Vulnerability of northern gannets to offshore wind farms; seasonal and sex-specific collision risk and demographic consequences

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A B S T R A C T

There is a pressing need to quantify the risks of renewable energy developments such as offshore wind farms for protected populations. However, assessments are often based on incomplete data, or fail to consider variation in risk between sexes and at different times of year. We tracked northern gannets foraging from the world's largest colony (Bass Rock, Scotland) across five consecutive breeding seasons. We examine how seasonal and sex differences in behaviour affect the collision risk from planned and operational wind farms within their foraging range and assess the likely consequences for long-term population viability. Both sexes made shorter trips during chick-rearing than prior to chick-hatching, spent a greater proportion of time within wind farm sites and had an eight times greater potential collision risk during chick-rearing. Females made longer trips than males at both these times of year, flew higher and spent more time within wind farm sites, leading to three times greater collision risk for females. After accounting for the potential additional mortality from collisions, and assuming that the death of a parent also led to the loss of its offspring, the breeding population was projected to increase by 3.57% (95% CI: 2.16–5.15%) per year, compared with 6.56% (95% CI: 4.59–8.73%) in the absence of turbines, suggesting a negligible effect on population viability. However, additional mortality could result in greater immigration from neighbouring colonies, potentially affecting their viability and highlighting a need for research within a metapopulation framework to assess the impacts of offshore wind developments on vulnerable species across multiple connected sites.

1. Introduction

Marine environments are facing increasing pressure from human activities including fisheries, shipping and offshore developments such as oil and gas installations and wind farms (Halpern et al., 2019; O'Leary et al., 2020). For instance, commitments to reduce reliance on fossil fuel energy are driving order-of-magnitude increases in offshore wind capacity in Europe, China and the US (GWEC 2019), making predicting the likely ecological impacts of these developments a conservation priority (May et al., 2017). Seabirds are key components of marine ecosystems and may be affected by offshore wind farms through direct mortality from collisions with turbines, as well as indirect effects such as forcing birds to travel further to forage (Furness et al., 2013; Masden et al., 2015), although some species may also be attracted to wind farms (Vanermen et al., 2015). Predicting the likely sizes of these effects on the populations of seabirds breeding at different colonies requires colony-specific information on the movements and behaviour of birds at sea, particularly when there may be cumulative impacts on a breeding colony from several different wind farms (Green et al., 2016). Such data can be obtained using bird-borne data loggers (Wade et al., 2014; Thaxter et al., 2015) but the use of such technology is often restricted to periods when devices can be deployed and retrieved from birds, which may not be representative of the entire breeding season. Changes in the distribution and abundance of prey may alter the movements and behaviour of birds over the course of a breeding season, as may changes in the constraints limiting individuals' foraging trip durations and hence the maximum ranges of trips (Kappes et al., 2015; Votier et al., 2017). In particular, nesting birds may face greater constraints when they need to return frequently to the nest to feed dependent offspring than at earlier stages of the breeding season (Ito et al., 2010; Widmann et al., 2015).

Behaviour may also differ between sexes, as a result of differing parental roles, competitive exclusion, niche partitioning or different nutritional requirements (Lewis et al., 2002). Hence assessments of interactions between seabirds and wind farms need to take account of variation in foraging movements and behaviour in relation to both stage of the breeding season and sex to properly evaluate the risks posed to populations at different sites.

Another key area of uncertainty concerns the population-level impacts of additional mortality caused by interactions with wind farms. Previous approaches to this question have often focused on determining the maximum number of additional mortalities a population could theoretically sustain through compensatory reductions in natural mortality, for instance using Potential Biological Removal (PBR) algorithms (Dillingham and Fletcher 2008). However these approaches are often prone to overestimating sustainable levels of offtake (Milner-Gulland and Akçakaya 2001) and several authors have strongly recommended that potential impacts should instead be assessed using matrix-based population projection models (Green et al., 2016; O'Brien et al., 2017). These models, however, require detailed information on age- or stage-specific vital rates, particularly adult survivorship, which has the greatest elasticity (i.e. the largest proportional effect on population growth) in species with high annual adult survival, delayed sexual maturity and low annual reproductive output, such as seabirds (Miller et al., 2019).

Northern gannets *Morus bassanaus* (hereafter gannets) are potentially at high risk of mortality from collisions with offshore wind turbines during the breeding season (Furness et al., 2013; Bradbury et al., 2014) due to their long foraging ranges (Hamer et al., 2007; Wakefield et al., 2013), their flight heights (particularly during periods of active foraging for prey; Cleasby et al., 2015a; Lane et al., 2019) and the proximity of several consented offshore wind developments to large gannet colonies of international importance (Warwick-Evans et al., 2018). However, tracking data for adult gannets have so far been confined to birds raising chicks, and they may not be representative of behaviour during earlier phases of breeding (Besel et al., 2018; Botha and Pistorius 2018). Similarly, while males and females are known to differ in their foraging distributions and diving behaviour during chick-rearing (Lewis et al., 2002; Cleasby et al., 2015b), differences earlier in the breeding season have not been examined, and the consequences of sex-specific foraging behaviour for potential collision risk have not been assessed.

Here we examine the foraging tracks of gannets at the world's largest colony, Bass Rock, UK (56° 6′ N, 2° 36′ W), to assess the incidence of seasonal and sex-specific differences in the movements and behaviour of birds at sea and the implications for collision risk. We examine how representative data for birds rearing chicks are of foraging trips earlier in the season, and we compare tracks of males and females at these different times of year. By combining this information with spatially-explicit data on the flight heights of males and females during periods of commuting and active foraging, we next calculate the potential collision risk across all proposed, consented or operational wind farms within the overall foraging ranges of birds. We then use capture-mark-recapture methods to estimate adult survival rates for males and females and construct population projection matrices to gauge the implications of potential additional mortality caused by wind turbines for the viability of this population.

2. Materials and methods

2.1. Study site and data collection

Fieldwork at Bass Rock took place between mid-April and mid-August over five consecutive years (2015–2019). Using a 6-m telescopic pole fitted with a metal noose or hook, adult gannets were caught at the nest site during April (prior to egg-laying) in 2017–2019 (n = 48 birds) or during June–August (while attending chicks) in 2015–2019 (n = 140 birds). To reduce disturbance, no attempt was made to capture

birds during incubation, when eggs are very vulnerable to predation by gulls (Nelson 2002). All birds caught prior to egg-laying had bred in the previous year and were holding a territory. Birds were sexed from observations of sex-specific behaviour (Redman et al., 2002) or in some cases from DNA (Cleasby et al., 2015b).

Unless already ringed, birds were fitted with a numbered metal British Trust for Ornithology (BTO) ring and a coloured engraved plastic ring with a unique alphanumeric code for easy identification at the nest site. We then equipped each bird with a GPS logger (igotU-GT600, Mobile Action Technology, Taipei, Taiwan) attached to the upper side of the central tail feathers and, during chick-rearing in 2015–2017, a subset of birds (n = 63) also had a pressure logger (MSR-145W, MSR Electronics, Seuzach, Switzerland) attached to the underside of the central tail feathers (Cleasby et al., 2015a; Lane et al., 2019). GPS loggers weighed 30–33 g and were programmed to record locations at 1- or 2-min intervals, with those deployed in April 2018 programmed to commence recording on 8 May (after most eggs were laid and well before the earliest chicks hatched at the colony; Nelson 2002). Pressure loggers weighed 18 g and recorded pressure and temperature at 1 Hz. Both loggers were attached using Tesa® tape (Beiersdorf AG, Hamburg, Germany).

Birds equipped with loggers in April each year were recaptured mainly in June, during the chick-rearing period at the colony, with trips recorded between 23 April and 3 June. Birds equipped with loggers during chick-rearing were recaptured after 7–14 days. Handling time of all birds at both deployment and retrieval of loggers was no longer than 15 min and, on both occasions, birds returned to their nest site and resumed normal behaviour almost immediately. The combined weight of loggers was <2% of body mass (~3 kg; Nelson 2002), which was well within recommended guidelines (Phillips et al., 2003), and previous studies at this colony confirmed that such deployments had no discernible impact on trip duration or body mass (Hamer et al. 2007, 2009; Cleasby et al., 2015a).

2.2. Trip metrics and spatial distribution

To account for any irregularities in the GPS data, all locations were interpolated to 2-min intervals using the R package adehabitatLT (Calenge 2006). For every foraging trip, we calculated the duration (h), total distance travelled (km) and maximum distance (km) on a direct bearing from the colony (Wakefield et al., 2013). In addition, we used speeds and turning angles derived from the GPS data to classify the behaviour of birds at sea as one of three categories: commuting, characterised by long step-lengths and small turning angles; active foraging, characterised by short step-lengths and large turning angles; resting on the water, characterised by short step-lengths and small turning angles (see Wakefield et al., 2013 for validation of these discrimination criteria; Grecian et al., 2018).

All trips recorded from birds tagged in April each year were undertaken well before the main chick-rearing period at the colony (median hatch date ~12 June; Nelson 2002). However, we could not be certain of a bird's reproductive status during individual trips, and so they were pooled into a single category termed 'pre-hatching period', including pre-laying and incubating pairs and potentially some failed breeders (not all of these birds had a chick when they were recaptured to retrieve the logger), for comparison with trips by birds that were confirmed as provisioning a chick (all birds tagged during chick-rearing were still attending a live chick when the logger was retrieved). Trip metrics (duration, distance travelled, maximum displacement from the colony and the proportion of each trip spent commuting, foraging and on the water) were then compared with respect to stage of season (pre-hatching or chick-rearing period) by fitting linear mixed models (LMM) using restricted maximum-likelihood (REML) in the R package 'nlme' (Pinheiro et al., 2018). Sex and year were included as fixed effects and bird identity nested within year was included as a random effect to account for repeated trips per individual and individuals repeated across years.

All trip metrics were right skewed and were therefore square-root transformed prior to analysis. Model selection was based on Akaike's Information Criterion (AICc), with the top model refitted to obtain χ^2 and *p* values. Where there was no clear top model (ΔAICc < 2; Burnham and Anderson 2002) model averaged parameters and their relative importance were extracted from all models with ΔAICc < 2 using the R package 'MuMIn' (Bartoń 2015).

Previous data have indicated that adult gannets are much more likely to fly at collision risk height (i.e. within the range of heights swept by turbine blades) when actively foraging than when commuting to or from the colony (Cleasby et al., 2015a). Hence in addition to examining the full tracks of birds at sea, we also assessed the spatial distribution of actively-foraging birds. Using only those GPS locations classified as active foraging, we estimated 50% and 95% utilization distributions (UDs; Fieberg and Kochanny 2005) for each sex and stage of the season (data sets pooled across years), using kernel analysis conducted with the R package 'adehabitatHR' (Calenge 2006) with a 1 km^2 grid and a smoothing parameter of 10 km (Cleasby et al., 2015b). We also calculated the 95% UDs for all GPS locations at sea, to determine the proportion of the overall foraging area encompassing wind farm sites for males and females during each stage of the season.

2.3. Flight height estimation

To compare the flight height of males and females during chick-rearing and enable us to include flight heights for individual wind farm sites in collision risk assessments, we used the barometric formula (Berberan-Santos et al., 1997; Wallace and Hobbs 2006) to estimate height *h* (meters) above sea level from pressure logger data:

$$h = -\frac{KT}{Mg}\ln\left(\frac{P}{P_o}\right) \tag{1}$$

where P_0 and *P* are the atmospheric pressures (Pascals) at sea level and at height *h* (meters) respectively; *K* is the universal gas constant for air (8.31432 N m mol^{-1} K^{-1}); *M* is the molar mass of air (0.0289644 kg mol^{-1}); *g* is the acceleration due to gravity (9.80665 ms^{-2}); and *T* is the temperature (K) of the atmosphere between h_0 and *h*. We obtained calibration pressures (P_0) when birds spent time on the water (Cleasby et al., 2015a) and we accounted for spatial and temporal changes in atmospheric pressure during long periods of sustained flight by adjusting calibration pressures throughout the duration of each flight bout using the ERA-Interim reanalysis sea surface pressure dataset (6-hourly data at 0.125 × 0.125° or approximately 8 × 8 km resolution; Dee et al., 2011) following Lane et al. (2019).

Flight heights were modelled using LMM with sex, behaviour (commuting or active foraging) and year as fixed effects. Models also included individual foraging trip identity nested within bird identity as a random effect, to account for repeated measures within each foraging trip and multiple trips per bird. A temporal autocorrelation structure was also included to control for non-independence of successive data within each trip (Lane et al., 2019).

2.4. Modelling collision risk

Birds are at risk of striking turbines only when in flight, and they tend to rest on the sea surface overnight (Hamer et al., 2009; this study). Hence following previous authors (Wakefield et al., 2013; Cleasby et al., 2015a) we first estimated the density, *d*, of males and females in flight during daylight hours (including twilight), within each 1 km^2 grid-square during pre-hatching and chick-rearing stages of the season as:

$$d = \hat{u}_{i,x}NZ \tag{2}$$

where $\hat{u}_{i,x}$ is the empirical probability density of use of cell *x* by bird *i* during daylight hours, *N* is the number of birds of each sex predicted to

be at sea, estimated by multiplying the number of breeding pairs (75,000 in 2014; Murray et al., 2015) by the observed proportion of time birds of each sex spent at sea, and *Z* is the proportion of time at sea that was spent in flight during daylight hours (defined separately for every trip to account for seasonal and latitudinal variation in day-length, and including civil twilight; Furness et al., 2018). For each sex and stage of the season, to estimate the mean density of birds in flight within each proposed wind farm site within the 95% UDs of birds, we then summed the number of birds expected in each 1 km^2 grid square within the boundaries of each site (from eqn. (2) above) and divided each sum by the total area of the site (km^2); boundaries and areas of sites were determined using shape files downloaded from The Crown Estate (2020) and The Crown Estate Scotland (2020).

For each wind farm site, we next calculated the proportion of time males and females spent in flight commuting and actively foraging during each stage of the season (see 2.2 above). For trips during chick-rearing, we then combined this information with spatially-explicit flight height data and specifications of turbines at each site (Table S1 in Supporting information) to calculate the proportion of time spent at collision risk height (i.e. within the height envelope swept by the turbine blades) during commuting and active foraging in each case. Flight height data were not obtained for birds tagged during the pre-hatching period so the proportions of flight at risk height during active foraging and commuting were presumed to be the same as those estimated at each site during chick-rearing. The total proportion of flight at collision risk height (P_H) was next calculated for each sex at each site during each stage of the season as:

$$P_H = P_F R_F + P_C R_C \tag{3}$$

where *P* = proportion of time spent foraging (P_F) or commuting (P_C) and *R* = proportion of flight at collision risk height during each activity.

We next applied these data to a mechanistic collision risk model (Band 2012) to assess the overall number of potential collisions across wind farm sites within the 95% foraging distributions of male and female gannets from Bass Rock at each stage of the season, assuming an overall turbine avoidance rate (combined macro-avoidance of wind farm areas and micro-avoidance of individual turbines when within a wind farm area; Garthe et al., 2017) of 0.989 (considered the most appropriate for gannets by Cook et al., 2018 based on a synthesis of available data; details of collision risk models in Appendix S1 in the Supporting Information).

2.5. Survival analysis

Between 2010 and 2016, 198 adult gannets breeding at Bass Rock (115 male, 83 female; see Table S3 in Supporting Information) were caught and fitted with an individually numbered colour-ring. During multiple return visits to the site in subsequent years, visual searches were undertaken for all marked birds and a record of re-sightings made to build up an encounter history of each marked individual. To estimate annual survival (ϕ) and resighting (*p*) probabilities of males and females, capture-mark-recapture (CMR) models were specified in MARK (Version 8.2, White and Burnham 1999). Following Deakin et al. (2019), a fully sex- and time-dependent Cormack-Jolly-Seber (CJS) model was evaluated for goodness-of-fit (GOF) and tested for evidence of transience (presence of individuals that permanently left the population after being caught and released) and trap-dependence (probability that recapture was not independent between years) using U-CARE (Choquet et al., 2009). The CJS model fitted the data well (GOF: $\chi^2_{25} = 14.84$, *P* = 0.94) with no evidence of transience (z = −0.84, two-sided test, *P* = 0.4) but there was evidence of trap dependence (z = −2.22, two-sided test, *P* = 0.026). The signed statistic for trap dependence (TEST2. CT) suggested trap happiness in females (z = −2.67, *P* = 0.007) but not males (z = −0.46, *P* = 0.65). The data were therefore split for time-dependence in U-CARE and a two-stage time-since-marking (TSM) structure was

applied to model resightings of females (Pradel 1993), with the first stage set as a constant. After accounting for trap-dependence a variance inflation factor (ĉ) of 0.457 was estimated by U-CARE, suggesting underdispersion in the data. We therefore set ĉ = 1, as recommended for cases where ĉ < 1 (White et al., 2001). The candidate model set was built adjusting the survival and resighting probability parameters so that they could vary by sex (*s*), with year (*t*) or remain constant over time (*c*). Estimates of survival and resighting probabilities (weighted means ± 95% confidence intervals, CI) were calculated using model averaging across the full model set (White et al., 2001).

2.6. Population projection models

To predict the potential population-level consequences of mortality from collision with turbines we constructed age-structured (Lefkovitch) matrix population models, in keeping with recommendations of previous authors (Green et al., 2016; O'Brien et al., 2017) (see Fig. S1 in Supporting Information for details). Survival rates of juveniles (birds in their first year) and immature birds (second to fifth year) were taken

from previous estimates based on BTO ring recoveries of birds from Bass Rock (Wanless et al., 2006). Annual adult survival rate was modelled as stochastic to account for uncertainty in our estimates of this parameter (Deakin et al., 2019). We first projected our population model over a period of 21 years from 1994 - 2014 to compare our model with observed nest counts (Apparently Occupied Sites, AOSs; Murray et al., 2015). Three different survival scenarios were then modelled, the first using random samples from the model-averaged survival estimates (ϕ_a) in the absence of operational offshore wind turbines, the second using the predicted mortality from collision with wind turbines to adjust the survival of adults assuming that wind farm mortality was entirely additive, and the third adjusting both adult survival and the probability of chicks fledging (ϕ_c) in this way, assuming that the death of a parent during the breeding season also resulted in the loss of its egg or chick. In each case, parameter uncertainty on the adult survival rates was incorporated by drawing 100,000 samples from a beta distribution (Deakin et al., 2019).

For each scenario, we modelled changes in breeding population size over a period of 25 years, corresponding with the proposed period of
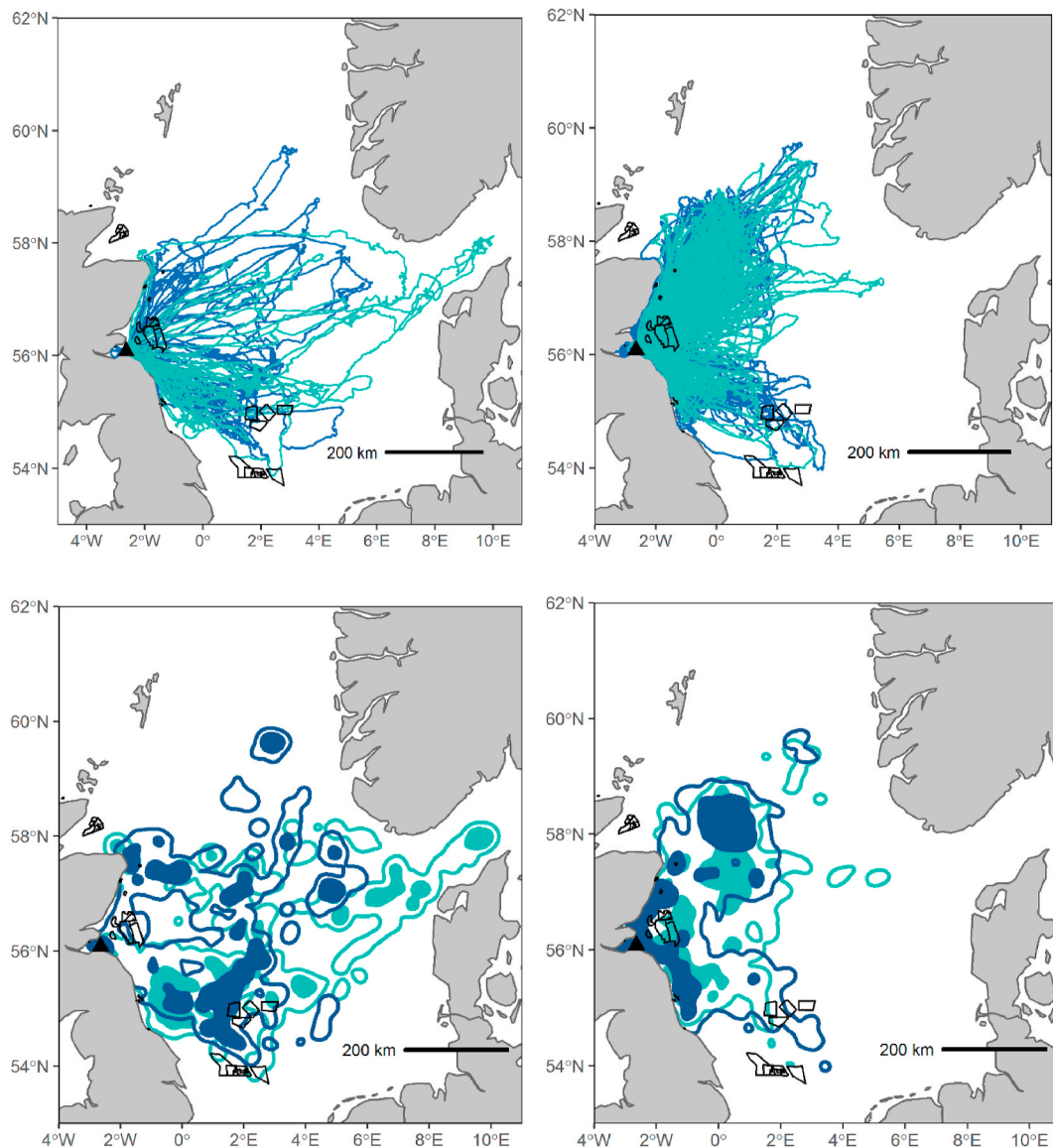

Fig. 1. (**Top**) foraging tracks and (**bottom**) utilization distributions (UDs) of female (green) and male (blue) gannets tracked from Bass Rock (black triangle) (**left**) prior to chick hatching (pooled data for 2017–2019) and (**right**) during chick-rearing (pooled data for 2015–2019). UDs are based on active foraging locations and shading denotes UD contours (filled, 50%; unfilled, 95%). Wind farm sites are outlined in black. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

operation of turbines (Bouty et al., 2017). In addition, to estimate the level of additional mortality that would be required to halt net population growth, the survival rate for females was adjusted until the simulated value for population growth (λ) became equal to 1, assuming that only adult birds experienced this additional mortality.

3. Results

We acquired high-resolution GPS data for 508 trips by 154 birds (288 trips by 84 males; 220 trips by 70 females; all recorded trips were included in the analysis but loggers were lost or malfunctioned on 34 of 188 deployments). Most trips by birds of both sexes travelled northeast or southeast of the colony, particularly during chick-rearing, with a higher proportion of trips travelling due east of the colony prior to chick-hatching (Fig. 1). Overall foraging areas of birds (95% UDs for all GPS locations at sea) covered a large area of ocean (~100,000 km^2 for each sex and stage of the season), of which ~2% encompassed wind farm sites (Table 1). Each adult on average spent 48% of time at sea during the pre-hatching period (males, 44%; females, 54%) and 50% of time at sea during chick-rearing (males, 49%; females, 51%).

3.1. Foraging trip durations, destinations and time-activity budgets at sea

Birds made significantly longer trips during the pre-hatching period than during chick-rearing in terms of duration (1.9–2.5 times longer on average; LMM; $\chi^2 = 63.3$, $p < 0.001$), distance travelled (1.5 times longer on average; $\chi^2 = 17.6$, $p < 0.001$) and maximum displacement (1.4 times longer on average; $\chi^2 = 9.9$, $p = 0.002$; Table 2), with core foraging areas (50% UDs of active foraging sites) in particular covering a much broader range of latitudes and longitudes during the pre-hatching period than during chick-rearing (Fig. 1). Females also made significantly longer trips than males in all three respects (duration, 1.1–1.4 times longer on average; $\chi^2 = 9.8$, $p = 0.002$; distance travelled, 1.1–1.2 times longer on average; $\chi^2 = 9.5$, $p = 0.002$; maximum displacement, 1.1 times longer on average; $\chi^2 = 8.7$, $p = 0.003$; Table 2), with only females during the pre-hatching period making trips that extended beyond 6°E, reaching as far as the Jutland coast, Skagerrak and the Norwegian trench (Fig. 1). Using an information theoretical approach, the best-supported models for trip duration, distance travelled and maximum displacement from the colony all included stage of season, sex and year (ΔAICc > 5 in each case; Tables S4 and S5 in Supporting Information).

Time-activity budgets of birds during foraging trips differed significantly between the two stages of the season, with a significantly smaller proportion of time at sea spent commuting and a significantly greater proportion of time spent resting on the sea surface during the pre-hatching period than during chick-rearing (LMM; $\chi^2_1 = 4.99$, $p = 0.025$ and $\chi^2_1 = 4.93$, $p = 0.023$, respectively; Fig. 2). There was no significant difference, however, in the proportion of time spent actively foraging ($\chi^2 = 0.63$, $p = 0.43$; Fig. 2). Using an information theoretical approach, there was support for a difference between stages of the season in the proportions of time spent commuting and resting on the sea surface, together with a marginally significant difference between sexes in the proportion of time spent commuting ($\chi^2_1 = 3.52$, $p = 0.06$;

Table 1
Total foraging area (95% UD for all GPS locations at sea) of male and female gannets from Bass Rock and the proportion of this area encompassing wind farm sites during pre-hatching and chick-rearing stages of the breeding season. Data pooled across years.

Season	Sex	Foraging area (km^2)	Proportion of foraging area containing wind farm sites (%)
Prior to chick hatching	Males	127,310	1.53
	Females	140,211	1.69
Chick-rearing	Males	97,739	2.12
	Females	100,508	2.20

Table 2
Characteristics of foraging trips by male and female gannets during pre-hatching and chick-rearing stages of the breeding season (n = 43 trips by 15 males, 24 trips by 9 females pre-hatching; 245 trips by 69 males, 196 trips by 61 females during chick-rearing).

	Sex	Pre-hatching		Chick-rearing	
		Median	IQR	Median	IQR
Duration (h)	Male	44.1	35.2–63.2	22.8	17.4–29.7
	Female	63.6	47.8–69.5	24.9	19.1–31.6
Distance (km)	Male	743.5	593.7–925.5	481.5	261.6–721.8
	Female	846.3	726.1–1121.9	554.3	374.5–716.4
Maximum displacement (km)	Male	292.6	215.7–333.7	205.1	107.6–300.5
	Female	308.2	254.3–419.3	224.4	149.3–293.5
Commuting flight height (m)	Male	–	–	15.3	5.9–32.7
	Female	–	–	19.7	7.5–42.9
Foraging flight height (m)	Male	–	–	25.0	9.8–42.4
	Female	–	–	34.6	13.9–54.6

Fig. 2), and for a difference among years in all three measures (Tables S6–S8 in Supporting Information).

3.2. Flight heights

Birds of both sexes flew higher when actively foraging than when commuting ($\chi^2_1 = 85.5$, $p < 0.001$) and females flew higher than males during both these activities ($\chi^2_1 = 6.32$, $p = 0.012$; Table 2). Using an information theoretical approach, there was strong support for differences in flight height between sexes, activities and years (Tables S9 and S10 in Supporting Information).

3.3. Collision risk

Irrespective of sex, the distribution of birds in flight at sea was much more diffuse during the pre-hatching period than during chick-rearing, resulting in much higher peak densities of birds km^{-2} during chick-rearing than pre-hatching (Fig. 3). In addition to high densities of birds in flight around the Bass Rock, densities were highest along the coast to the south-east of the colony during the pre-hatching period and to the north-east of the colony during chick-rearing, resulting in higher densities within the proposed wind farm sites in the outer Firth of Forth during chick-rearing than pre-hatching, particularly for females. Densities of both sexes were relatively low at other wind farm sites within birds' overall foraging ranges at both stages of the season (Fig. 3).

Both sexes spent a high proportion of their flight time within wind farm sites commuting at relatively low height rather than actively foraging (mean ± SD; pre-hatching = 83.5 ± 14.0% for males, 94.6 ± 12.4% for females; during chick-rearing = 74.8 ± 14.2% for males, 64.7 ± 28.5% for females). The predicted number of collisions across all wind farm sites within the ranges of birds from Bass Rock was 59 per month during the pre-hatching period and 452 per month during chick-rearing, with ~75% of predicted collisions being by females in each case (Table 3). Combining the monthly totals for males and females from April to August, an estimated 1474 collisions would be predicted to occur each breeding season, with three times the number of collisions for females than for males (Table 3).

3.4. Survival analysis

Of the 198 birds colour ringed on Bass Rock between 2010 and 2016, 192 (115 males, 83 females) were resighted at least once. The top model included constant survival but the model set included support for effects of both sex and time on survival, and there was also support for sex- and time-dependent resighting probability in the top models (Table 4). Model averaging therefore resulted in separate survival and resighting probabilities for males and females each year. Annual survival estimates
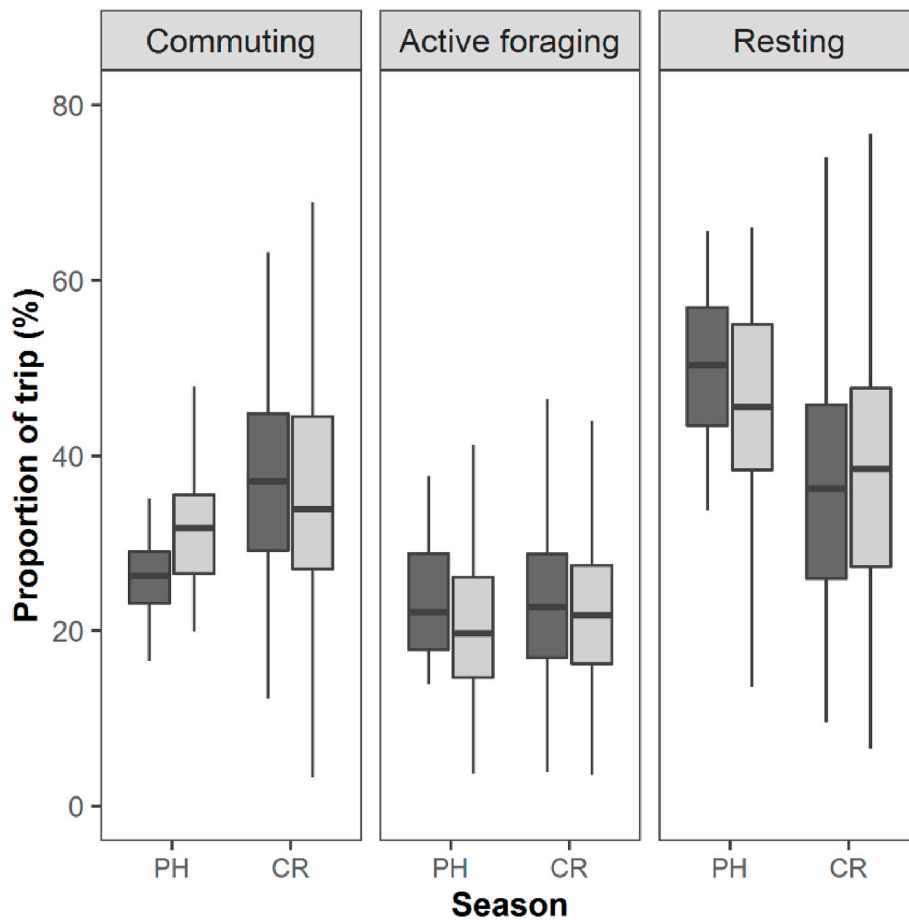
Fig. 2. At-sea time-activity budgets of gannets at Bass Rock. Data show the proportion of total daylight hours (medians, IQRs and ranges) spent in commuting, active foraging and resting on the water for females (dark grey) and males (light grey) prior to hatching and during chick-rearing stages of the breeding season (PH and CR, respectively). Data pooled across years.

ranged from 0.949 (95% CI: 0.830–0.986) to 0.965 (0.911–0.987) for males and from 0.944 (0.836–0.983) to 0.961 (0.898–0.985) for females, with mean (SD) survival for males and females of 0.959 (0.005) and 0.955 (0.005), respectively. Resighting probability of males varied between years, from 0.936 (0.869–0.970) to 0.941 (0.890–0.970), while resighting probability of females was 0.936 (95% CI: 0.834–0.976) in the first year after marking and varied between years thereafter, from 0.811 (0.683–0.896) to 0.831 (0.731–0.899).

3.5. Potential population impacts

The annual survival estimates for gannets from Bass Rock were predicted to decrease to a greater extent among females than males as a result of collisions with wind turbines; from 0.955 to 0.940 among females, from 0.959 to 0.954 among males. Hence our population projection model (PPM) focused on the impact of changes in female survivorship on population growth. The current survival estimate for females (0.955) gave a mean population growth rate (λ) of 1.040 (95% CI: 1.031–1.047) that closely matched the observed increase in breeding pairs between 1994 and 2014 (see Fig. S2 in Supporting Information), resulting in a projected population of 77,771 (65,314 - 91,013) pairs in 2014 (observed count = 75,259 AOSs.) The predicted mean population growth rate decreased to 1.027 (95% CI: 1.019–1.035) when the adult survival estimate was decreased to 0.940 to include the predicted additional mortality from collision with turbine blades and to 1.026 (1.017–1.034) when fledging success was additionally decreased to 0.705, assuming that the death of a parent during the breeding season also resulted in the loss of its egg or chick. However, the number of

breeding pairs was still predicted to increase by 3.57%–3.81% per annum in the presence of wind turbines, reaching between 142,364 and 146,861 in 25 years' time (Fig. 4). Assuming the death of a parent also led to the loss of its offspring, for population growth rate to be halted (λ = 1) annual survival of females would need to decline by 0.045–0.910, an additional 3375 deaths during the breeding season each year above the current (pre-construction) level.

4. Discussion

Gannets rearing chicks made much shorter trips than those recorded earlier in the breeding season in terms of both durations and distances travelled, with a smaller proportion of each trip spent resting on the sea surface during chick-rearing, presumably reflecting a benefit in returning quickly to the colony at this stage of the season to feed dependent offspring (Hamer et al., 2007; Lane et al., 2019). Trips recorded during the pre-hatching period probably included some that were from pre-laying or failed breeders in addition to birds whose partners were incubating, but they were nonetheless consistently longer than trips by birds rearing chicks, with no overlap between these two stages of the season in interquartile ranges (IQRs) for trip durations by either sex and little overlap in IQRs for distances travelled (Table 2). This consistency in trips recorded pre-hatching probably arose because all these birds were acting as central-place foragers (birds occupy and vigorously defend nest sites throughout the breeding season regardless of whether or not they have an egg or chick; Nelson 2002) but with fewer constraints on trip duration during this period than post-hatching. Hence while there may have been some differences in foraging behaviour
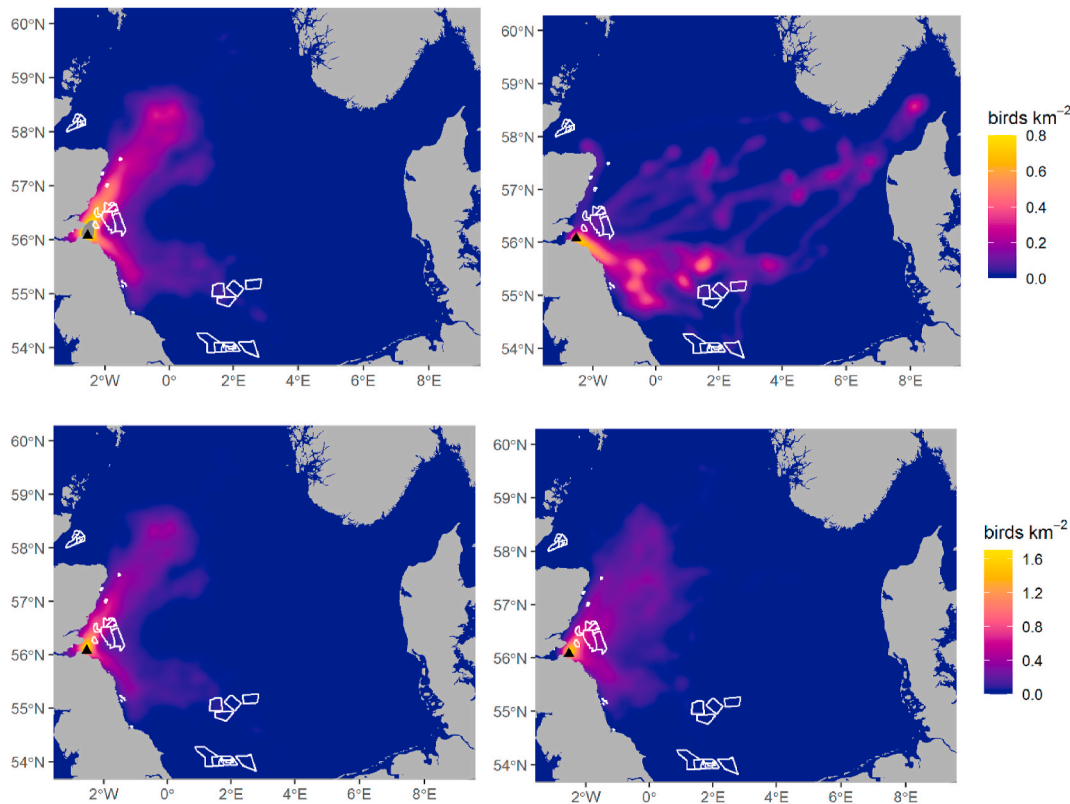
Fig. 3. Estimated density of **(left)** male and **(right)** female northern gannets in flight (birds km^{-2}) tracked from the Bass Rock (black triangle) during **(top)** pre-hatching and **(bottom)** chick rearing stages of the breeding season. Wind farm sites are outlined in white. Note different scales for densities pre- and post-hatching.

Table 3

Predicted number of potential collisions per month during the pre-hatching period (April–May) and chick-rearing period (June–August) for male and female gannets from Bass Rock, summed across wind farm sites within foraging areas of birds, plus total predicted numbers of collisions for each sex across the core breeding season (April–August) each year.

	Pre-hatching	Chick-rearing	TOTAL
Male	24	103	**357**
Female	35	349	**1117**

before and after egg-laying or between failed and successful breeders during incubation, as have been found in some other species (Fijn et al., 2014; Ponchon et al., 2017), any such differences were small compared to those between trips recorded during the pre-hatching period and those made by birds rearing a chick. Ponchon et al. (2019) similarly recorded no difference in the foraging behaviour of failed and successful black-browed albatrosses *Thalassarche malanophris* except during chick-rearing, when successful birds foraged more intensively to meet the food requirements of their chick as well as themselves.

Variation in the foraging movements and behaviour of birds across the breeding season could have resulted from seasonal changes in habitat usage (Thaxter et al., 2015) or in the distribution and abundance of prey in addition to differences in time-constraints acting upon birds. For instance, gannets focus their foraging activity around meso- and sub-mesoscale features such as oceanographic fronts (Hamer et al., 2009; Grecian et al., 2018) and there may have been seasonal differences in the position, size, intensity and/or duration of such features, requiring birds to travel further from the colony to locate prey earlier in the season. However, we recorded no significant difference in the proportion of each trip spent in active foraging during pre-hatching and chick-rearing periods, which suggests that any seasonal differences in overall prey availability were not large. There was nonetheless some

Table 4

Top six models (ranked by QAIC$_c$) of survival and resighting probabilities of adult female and male northern gannets breeding on Bass Rock, Scotland (2010–2017). Inflation factor ($\hat{c}$) = 1.000. Model subscripts relate to effects fitted to survival (ϕ) and resighting (p) probabilities (s: sex; c: time constant; t: time dependent; m: male; f: female). QAIC$_c$: quasi-likelihood adjusted Akaike's information criterion (AIC); ΔQAIC$_c$: difference in QAIC$_c$ between the best model and the model in question; Num. Par.: number of parameters estimated in the model; QDeviance: quasi-likelihood adjusted deviance.

Model	QAICc	ΔQAICc	AICc Weights	Model Likelihood	Num. Par.	QDeviance
φ (c) p (m:c, f:c/c)	519.93	0	0.481	1	4	130.78
φ (s) p (m:c, f:c/c)	521.31	1.38	0.241	0.502	5	130.13
φ (t) p (m:c, f:c/c)	522.45	2.52	0.136	0.284	10	120.97
φ (c) p (m:c, f:c/t)	523.95	4.01	0.065	0.135	9	124.53
φ (c) p (m:t, f:c/c)	524.83	4.90	0.042	0.086	10	123.35
φ (s) p (m:c, f:c/t)	525.14	5.20	0.036	0.074	10	123.65

annual variation in the movements and behaviour of birds at each stage of the season, presumably reflecting year-to-year variation in prey distribution and abundance (Hamer et al., 2007), and we accounted for this variation by using data pooled across years to calculate collision risks during pre-hatching and chick-rearing periods.

In addition to variation across the breeding season, our data also revealed consistent sex differences in colony attendance and foraging behaviour. Females spent a greater proportion of time at sea than males, particularly prior to chick-hatching, probably due to males having a greater role than females in defending nest sites and an exclusive role in providing and augmenting nest material, particularly prior to chick-hatching (Nelson 2002; Redman et al., 2002). Females also made consistently longer foraging trips than males in terms of both durations and distances travelled, indicating that sex differences during chick-rearing (Lewis et al., 2002; Malvat et al., 2020) also occur earlier
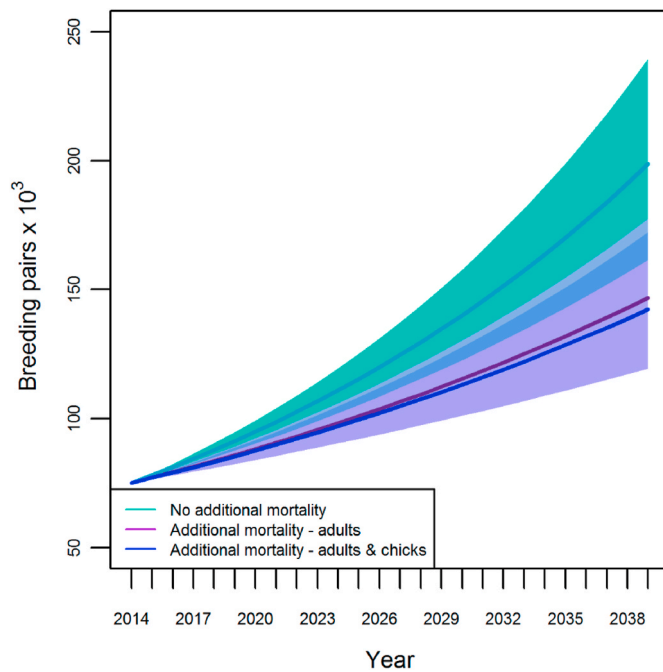
Fig. 4. Predicted mean population trajectory (number of breeding pairs) for the Bass Rock gannet colony under three scenarios: (1) without additional mortality from wind turbines (green line); (2) including additional adult mortality from wind turbines (purple line) and; (3) including additional adult mortality from wind turbines and associated decrease in breeding success (blue line). All models are based on a starting population of 75,259 breeding pairs in 2014 with a stable age distribution. Model predictions assume a closed population and are applied over 25 years, the expected operational lifetime of an offshore wind farm. Coloured polygons show the bootstrapped 95% CI (2.5th and 97.5th percentiles) from 100,000 model runs. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

in the breeding season. At Bass Rock, sexual segregation is driven largely by differences in habitat usage, with males foraging more in mixed waters along the coast and over offshore banks, and females foraging more in stratified waters (Cleasby et al., 2015b, Fig. 1). This habitat segregation in turn results in sex-specific foraging behaviour, with females diving to greater depths than males, particularly during V-shaped dives when birds rely on momentum to attain depth (Lewis et al., 2002; Cleasby et al., 2015b). We found that females also flew at greater heights than males, particularly during periods of active foraging, presumably to provide additional dive momentum allowing them to penetrate further beneath the water surface (Garthe et al., 2014).

We did not record flight heights prior to chick-hatching, but our data were similar to heights recorded elsewhere in studies lasting throughout the year. For instance, birds moving through an offshore wind farm in the English Channel flew at a median height of 17m (recorded using video and radar; Figure 5.11 in Skov et al., 2018), while birds in the North Sea and Baltic Sea, recorded using laser rangefinders, flew at a median height of 14m during periods of commuting (i.e. no rapid changes in height; Table 1 in Borkenhagen et al., 2018), compared to median heights of 15m for males and 19m for females during commuting flight in this study. Similarly, data obtained mainly during the incubation period at a colony in Canada recorded that birds initiated plunge dives from a mean height of 37m (Garthe et al., 2014) compared to median foraging flight heights of 25m for males and 35m for females in this study. Accordingly, we used data from birds rearing chicks to characterise flight heights throughout the breeding season. Average flight heights vary spatially due to variation in the likelihood of foraging versus commuting and differences in foraging flight heights over mixed and stratified waters (Cleasby et al., 2015a), and we accounted for this

variation by using spatially explicit data on heights during each of these activities to calculate collision risks at wind farm sites. Flight heights also vary between years (Cleasby et al., 2015a; this study) and we accounted for this variation by using data pooled across years. Over shorter time scales, birds fly lower into head winds than with tail winds when commuting (Skov et al., 2018; Lane et al., 2019) but most flight at collision risk height is during periods of active foraging, when heights are not affected by wind speed or direction (Lane et al., 2019).

In keeping with spatial density estimates from survey data (Waggitt et al., 2020) and previous tracking data from Bass Rock (Hamer et al., 2007; Cleasby et al., 2015a), areas with the highest densities of gannets at sea were close to the colony and overlapped with wind farm sites in the outer Firth of Forth. Many of these birds were commuting to or from foraging areas further from the colony, at heights typically below collision-risk height. However, gannets also forage during the outward portions of trips (Hamer et al., 2009), increasing their potential collision risk. Combined with the high density of birds close to the colony, this resulted in >99% of predicted collisions occurring within these sites, with fewer than 1% predicted to occur across remaining sites within birds' overall foraging ranges. There was also a much higher density of birds within wind farm sites close to the colony during chick-rearing than pre-hatching, corresponding with longer trips pre-hatching and resulting in the total predicted monthly collisions prior to chick-hatching being only ~10% of those during chick-rearing (calculated from data in Table 3). In addition, despite females making longer trips than males there were a higher density of females than males within wind farm sites in the outer Firth of Forth, associated with males foraging more than females in mixed waters closer inshore (Cleasby et al., 2015b, Fig. 1). This higher density of females combined with a higher proportion of flight at collision risk height by females resulted in the total number of predicted collisions by females being three times that of males. These data highlight the importance of accounting for seasonal and sex-specific variation in collision risks when assessing impacts on potentially vulnerable populations.

Our overall prediction of 1474 collisions across the core breeding season (April to August) each year (hence excluding migration periods; MacArthur Green 2018; Deakin et al., 2019) was slightly higher than that obtained from aerial survey data at sites in the outer Firth of Forth during the same period of year and with same assumed turbine avoidance rate (98.9%) as in our study (1281 predicted collisions per breeding season; Table 13.75 in MacArthur Green, 2018). Survey data are not able to determine the origins of birds observed at sea but gannets have mutually exclusive colony-specific home ranges during the breeding season (Wakefield et al., 2013) and hence all those recorded in the outer Firth of Forth during these months were probably from Bass Rock. Our estimate assumed that data obtained from birds rearing chicks were representative of the entire breeding population at this time of year, whereas 18% of breeding attempts by gannets typically fail prior to hatching (Nelson 2002). Failed breeders are not constrained to return to the colony frequently to feed chicks and so, unlike successful breeders, their trip durations and foraging ranges may be no shorter during the chick-rearing period than earlier in the year. Assuming that their collision risk is unaltered accordingly, the predicted number of collisions per month during the chick-rearing period would be reduced from 452 to 382 ([452 × 0.82] + [59 + 0.18]; calculated from data in Table 3) resulting in an overall prediction of 1264 collisions each core breeding season, which is very similar to that based on aerial survey data.

Our PPM predicted that additional mortality from wind farms would reduce the growth rate of the gannet population at Bass Rock but would be insufficient to drive the population into decline. We did not consider potential displacement and barrier effects (Masden et al., 2015) but these are unlikely to be large because currently planned and operational wind farm sites comprised <2.5% of the area encompassed by the foraging ranges of birds. We assessed only the core breeding season and did not consider mortality during spring and autumn migration periods. Nor did we consider impacts of wind farms on immature birds, which

also act as central-place foragers during the breeding season (Votier et al., 2017; Grecian et al., 2018). However, we estimate that an additional mortality of ~3300 breeding females per year would be needed to halt population growth, which is around three times our predicted number of collisions by females each breeding season (~950–1120, depending on the foraging trip characteristics of failed breeders during the chick-rearing period at the colony). Moreover, as recommended (Green et al., 2016), our model assumes that mortality from wind farms is entirely additive and takes no account of density-dependence (Lewis et al., 2001; Davies et al., 2013), which might off-set losses from collisions. This was a precautionary approach, in keeping with conclusions from recent analyses that any compensatory responses are unlikely to offset losses from breeding populations due to additional mortality associated with wind farms, and that depensatory responses (i.e. positive density-dependence) are unlikely to occur except in small populations of species that are more vulnerable than gannets to predation (Horswill et al., 2017; Miller et al., 2019). Population extinction risk can also be increased by stochastic variation in environmental conditions (Lande et al., 2003), although gannets are comparatively robust in this respect due to their life history and breeding ecology (Hamer et al., 2007; Montevecchi et al., 2009) making impacts of environmental stochasticity on population dynamics much less of an issue for gannets than for many other species (Miller et al., 2019).

Our results suggest that despite additional mortality from collisions with turbines, currently planned and operational wind farms would be unlikely to materially affect the viability of the gannet population at Bass Rock. Nonetheless, our PPM predicted that over a period of 25 years, uncompensated additional mortality of adults due to wind turbines would result in a breeding population only 71% of the predicted size in the absence of wind farms (data in Fig. 4, assuming death of one parent also resulted in loss of offspring). In practice, such sustained population growth is unlikely to occur under either scenario because the population at Bass Rock is probably approaching carrying capacity due to limited space for additional nesting sites (Murray et al., 2015). However, additional mortality at Bass Rock could result in changes to dispersal and recruitment (Seward et al., 2018; Bosch et al., 2019) with enhanced net immigration into this site potentially having adverse effects on population sizes at other colonies (Sanz-Aguilar et al., 2016; Miller et al., 2019). Hence our findings highlight a need for empirical data and theoretical research within a metapopulation framework (Votier et al., 2011) to assess impacts of offshore wind developments across multiple connected sites.

CRediT authorship contribution statement

Jude V. Lane: Methodology, Investigation, Formal analysis, Writing - original draft, Project administration. **Ruth Jeavons:** Data collection, Writing - review & editing. **Zoe Deakin:** Formal analysis, Writing - review & editing. **Richard B. Sherley:** Formal analysis, Writing - review & editing. **Christopher J. Pollock:** Data collection, Writing - review & editing. **Rebecca J. Wanless:** Data collection, Formal analysis. **Keith C. Hamer:** Conceptualization, Methodology, Data collection, Writing - review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2020.105196.

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