colony) competition effects and environmental suitability (e.g. sea surface temperature, chlorophyll). Model selection was applied in two stages, in order to account for the effects of parapatric competition: (1) fitting models that included only effects of accessibility (e.g. distance to colony by sea) as explanatory variables and using these to calculate an index of parapatric competition; and then (2) fitting models that also included variables relating to environmental suitability and the parapatric competition index as potential explanatory variables. Final models for each species were then used to generate predicted maps of spatial distributions for each colony

(rescaled so that the maps sum to one), including both colonies with GPS tracking data and those without.

The maps produced for SEANSE used a similar approach to Wakefield et al. (2017), but whilst the focus of Wakefield et al. (2017) was on the production of national-scale maps (including a large number of colonies without GPS tracking data) the SEANSE project was focused on a specific area with good coverage, in which colony-specific GPS tracking data were available for the key colonies of interest. Rather than explaining environmental heterogeneity in terms of explanatory variables (such as sea surface temperature) SEANSE therefore instead focused solely upon providing an empirical map of environmental heterogeneity. The second stage of modelling for SEANSE therefore used a Generalized Additive Model (GAM) rather than GLM, which contained the explanatory variables for accessibility and competition considered in Wakefield et al (2017) and a smooth spatial term for “location” (in place of explanatory variables that aim to describe environmental suitability). This semi-parametric approach assumes that the maps vary smoothly with location but imposes no other constraints upon the form (shape) of the relationship between bird density and environment, in contrast to the parametric habitat association model used in Wakefield et al. (2017). The degree of smoothing is determined automatically via a form of cross-validation; the model uses a fixed effect for “colony” to adjust for overall differences in abundance between colonies. The models were fitted in R using the ‘bam’ function within the ‘mgcv’ package (Wood, 2001), using a regular grid with a spatial resolution of 1x1 km. For further information on the modelling approach used in SEANSE, and how it relates to Wakefield et al. (2017), please see Appendix A of Searle et al. (2020).

1.1 Method for deriving distance decay maps

Where there is limited or no tracking data available, we recommend creating bird distribution maps using a simple distance-decay relationship. In this case, users provide parameters that are used to create a bird density map associated with a simple distance-decay function.

The distance-decay model used within SeabORD assumes that the proportion of time that birds from the colony of interest spend within each grid cell (the utilisation distribution) is proportional to $\exp(-\beta d)/d$, where d represents the distance (in a straight line along a great circle) from the colony of interest to the midpoint of this grid cell. The values of the distribution are normalised so that they sum to one across all grid cells. The parameter β determines the rate of distance decay.

This model is motivated by two assumptions:

1. That the *total* number of birds within each distance band decays exponentially with distance - i.e., that the total number of birds that lie at distance d from the colony is proportional to

$\exp(-\beta d)$. The exponential decay model is not the only possible model for decay with distance but is a widely used model and has the advantages of (a) only containing a single unknown parameter and (b) having a finite value at a distance of zero.

2. That birds within this distance band are distributed uniformly throughout the band, which seems a reasonable assumption in the absence of any other information. The division by distance within the model ($1/d$) then follows directly from geometric considerations: there are fewer grid cells within distance bands close to the colony than within distance bands far from the colony, with the circumference of each distance band being equal to $2\pi d$. The normalisation step renders the constant, 2π , irrelevant. If birds were equally likely to visit each distance band the density of birds in space would therefore decay with distance at a rate $1/d$, but since the overall probability of being within each distance band is $\exp(-\beta d)$ the density of birds in space is instead proportional to $\exp(-\beta d)/d$.

If the parameter β were taken to be equal to zero then the model would assume that birds are uniformly distributed across distance to colony, so that the density decays with distance solely due to geometric considerations. If the parameter β is taken to be large, then the model assumes a very rapid decay of density with distance: far more rapid than would be explained by geometry alone.

1.1.1 User specification of the parameters for distance-decay

Users specify the foraging range, and a parameter that controls the rate of decays with distance within the distance decay model. The exponential decay parameter β does not have a straightforward ecological interpretation, so may not be a parameter that users can readily specify based on expert judgement.

Users therefore instead provide a parameter q that specifies the proportion q of the foraging range that (in an idealised situation without land) contains half the population, on the basis that this is more ecologically interpretable than β and so will be easier to specify based on expert judgement. If this proportion is equal to 0.5 then it implies that the number of birds is the same in every distance band out to the foraging range (so that the decline in bird density is solely because of the increasing area covered by each distance band). If this proportion is close to zero then it implies, in contrast, that the distribution is heavily concentrated towards the colony.

The value of the parameter q can be converted into the parameter β by using standard numerical optimisation (implemented in R via the `optimise` function) to identify the value of β such that

$$\frac{\text{Probability of distance from colony being less than } rq}{\text{Probability of distance from colony being less than } r} = \frac{1 - \exp(-\beta rq)}{1 - \exp(-\beta r)} = \frac{1}{2}$$

Note that previous versions of SeabORD (Searle et al. 2014, 2018) used an alternative parameterisation, which relied on the user defining the proportion of the total distribution that lies within the foraging range, but the current approach has been adopted following user feedback on the basis that it involves users specifying a parameter that has a clearer ecological interpretation, and so may be easier to specify based on expert judgement.

2. Method for simulating competition within SeabORD

We provide mathematical details around the simulation of the number of competing birds, from all colonies except the colony of interest, for each grid cell at each time point. The number of competing birds from the colony of interest is simulated directly within SeabORD and is added on to the number of birds simulated to arise from other colonies.

2.2.1 User-defined inputs relevant to calculation of competition

Users provide a competition map representing the number of individuals per grid cell from all colonies other than the colony of interest, from which it is possible to extract:

- the number of grid cells n :
- T : the total abundance of birds from all non-focal colonies (i.e., the sum of the competition map)
- (u_1, \dots, u_n) : the normalized competition map i.e., the probability of birds from non-focal colonies being in grid cell $j = 1, \dots, n$ at any given time step. This is calculated by dividing the competition map by T .

Users also specify:

- the displacement rate, d , which represents the proportion of individuals that are susceptible to displacement by windfarm
- windfarm polygons, which can be used to define a binary variable λ_j that indicates for each cell j whether the cell lies within any wind farm
- the width of buffer and displacement zone, which can be used, in conjunction with the windfarm polygons, to construct a binary variable θ_{jk} for each pair of grid cells j and k . This binary variable indicates whether birds foraging in grid cell j have the potential to be displaced to grid cell k or not: this will be equal to one if grid cell j is within a wind farm and grid cell k is in the area surrounding the same wind farm into which birds from that wind farm are displaced (the “displacement zone”), and zero for all other pairs of grid cells.

2.2.2 Simulation of number of non-focal colony birds foraging in each grid cell in the baseline

The total number of birds B_{ij} from non-focal colonies that are simulated to forage in each of the $j = 1, \dots, n$ grid cells at each timestep t under the baseline (i.e. without windfarms) can be simulated

using an independent multinomial simulation for each time step, using the colony size as the multinomial size and the normalized competition map as the multinomial probability, so that:

$$(B_{t1}, \dots, B_{tn}) \sim \text{Multinomial}(T, (u_1, \dots, u_n))$$

2.2.3 Simulation of number of non-focal colony birds foraging in each grid cell with a windfarm

We can simulate the number of birds that are displaced away from grid cell j at a particular time point t via a binomial simulation

$$M_{jt} \sim \text{Binomial}(B_{jt}, \lambda_j d)$$

which will always be zero for grid cells not in a windfarm ($\lambda_j = 0$).

The probability that a bird which was displaced away from foraging in grid cell j will choose to forage in grid cell k can be calculated as

$$q_{jk} = \frac{\theta_{jk} u_k}{\sum_{l=1}^n \theta_{jl} u_l}$$

which represents the part of the competition map (rescaled to sum to one) that lies in the area that birds are displaced into from the wind farm containing grid cell j . The number of displaced birds D_{jkt} that are simulated to move from grid cell j to grid cell k at time step t is simulated via a multinomial distribution that determines the destinations of the displaced birds originating from each grid cell j :

$$(D_{j1t}, \dots, D_{jnt}) \sim \text{Multinomial}(M_{jt}, (q_{j1}, \dots, q_{jn}))$$

In practice, this only needs to be calculated for pairs of grid cells in which cell j lies in a wind farm and cell k lies in the displacement zone for the wind farm associated with grid cell j , because values will be zero by definition for all other grid cells.

Finally, we can calculate B_{jt}^* , which we define to be the number of birds from this colony foraging in this grid cell at this time step over once one or more wind farms have been introduced, to be:

$$B_{jt}^* = B_{jt} + \sum_{k=1}^n (D_{kjt} - D_{jkt})$$

i.e., to be the number of birds that were foraging at this grid cell in this baseline, plus the number of birds moving into this grid cell from the wind farm (non-zero only for grid cells in the displacement zone around a wind farm into which displacement occurs), minus the number of birds moving away from this grid cell (non-zero only for grid cells in a wind farm or buffer).

3. Extended sensitivity analysis results

Table S9: Resulting calibrated prey ranges, where possible, for all parameter variations used in the sensitivity analysis

Parameter name	Description	New parameter value	Calibration indicating new prey range?	Prey range
default	The prey range for default parameter set	NA	NA	170.5 - 172.5
adult_mass_KG	Energy density of the bird's tissue (kJ g ⁻¹)	34.65	yes	171.5 - 174
		36.575	yes	171 - 173
		40.425	yes	169.5 - 171.5
		42.35	yes	169-171
BM_adult_abdn	Critical mass below which adult abandons chick	0.72	not possible	NA
		0.76	just	168.5 - 169.5
		0.84	not possible	NA
		0.88	not possible	NA
BM_Chick_mortf	Critical mass below which chick is dead	0.54	yes	170.5 - 172.5
		0.57	no	170.5 - 172.5
		0.63	no	170.5 - 172.5
		0.66	no	170.5 - 172.5
unattend_max_hrs	Critical time threshold for unattendance at nest above which a chick is assumed to die through exposure or predation	16.2	yes	171 - 173
		17.1	no	170.5 - 172.5
		18.9	yes	170-172
		19.8	yes	170-172
IR_half_b	Competition effect on intake rate parameter	0.005	yes	167 - 168.5
		0.01	yes	168 - 169.5
		0.04	yes	176 - 177.5
		0.08	yes	189 - 191
Displacement zone extent	How far the displacement zone buffer extends (km)	1	not required	170.5 - 172.5
		2.5	not required	170.5 - 172.5
		10	not required	170.5 - 172.5
		20	not required	170.5 - 172.5

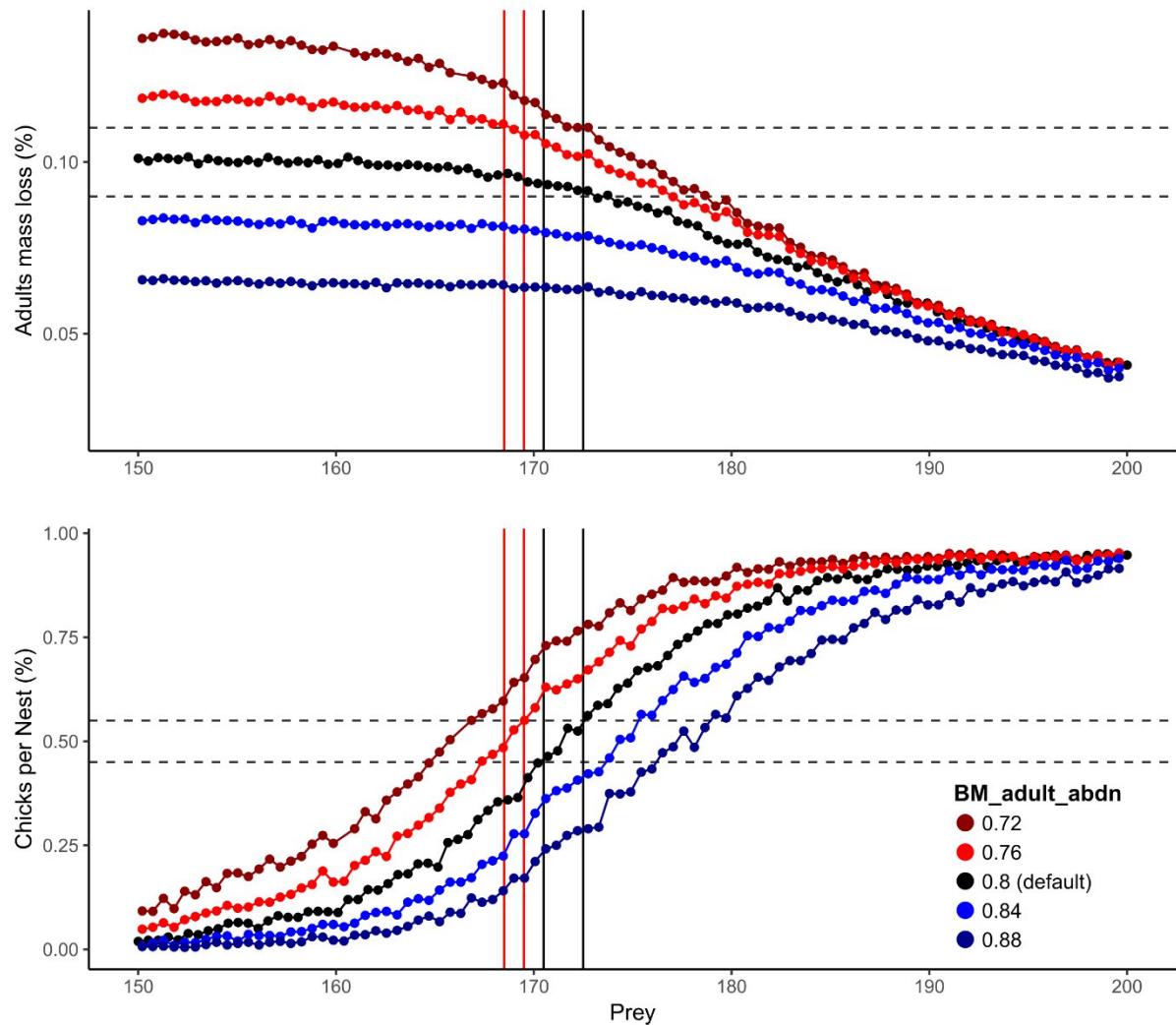


Figure S10: Calibration plots showing 90 baseline simulations with varying prey values for each **BM_adult_abdn** parameter variation used in the sensitivity analysis, including the default values in black, dark red 0.72 (-10%), light red 0.76 (-5%), light blue 0.84 (+5%), and dark blue 0.88 (+10%). Upper and lower horizontal dashed lines indicate the range for moderate conditions for respective outputs, adult mass loss and chicks per nest. Vertical solid lines indicate any shared overlap across these two outputs, with colours respective to parameter variations - i.e., there was only overlap for the default parameter value and 0.76 (-5%).

4. Extended modelling of cumulative effects

4.1 Introduction

One advantage of IBMs is that you can start to examine how complex behaviours accumulate and reflect in emergent properties at the population level. In the context of SeabORD, there is nothing in the model that explicitly tells demographic rates how they should change in relation to a barrier or displacement effect, whether relating to one or several wind farms within their modelled foraging distribution.

A simplifying assumption often seen in cumulative impact assessments is that the impacts are additive, but it is accepted that it may contradicted by varying behaviour of individuals towards developments, resulting in sublethal effects that are likely to be non-linear and possess threshold characteristics (Masdene et al., 2010) driven by behaviour seen in long-lived seabird where adults favour their own survival over that of their chick. We explore this further in our paper by using our IBM, SeabORD, to model extensive hypothetical ORD arrays to predict how increasing cumulative effects on populations of two seabird species, common guillemot *Uria aalge* and black-legged kittiwake (hereafter “guillemot” and “kittiwake”, respectively), breeding at the Isle of May NNR, in eastern Scotland, drive predicted changes in breeding success and adult survival during the chick-rearing period.

4.2 Methods

In addition to assessing our three output metrics (ORD adult mass change, adult year-round survival and breeding success) against number of ORDs in the main report, we also investigated three response variables used to assess the magnitude of cumulative effects:

- (i) Energetic cost of extra km flown due to barrier effects
- (ii) Proportion of individuals displaced per time step
- (iii) Expected total number of additional pairwise competition events occurring per grid cell per time step in the displacement zone as a result of the windfarm

These variables were calculated for each ORD scenario ($n = 63$) and species ($n = 2$) combination (total $n = 126$). Variable (i) was achieved by estimating the time taken to fly the model output ‘total extra km flown’, which is the extra distance flown through experiencing barrier effects, and then multiplying this by the kJ/sec cost of flight (Leedham et al., 2025), while (ii) was extracted directly from model outputs, and is a proxy for displacement effects. Variable (iii) can be calculated from model inputs by multiplying together:

- (a) the number of grid cells in the displacement zone;
- (b) the expected number of adults foraging within each grid cell of the displacement zone in the baseline, which is equal to the population for the focal colony (i.e. total number of adults being simulated) multiplied by the proportion of the bird map's UD cells contained within the displacement zone(s) of the ORD(s), divided by the number of grid cells in the displacement zone; and
- (c) the expected number of adults displaced into each grid cell within the displacement zone as a result of the windfarm, which is equal to the population size of the focal colony multiplied by the proportion of the bird map contained by the ORD footprint(s) and their 2km buffers and the proportion of individuals susceptible to displacement (the displacement rate, set at 60% for all simulations), and then divided by the number of grid cells in the displacement zone.

4.3 Results & discussion

Table S10: The mean effect of different numbers of ORDs on key model outputs with minimum and maximum outputs where relevant (n>1).

Species	Output	Number of ORDs						
		0 (baseline, n=63)	1 (n=6)	2 (n=15)	3 (n=20)	4 (n=15)	5 (n=6)	6 (n=1)
Kittiwake	Adult mass loss (g)	34.22 (34.21, 34.23)	34.32 (34.26, 34.38)	34.44 (34.31, 34.58)	34.57 (34.40, 34.72)	34.72 (34.51, 34.84)	34.87 (34.77, 34.94)	35.03
	Adult survival	0.743 (0.742, 0.745)	0.743 (0.742, 0.744)	0.743 (0.741, 0.744)	0.742 (0.741, 0.743)	0.741 (0.739, 0.742)	0.741 (0.740, 0.741)	0.740
	Chicks per nest	0.538 (0.536, 0.539)	0.529 (0.524, 0.534)	0.519 (0.506, 0.530)	0.506 (0.494, 0.524)	0.492 (0.479, 0.514)	0.476 (0.466, 0.489)	0.457
Guillemot	Adult mass loss (g)	60.51 (60.50, 60.52)	60.81 (60.43, 61.32)	61.20 (60.40, 62.27)	61.68 (60.59, 63.46)	62.22 (61.00, 63.71)	62.89 (62.06, 63.69)	63.66
	Adult survival	0.888 (0.888, 0.888)	0.888 (0.887, 0.888)	0.887 (0.885, 0.888)	0.886 (0.884, 0.888)	0.886 (0.883, 0.887)	0.885 (0.883, 0.886)	0.884
	Chicks per nest	0.830 (0.829, 0.830)	0.826 (0.820, 0.831)	0.822 (0.810, 0.830)	0.816 (0.794, 0.828)	0.809 (0.790, 0.823)	0.801 (0.790, 0.812)	0.79

Table S11: R-squared and Delta-AIC values (i.e. AIC values relative to the model with lowest AIC) for the alternative linear and quadratic models considered for the mean value of each response variable on birds from the scenario (ORDs included) runs only. An asterisk indicates when one of the paired models (linear versus quadratic) received considerably more support in the data compared to the alternative model (delta AIC (Δ AIC) values >2).

Response variable	Model structure	Kittiwake		guillemot	
		R-squared	Δ AIC	R-squared	Δ AIC
Adult mass lost	Cost of extra km flown	91.9	0	94.2	0
	Cost of extra km flown + Cost of extra km flown ²	91.9	1.91	94.4	0.64
	Proportion displaced per tstep	94	0.76	77.6	5.43
	Proportion displaced per tstep + Proportion displaced per tstep ²	94.2	0	80.2	0*
	Number competition events	78.2	0	63	0.03
	Number competition events + Number competition events ²	78.2	1.99	64.1	0
Adult survival	Cost of extra km flown	60.8	0.54	94.3	0
	Cost of extra km flown + Cost of extra km flown ²	62.4	0	94.4	1.47
	Proportion displaced per tstep	67.9	0	72.8	7.04
	Proportion displaced per tstep + Proportion displaced per tstep ²	68.7	0.33	76.4	0*
	Number competition events	54.5	0	58.4	0.93
	Number competition events + Number competition events ²	55.2	0.92	60.3	0
Chicks per nest	Cost of extra km flown	92.2	2.5	93.7	0
	Cost of extra km flown + Cost of extra km flown ²	92.7	0*	93.7	1.8
	Proportion displaced per tstep	93.7	12.33	77.4	9.29
	Proportion displaced per tstep + Proportion displaced per tstep ²	95	0*	81.1	0*
	Number competition events	77.3	0	60	0.94
	Number competition events + Number competition events ²	77.6	1.32	61.8	0

Adult mass loss appeared to increase in an approximately linear fashion with mean energetic cost of extra km flown in simulations including ORDs for both kittiwakes and guillemots (Table S11, Figure S11 A & B), which represents the energetic cost when experiencing barrier effects occurring as a

result of ORD interactions. The mean total extra km flown for adults due to barrier effects when including all six ORDs was ~120km, compared to guillemots which flew ~38km further for their configuration, but the energy cost between species was comparable (Figure S11 A & B), attributed to the difference in flight costs and speeds between the two. Increases in adult mass loss also appeared approximately linear for kittiwakes in relation to the proportion of birds being displaced per time step (Figure S12 A), whilst for guillemot there was some evidence for a quadratic rather than linear effect (Table S11). When comparing adult mass loss against the estimated number of competition events, the linear model was the best supported for both species (Figure S13 A & B, Table S11) and adult survival generally decreases with increasing exposure to ORDs. This was also reflected in the models that were supported, with all linear models receiving greater support in the data, apart from the proportion of birds displaced per time step where the model including the quadratic term again received the greater support ($R^2 = 76.4\%$, $\Delta AIC = 7.04$, Table S11).

Chicks per nest showed consistent declines in relation to increasing ORD interactions. For mean energetic cost of extra km flown, the model including the quadratic term was the best supported for kittiwakes ($R^2 = 92.7\%$, $\Delta AIC = 2.5$, Table S11) indicating that as barrier effects increased the decline in chicks per nest also increased (Figure S11 E). Whereas, for guillemots, this decline was linear ($R^2 = 93.7\%$, $\Delta AIC = 1.8$, Table 3, Figure S11 F). The decrease in chicks per nest against the proportion of birds displaced per time step was nonlinear for both kittiwakes and guillemots (Table S11, Figure S12 E & F). In response to the estimated number of competition events, chicks per nest decreased in an apparently linear fashion for both kittiwakes and guillemots (Table S11), but for guillemots the explanatory power of the model was relatively low ($R^2 = 60\%$), (Figure S13 E & F).

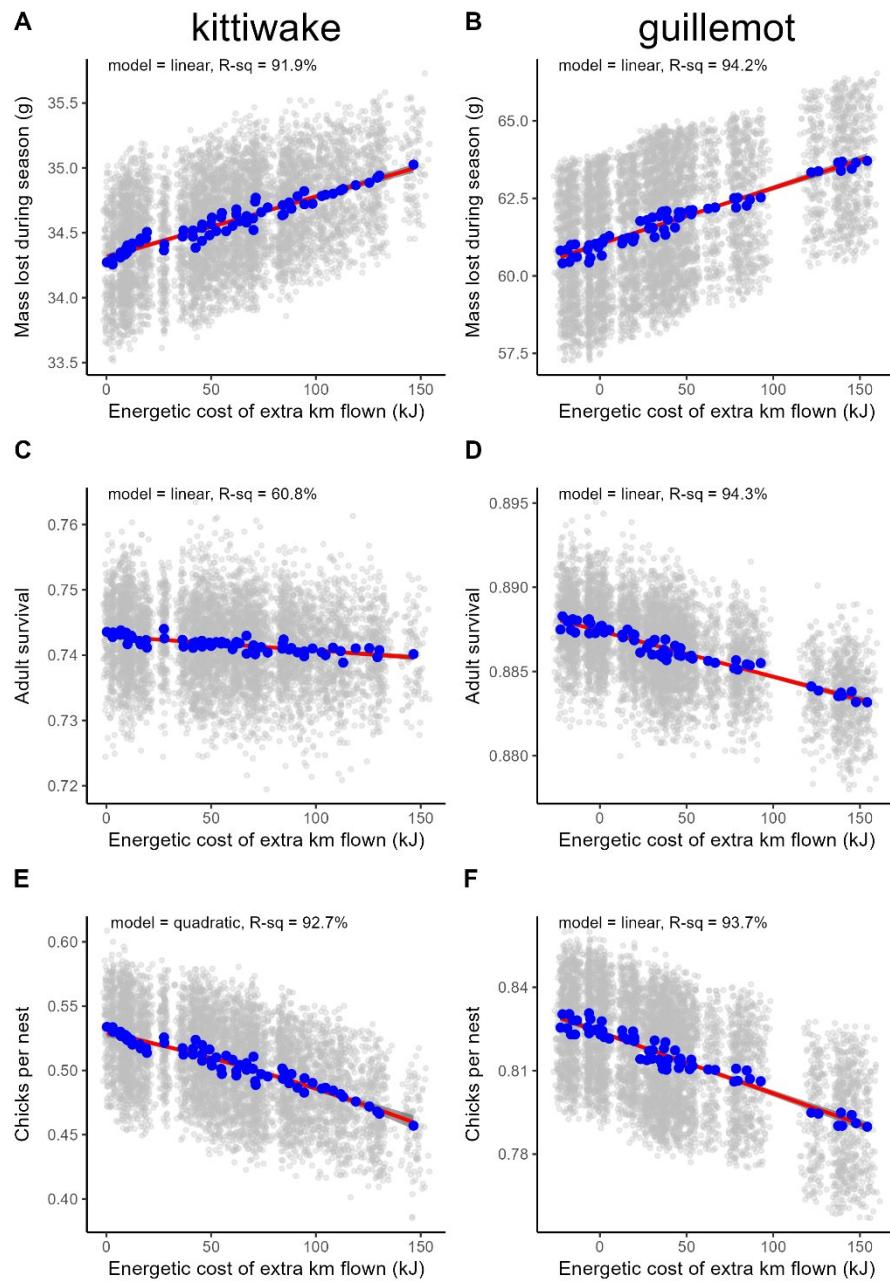


Figure S11: Mean energetic cost of extra km flown (kJ), experienced as consequence of barrier effects, plotted against three primary SeabORD outputs from scenario birds only (no baseline included) for the two modelled species. In each plot (A-F), the blue points represent the modelled means of the 63 different ORD scenarios, with the spread of each point's respective 100 replicates (not modelled) shown in grey. The red line and 95% confidence intervals represent the most supported model which is alluded to at the top of respective plots.

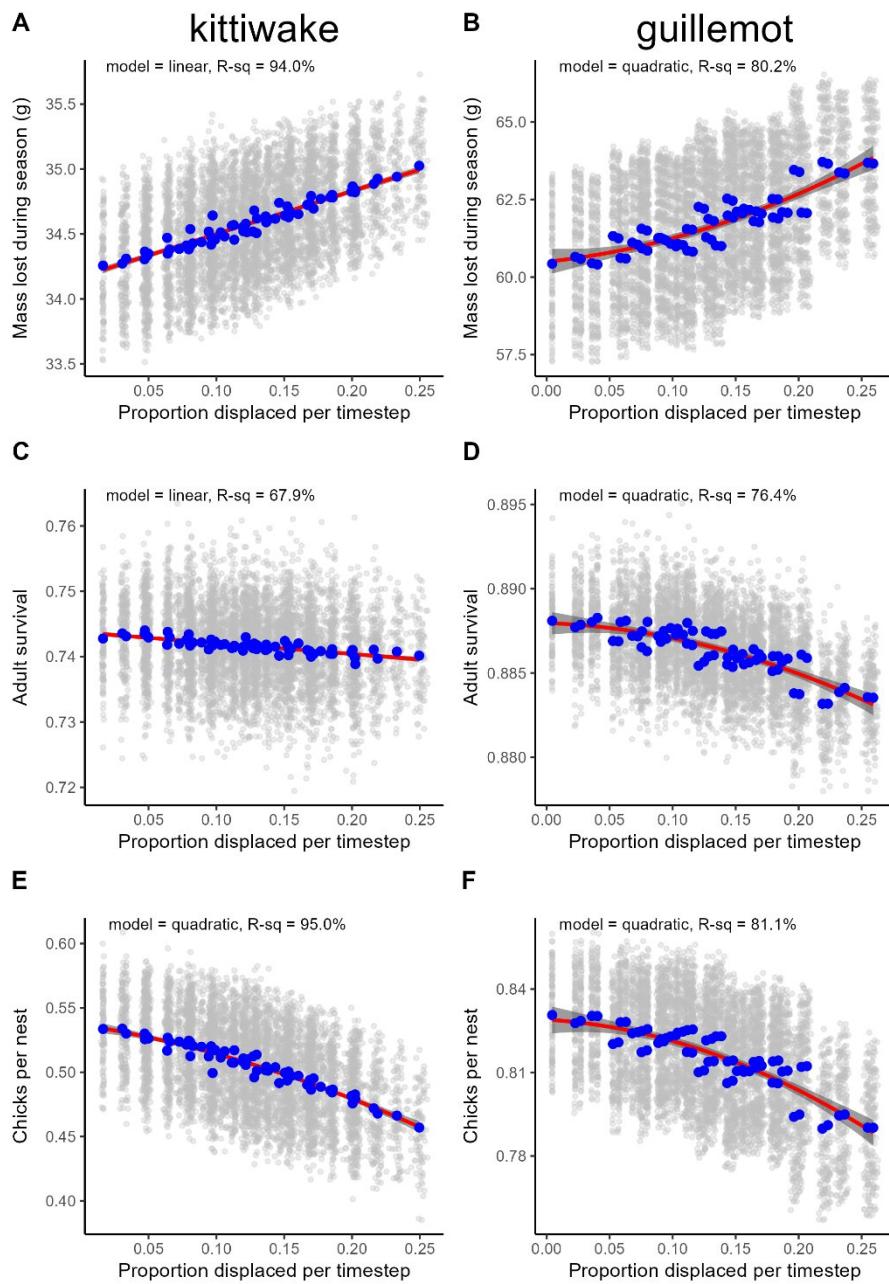


Figure S12: Proportion displaced per time step plotted against three primary SeabORD outputs from scenario birds only (no baseline included) for the two modelled species. In each plot (A-F), the blue points represent the modelled means of the 63 different ORD scenarios, with the spread of each point's respective 100 replicates (not modelled) shown in grey. The red line and 95% confidence intervals represent the most supported model which is alluded to at the top of respective plots.

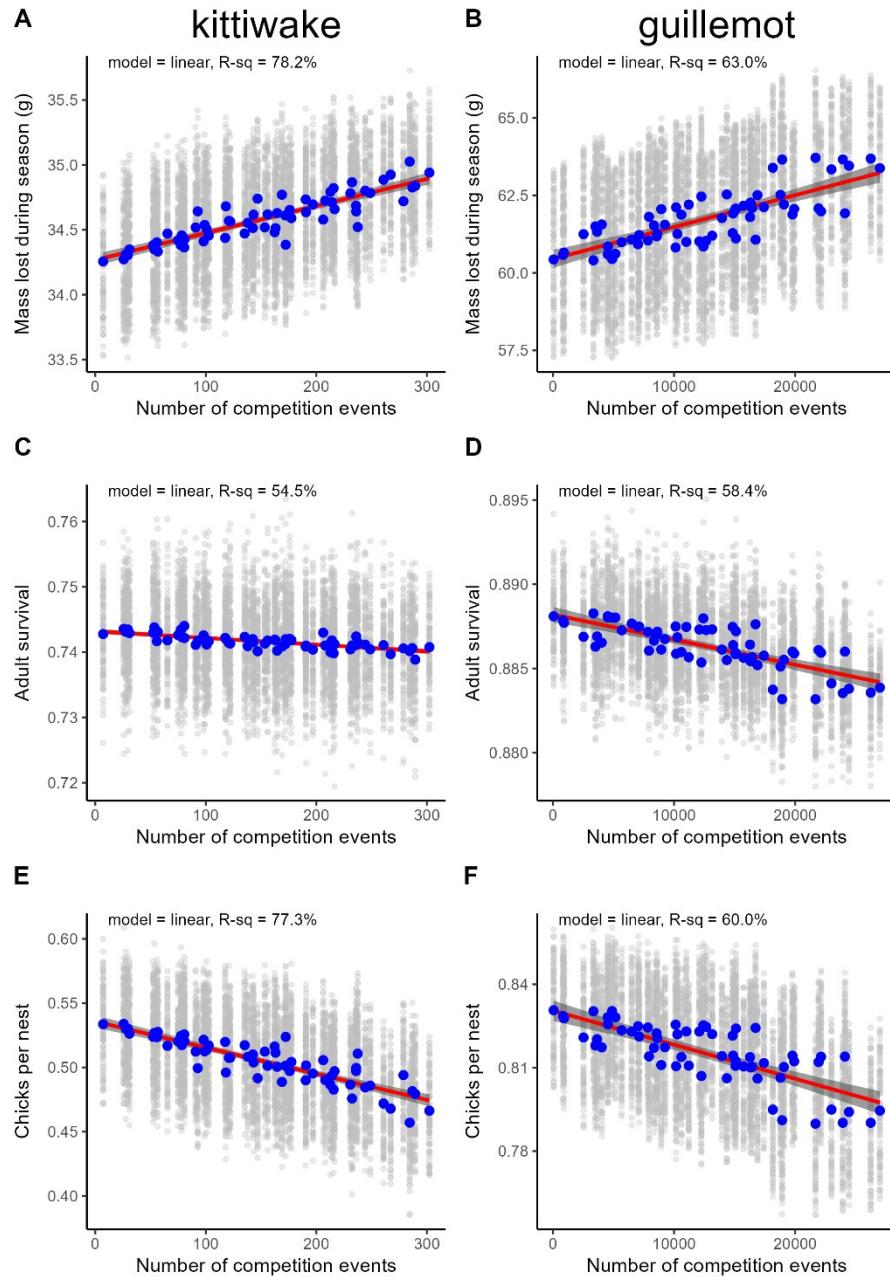


Figure S13: The estimated number of competition events plotted against three primary SeabORD outputs from scenario birds only (no baseline included) for the two modelled species. In each plot (A-F), the blue points represent the modelled means of the 63 different ORD scenarios, with the spread of each point's respective 100 replicates (not modelled) shown in grey. The red line and 95% confidence intervals represent the most supported model which is alluded to at the top of respective plots.

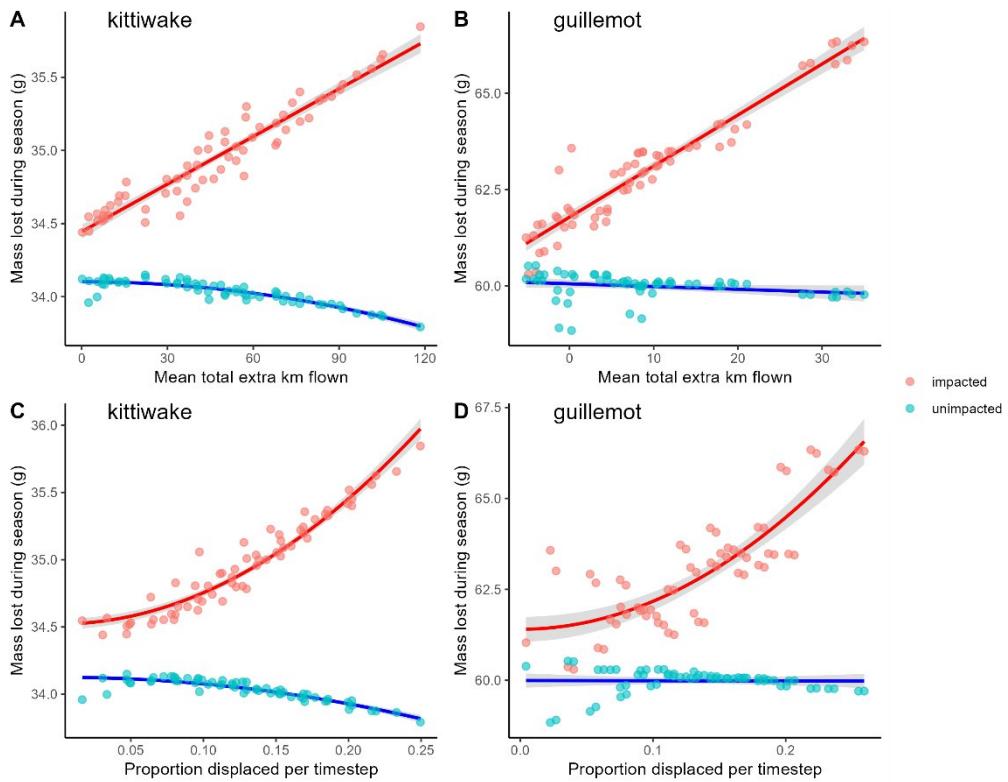


Figure S14: Plots showing birds impacted at least once (“impacted”, red) and birds never directly impacted (“unimpacted”, blue), which includes scenario birds only (i.e., no baseline runs without ORDs). Kittiwake adult mass loss during the season versus mean total extra km flown (A), and proportion displaced per time step (C), and the same respective plots for guillemots (B & D).

For further insight into the relationship between adult mass loss during the simulations we partitioned the results into birds impacted at least once, and those that were never impacted and fitted linear and non-linear models of each response variable to the mean total extra km flown (analogous to the energetic cost of extra km flown due to barrier effects) and the proportion of birds displaced per time step. Kittiwakes that were impacted at least once by an ORD (i.e. suffered a barrier or displacement event) saw increases in mass loss with increasing total extra km flown in an approximately linear fashion, while unimpacted kittiwakes resulted in a nonlinear decrease in mass losses with increasing exposure. A similar pattern was seen in guillemots with respect to increasing total extra km flown, however both impacted and unimpacted birds lost mass in an apparently linear fashion. With increasing proportion of birds displaced per time step adult mass loss increased in a nonlinear fashion, with effects becoming stronger as this proportion increased (Figure S14 C), with the same pattern observed for guillemots (S14 C).

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