Three-dimensional tracking of a wide-ranging marine predator: flight heights and vulnerability to offshore wind farms

Ian R. Cleasby[1,2], Ewan D. Wakefield[1,3,4], Stuart Bearhop[2], Thomas W. Bodey[2], Stephen C. Votier[5] and Keith C. Hamer[1]*

[1]School of Biology, University of Leeds, Irene Manton Building, Leeds LS2 9JT, UK; [2]Centre of Ecology and Conservation, University of Exeter, Cornwall Campus, Falmouth TR10 9EZ, UK; [3]RSPB Centre for Conservation Science, Sandy SG19 2TL, UK; [4]UK and Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Glasgow G12 8QQ, UK; and [5]Environment & Sustainability Institute, University of Exeter, Cornwall Campus, Falmouth TR10 9EZ, UK

Abstract

1. A large increase in offshore wind turbine capacity is anticipated within the next decade, raising concerns about possible adverse impacts on birds as a result of collision risk. Birds' flight heights greatly influence this risk, yet height estimates are currently available only using methods such as radar- or ship-based observations over limited areas.

2. Bird-borne data-loggers have the potential to provide improved estimates of collision risk and here, we used data from Global Position System (GPS)-loggers and barometric pressure loggers to track the three-dimensional movements of northern gannets rearing chicks at a large colony in south-east Scotland (Bass Rock), located < 50 km from several major wind farm developments with recent planning consent. We estimated the foraging ranges and densities of birds at sea, their flight heights during different activities and the spatial variation in height during trips. We then used these data in collision-risk models to explore how the use of different methods to determine flight height affects the predicted risk of birds colliding with turbines.

3. Gannets foraged in and around planned wind farm sites. The probability of flying at collision-risk height was low during commuting between colonies and foraging areas (median height 12 m) but was greater during periods of active foraging (median height 27 m), and we estimated that ˜1500 breeding adults from Bass Rock could be killed by collision with wind turbines at two planned sites in the Firth of Forth region each year. This is up to 12 times greater than the potential mortality predicted using other available flight-height estimates.

4. *Synthesis and applications.* The use of conventional flight-height estimation techniques resulted in large underestimates of the numbers of birds at risk of colliding with wind turbines. Hence, we recommend using GPS and barometric tracking to derive activity-specific and spatially explicit flight heights and collision risks. Our predictions of potential mortality approached levels at which long-term population viability could be threatened, highlighting a need for further data to refine estimates of collision risks and sustainable mortality thresholds. We also advocate raising the minimum permitted clearance of turbine blades at sites with high potential collision risk from 22 to 30 m above sea level.

Key-words: climate change, collision risk, environmental impact, foraging, *Morus bassanus*, offshore renewables, population model, wildlife telemetry

Introduction

The number of offshore wind turbines is predicted to increase tenfold over the next decade, particularly in the

shallow seas of Europe, making predicting the likely ecological impacts of these developments a conservation priority (Infield 2013). The impact of offshore wind farms on the internationally important populations of seabirds that forage in the seas around the UK is of particular concern (Masden *et al.* 2012; Furness, Wade & Masden

2013). Evidence from both onshore and offshore wind farms shows that, for some birds, both direct mortality due to collisions and indirect disturbance could have significant negative impacts (Marques *et al.* 2014). However, estimates of mortality from collisions with turbines are frequently based on partial or subjective data (Ferrer *et al.* 2012). Moreover, accurate data on spatial, temporal and activity-specific variability in flight heights are lacking, especially for seabirds (Johnston *et al.* 2014).

To date, seabird flight heights have largely been estimated using ship-based surveys involving surveyors' subjective assessment by eye, the accuracy of which remains unquantified (Cook *et al.* 2012; Johnston *et al.* 2014). Radar can quantify flight heights and tracks much more accurately (Desholm *et al.* 2006), but provides data over only a limited area (maximum range typically 6 km) and is costly. An additional limitation of both ship-based surveys and radar is that the provenance, breeding status and in many cases age and sex of birds cannot be determined, yet these parameters are needed to model population-level consequences of predicted mortality more accurately.

A recent review of the vulnerability of marine bird populations to wind farms identified northern gannets *Morus bassanus* (Linn.) as a species of particular concern (Furness, Wade & Masden 2013). Britain and Ireland hold ~65% and 85% of the world and European breeding populations of gannets, respectively (Wanless, Murray & Harris 2005; Murray, Harris & Wanless 2015). Planning consent for several major offshore wind farms has just been granted in close proximity to major North Sea Gannet colonies (Furness & Wanless 2014). Tracking studies suggest that gannets typically travel at heights below 10 m but may ascend to above 20 m during foraging, as they search for prey and attain height, and therefore potential energy, prior to plunge-diving (Garthe *et al.* 2014). Foraging gannets may thus be at significant risk of colliding with wind turbine blades, which may sweep an area from 22 m above sea level at highest astronomical tide (the lowest blade clearance currently permitted; UK Maritime and Coastguard Agency 2008) to around 160 m above sea level or higher (Rothery, Newton & Little 2009; Furness, Wade & Masden 2013). However, collision risk is currently difficult to estimate because accurate data on flight heights and behaviour in proposed wind farm sites are lacking.

Global Position System (GPS) loggers are increasingly used to record the movements of birds (e.g. Wakefield *et al.* 2013), and can provide information on height as well as latitude and longitude. However, whilst they are accurate to <10 m in the horizontal plane, vertical measurement errors may be an order of magnitude greater (Ladetto *et al.* 2000). Alternatively, height may be estimated by recording atmospheric pressure and comparing it to that at sea level using the barometric formula (Berberan-Santos, Bodunov & Pogliani 1997; Wallace & Hobbs 2006). For example, the flight heights of tropical seabirds have been estimated by assuming that atmospheric pressure recorded at a reference location, such as a bird's breeding colony, is representative of that at tracking locations (Weimerskirch *et al.* 2005). Errors incurred using this approach are tolerably small in tropical regions, where atmospheric pressure usually varies little over wide areas, but at temperate latitudes, surface atmospheric pressure is much more labile in time and space, potentially introducing large errors. To obtain more accurate estimates of flight height in these areas, pressure loggers must therefore be calibrated frequently against pressure at sea level in their vicinity (Li, Harvey & Gallagher 2013). The reliability of such barometric altitude estimates can be assessed by examining the correlation with GPS altitude because, whilst individual GPS altitudes are unreliable, errors have a Gaussian distribution with a mean of zero (Whang & Ra 2008). Hence, a reliable pressure-logger-based estimate should correlate with GPS-derived altitude.

The Bass Rock (56°6′N, 2°36′W) supports the world's largest breeding population of gannets (~75 000 breeding pairs in 2014; Murray, Harris & Wanless 2015), yet several large wind farms have been scheduled for construction in its vicinity within the next 5 years (Marine Scotland 2014; Fig. 1). Taking this system as an example of one in which the potential effects of offshore wind farms on seabirds are of concern, we aimed to assess how the use of different flight-height estimation methods affects the predicted risk of birds colliding with turbines and hence the potential impact on seabird population viability. We combined GPS tracks of gannets breeding at the Bass Rock in three consecutive years (2010–2012) with data from bird-borne pressure loggers in 2011 and 2012 to estimate the foraging ranges and densities of birds at sea, their flight heights during different activities, and spatial variation in flight height and potential collision risk during foraging trips. We then compared these results to collision risks predicted using flight heights reported from ship-based and radar-based studies.

Materials and methods

STUDY SITE AND SAMPLING

Fieldwork took place at Bass Rock between mid-June and mid-August over three consecutive breeding seasons (2010–2012). Adult gannets raising chicks (*n* = 49 in 2010, 25 in 2011, 33 in 2012) were caught at the nest using a 6-m telescopic pole fitted with a wire crook (*n* = 55 birds in total; most were sampled in >1 year). Upon initial capture, birds were fitted with a metal British Trust for Ornithology ring and an individually numbered plastic colour-ring (Wakefield *et al.* 2013). An i-gotU 200/600 GPS logger (Mobile Action Technology, Taipei, Taiwan) weighing ~30 g was attached to the upper side of the central three tail feathers of each bird using Tesa© tape (Milton Keynes, UK). In addition, a subset of these birds caught in 2011 (*n* = 11) or 2012 (*n* = 5) was equipped with a pressure logger (MSR-145; MSR Electronics, Seuzach, Switzerland) weighing 18 g and taped to the underside of the central tail feather. Air pressure and temperature were logged at 1 Hz, which resulted in a pressure logger battery life of ≥7 days. GPS-loggers, programmed to record at either high
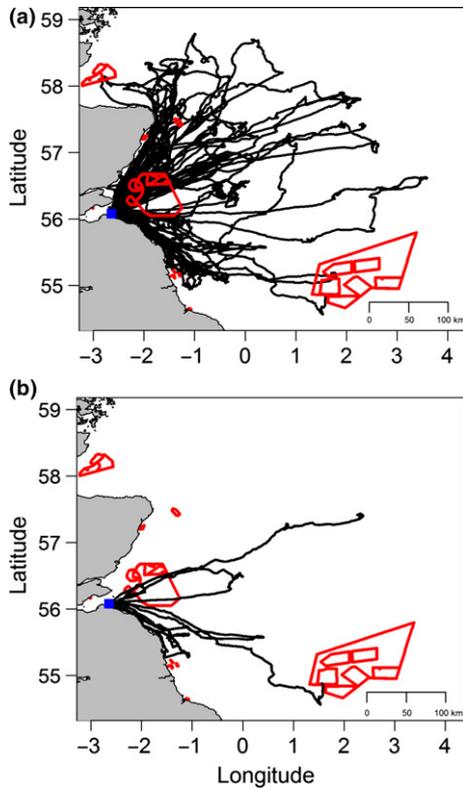
Fig. 1. Foraging tracks of chick-provisioning northern gannets from Bass Rock during June–August in 2010–2012 (black) and locations of proposed wind farms: (a) all tracks for birds equipped with Global Position System-loggers and altitude loggers (n = 54 trips by 16 birds); (b) tracks recorded at high resolution (1 Hz; n = 7 trips by 7 birds). For details of wind farm sites, see Marine Scotland (2014). *Square* shows location of Bass Rock.

resolution (1 Hz; i.e. once per second) or standard resolution (2-min intervals), were deployed along with pressure loggers. We collected high-resolution GPS data to discriminate behaviours over very short time intervals, allowing us to assess flight heights during different activities accurately. However, GPS battery life was ~20 h at this resolution, which is less than the average trip duration in some years (Hamer *et al.* 2007; Wakefield *et al.* 2015). Standard-resolution data were not used to examine activity-specific heights but covered much longer time periods, allowing us to track individual birds for up to 7 days and examine broad-scale spatial variation in flight heights during trips. Birds were recaptured and loggers retrieved after ≤10 days (total handling time ~15 min on each capture). After release, birds returned immediately to their nest and resumed normal behaviour. The maximum weight of loggers deployed on birds (48 g) was <2% of body mass (3 kg). Trip durations of instrumented birds were very similar to those of non-instrumented birds observed via a remote radio link using a Mobotix© (Uxbridge, UK) surveillance camera installed in the same area of the colony (Cleasby *et al.* 2015b), and previous studies (e.g. Hamer *et al.* 2000) found that similar devices had no discernible effects on trip durations or body mass.

BAROMETRIC ESTIMATION OF HEIGHT

We used the barometric formula (Berberan-Santos, Bodunov & Pogliani 1997; Wallace & Hobbs 2006) to estimate height z (m) above sea level:

$$z = -\frac{kT}{mg}\ln\left(\frac{P}{P_0}\right),\qquad\text{eqn 1}$$

where P_0 and P are the atmospheric pressures (Pascals) at sea level and at height z (m), 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 (m s^{-1}); and T is the temperature of the atmospheric layer between z_0 and z. Validation of this method using loggers placed at different known heights (see Appendix S1 in Supporting Information for details) indicated that the mean absolute error of height estimated by recording pressure was 0·88 m (range 0·32–1·92 m). Precision of height estimates (σ_z) decreased linearly as the interval, Δt, between observations of P_0 and P increased (Fig. S1). At Δt = 11·5 min (the median value used in our study), σ_z was 1 m.

For both the high-resolution and standard-resolution data sets, we used GPS data to categorize the behaviour of birds based on their location and speed of travel as (i) at the colony, (ii) in flight or (iii) on the water (Wakefield *et al.* 2013). Dives were identified by a rapid increase in pressure above ambient. To calculate birds' heights during periods of flight, pressure data P were smoothed using a running median calculated using a moving window of 11 observations (i.e. over a period of 11 s), centred on each successive location. Prior to smoothing, estimates of pressure ≤5 s before and ≤3 s after dives were removed, as there was typically high variation in pressure within these periods due to acceleration and turbulence. Similarly, following smoothing, we discounted short periods of flight (<3 min) and both the initial and final 60 s of each flight period. For the remaining cases, P_0 was defined where we had high-resolution GPS data as the value of P measured 5 s after the current flight period began. We assumed that whilst at this point the bird would still be flying at low altitude, initial Bernoulli effects associated with increasing airspeed during take-off (Chanson 2009) would have subsided. However, this degree of behavioural discrimination was not possible using the standard-resolution GPS data, so we defined P_0 in these cases as the value of P 10 s before the end of the previous period spent on the water. At the onset of a foraging trip, during the initial bout of flight, P_0 was defined as the pressure at the colony reduced to sea level using eqn 1 (the height of the colony was known). We also assessed the accuracy of a simpler calibration method in which this value of P_0 was used to estimate height throughout foraging trips.

DATA ANALYSIS

Density of birds at sea

The utilization distribution (UD) of breeding birds from Bass Rock was estimated by calculating the kernel density of bird locations (data sets pooled across all 3 years). Kernel density was estimated on a 1-km^2 grid using the R package adehabitatHR (Calenge 2006). Following Wakefield *et al.* (2013), we then estimated the density of birds within each grid-square (d) as:

$$d = \hat{u}_{i,x}N,\qquad\text{eqn 2}$$

where $\hat{u}_{i,x}$ is the empirical probability density of use of cell x by bird i and N is the size of the colony (75 000 breeding pairs in 2014; Murray, Harris & Wanless 2015). The number of breeding

pairs was used as a measure of *N*, rather than the number of breeding individuals, because one member of a pair usually remains at the colony attending the chick (Lewis *et al.* 2004). This approach generated an estimate of the number of breeding gannets expected in each grid cell during the peak chick-rearing period (June–August) each year.

Discrimination of foraging and commuting behaviour

Gannets primarily forage by plunge-diving during daylight (Hamer *et al.* 2009). Following Wakefield *et al.* (2013), we assumed therefore that daytime GPS locations characterized by slow flight speeds and high turning rates indicated foraging (excluding periods when birds were on the water; details and validation of discrimination criteria in Appendix S3). We used the 50% and 95% UDs of foraging locations to represent the core and wider foraging areas, respectively.

Variation in flight heights

We used high-resolution tracking data to examine flight heights during periods of commuting and foraging, and standard-resolution data (i.e. locations at 2-min intervals) to examine spatial variation in flight height (high-resolution data were more precise but included incomplete trips, which could have biased any spatial analysis of heights because birds seldom forage on the return legs of trips; Hamer *et al.* 2009). Flight height was modelled as a log-transformed response variable using a generalized additive mixed model (GAMM) with Gaussian errors in the ʀ package mgcv (Wood 2006). There were some estimated heights ≤0 m (2·7% of values), and these were included in the analysis by adding the minimum estimated height (absolute value) to all cases (to permit log-transformation); data are then presented following back-transformation including subtraction of minimum estimated height in each case. The model included an isotropic spatial smooth of longitude and latitude, permitting spatial predictions of flight height (Wood 2003). Trip identity, nested within bird identity, was included as a random effect. To assess the decay in precision of pressure calibrations over long periods of flight, we also modelled the residual variance in flight height as a function of time elapsed since the most recent calibration of P_0 using the varPower variance function in the nlme ʀ package (Pinheiro & Bates 2000). Flight-height estimates (including negative values) are quoted as medians plus interquartile ranges (IQR).

In addition, we used a binomial GAMM to examine spatial variation in the probability of a bird flying at collision-risk height, that is within the height envelope swept by wind turbine rotors. For this analysis, flight heights between 30 and 160 m above sea level (asl) were scored as 1 (at risk of collision) and all other observations were scored as 0 (not at risk of collision). The risk envelope used here represents a general case rather than a specific turbine design. Fixed and random explanatory covariates were as for the flight-height model described above.

Modelling collision risk

We used a mechanistic collision-risk model (Band 2012; the de facto standard in UK wind farm impact assessments) to assess the potential impact on gannets from Bass Rock of the two closest proposed wind farms within the Firth of Forth area (sites A and B in Fig. 2). Other wind farm developments are also planned,
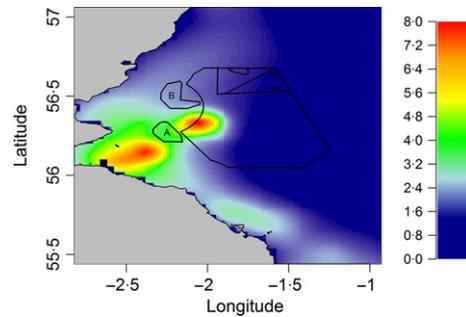
Fig. 2. Estimated density of chick-provisioning northern gannets (birds km^{-2}) in the vicinity of Bass Rock (black square) and the proposed wind farms close to the Firth of Forth (solid lines; sites A and B labelled). Based on all birds equipped with Global Position System-loggers (*n* = 516 trips by 55 birds).

but our aim was to investigate the importance of accurate flight-height assessments for collision-risk modelling rather than to predict the potential cumulative impact of all proposed wind farms in the region. For comparison, we used both 'basic' and 'extended' versions of the model, treating flight-height data as categorical and continuous, respectively (see Appendix S2 for details).

We ran the models for putative turbine avoidance rates of 98·5% and 99%; a recent comprehensive review of behavioural responses to turbines by different species of seabirds (Cook *et al.* 2014) recommended an avoidance rate of 99% for use with gannets in the basic collision-risk model but considered there were insufficient data to derive a rate for use with the extended model. However, for species with more reliable data on turbine avoidance rates at different spatial scales, the recommended avoidance rate for use in the extended model was consistently 0·5–0·6% lower than that for use in the basic model (Table 7·2 in Cook *et al.* 2014). Hence, taking a precautionary approach, we considered that the lower avoidance rate may be more appropriate for the extended model, although further data are needed to confirm or refute this. To account for the fact that birds do not fly continuously at sea (Hamer *et al.* 2000), we multiplied collision-risk estimates in each case by the proportion of occasions when birds were classified as in flight at each site (average of 82%).

To examine how different methods of recording flight height affected collision-risk estimates, we also ran collision-risk models using published gannet flight heights estimated subjectively by human observers (Cook *et al.* 2012; Johnston *et al.* 2014) in conjunction with our spatial distribution data. Cook *et al.* (2012) modelled gannet flight heights, allowing estimation of the proportion of flights within different collision-risk envelopes, based on ship-based, land-based and radar-based surveys, whilst Johnston *et al.* (2014) presented a continuous gannet flight-height distribution estimated using observer data from 32 wind farm sites. In summary, we compare collision risks estimated: using altimeter data collected during this study in (i) the basic and (ii) the extended models; (iii) using data from Cook *et al.* (2012) in the basic model; and (iv) using data from Johnston *et al.* (2014) in the extended model.

Results

FORAGING TRACKS AND DENSITIES OF BIRDS AT SEA

The foraging ranges of birds extended up to 536·5 km from the colony (mean ± SD = 180·9 km ± 106·0,
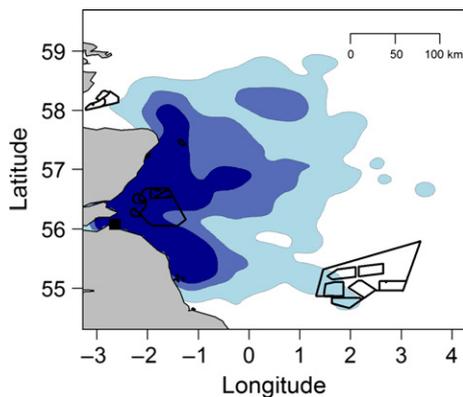
$n = 516$ trips by 55 individuals) and encompassed proposed wind farm sites close to the Firth of Forth and elsewhere in the North Sea (Fig. 1). Gannet densities during 2010–2012 were high not only close to the Bass Rock but also within proposed wind farm sites close to the Firth of Forth (Fig. 2). Moreover, the foraging UD indicated that the core area of foraging activity (50% foraging UD) overlapped extensively with proposed wind farm sites close to the colony (Fig. 3).
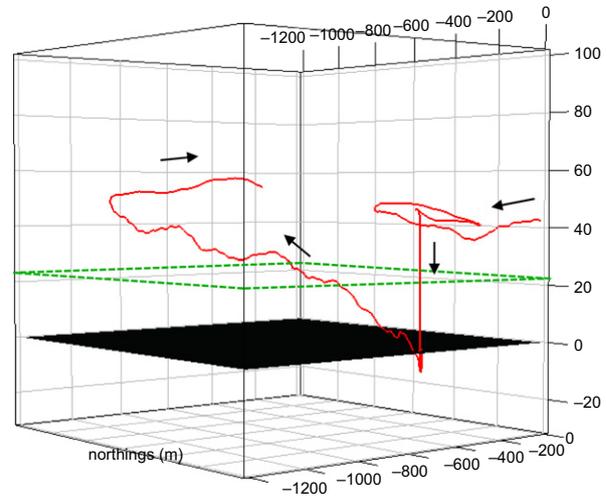
FLIGHT HEIGHTS

High-resolution data

Data collected using GPS and pressure loggers allowed us to reconstruct the three-dimensional movements of birds (Fig. 4). Estimates of height obtained using pressure loggers were significantly positively correlated with GPS-estimated heights ($r = 0.58$, $P < 0.01$), with a median precision of ±1 m (see Materials and methods section). We are therefore confident that they accounted appropriately for spatiotemporal variation in atmospheric pressure at sea level. In contrast, using P_0 values recorded at the colony at the beginning of each trip gave estimates that were about 40% higher on average and poorly correlated with GPS-estimated heights ($r = 0.23$, n.s.). We therefore deemed this technique unreliable and did not consider it further.

Flight height was bimodal, with significantly lower heights during commuting bouts (median = 11·5 m, $n = 738$, IQR = 6·1–21·7 m) than during foraging bouts (median = 26·5 m, $n = 464$, IQR = 9·7–46·1 m; randomization test, $P < 0.001$; see Appendix S4 for details). Hence, foraging birds tended to be at or around collision-risk height (Fig. 5). Although the second peak was discernible across all locations visited by birds (Fig. 5a), it was more prominent within the locations of proposed wind farms (Fig. 5b), where a risk envelope of 20–120 m

Fig. 4. Five-minute section of a three-dimensional foraging track of a gannet breeding at Bass Rock, recorded using Global Position System (x, y) and pressure difference (z). The bird moves from right to left, circling once, before plunge-diving to 6 m below sea level. On returning to the surface, it takes off and again begins circling. The dotted green line indicates that the bird spent most of this time above the minimum collision-risk height (22 m above sea level).

Fig. 3. Foraging utilization distribution (UD) of chick-provisioning northern gannets tracked from Bass Rock (black square) during June–August in 2010–2012, together with locations of proposed wind farm sites. Contours show 50% (darkest), 75% (intermediate) and 95% (palest) UDs.
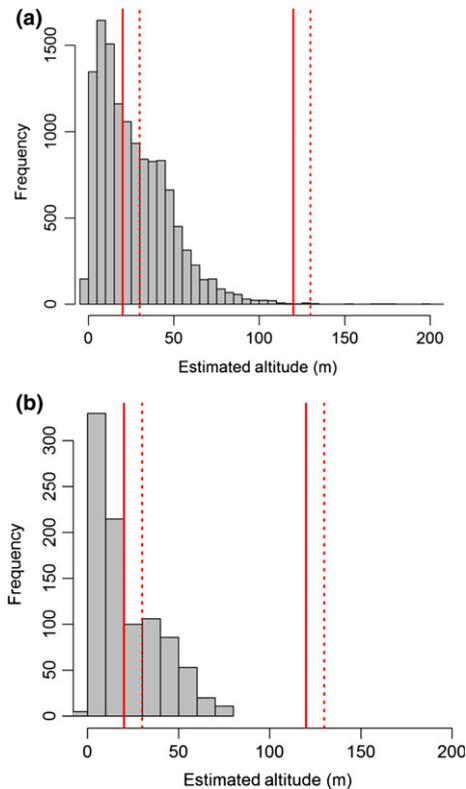
Fig. 5. Distribution of estimated flight heights for (a) all locations visited by birds ($n = 16$ birds, 12989 observations) and (b) area encompassed by proposed wind farms close to the Firth of Forth ($n = 11$ birds, 962 observations; five birds equipped with altitude loggers never visited this area). Vertical lines denote two potential collision-risk envelopes (solid lines, 20–150 m above sea level; dashed lines, 30–160 m above sea level).

asl contained ~10% more observations than one of 30–130 m asl. There was no significant difference between flight heights determined using high-resolution GPS data (median = 13·3 m, *n* = 1202 height estimates, IQR = 6·9–34·6 m) and those determined using the much larger standard-resolution data set (median = 22·0 m, *n* = 12621 height estimates, IQR = 10·1–40·0 m; randomization test, *P* = 0·5; see Appendix S5).

Spatial analysis

There was significant spatial variation in flight heights of birds (Table 1) and in the probability of flying at collision-risk height (Table 2). Areas of high average height were all >100 km from the colony, with lower average heights occurring mainly, though not entirely, inshore and closer to the colony (Fig. 6). There was also significant variation among individuals in flight height (Table 1) and in the probability of flying at collision-risk height (Table 2). Although the precision of our height estimates decreased linearly as the interval between observations of P_0 and P increased (Fig. S1), the time elapsed since measuring P_0 had no effect on the variance of flight-height estimates and including this term in the model of flight height did not improve its performance (Table 1).

COLLISION-RISK ESTIMATES

Mortality predicted using combined altimeter and GPS data was 11·6 times that obtained using the overall distribution of flight heights estimated by observers at sea combined with GPS data (cf. extended models, Table 3) and 5·9 times that obtained by assuming that 5% of birds fly at collision-risk height, based on observer and radar data (cf. basic models, Table 3). Using combined altimeter and GPS data, the basic model with 99% avoidance, which we consider the most reliable estimate, suggested that ~300 breeding adults could be killed per month during the chick-rearing period each year as a result of collisions with turbines at the two planned wind farm sites included in the model (Table 3).

Table 2. Generalized additive model of the probability of gannets flying within a collision-risk envelope of 30–160 m)

Variable	Estimate	Lower 95% CI	Upper 95% CI	P-value	ΔAICc
Fixed effects					
Intercept	−0·78	−1·13	−0·42	<0·001	NA
Isotropic smoothers					
s (Lon, Lat)	d.f. = 26·29			<0·001	+948
Random effects					
Trip ID	0·72	0·55	0·94		+98
Bird ID	0·53	0·29	0·96		+592

## Discussion

DATA COLLECTION

We found that standard-resolution and high-resolution GPS data (recorded at intervals of 2 min and 1 Hz, respectively), combined with pressure data collected at 1 Hz, resulted in similar gannet flight-height estimates. The use of the standard-resolution GPS-tracking may resolve changes in behavioural state less finely but allows birds to be tracked for longer periods. Time since last calibration had little effect on the precision of our flight-height estimates, perhaps because atmospheric conditions were relatively quiescent during our study. However, it would be desirable to establish how precision decays with this parameter in more dynamic weather conditions, for which further study would be required. Our data show that calibration using pressure recorded in the colony at the beginning of the trip resulted in biased and unreliable estimates of height, so we do not recommend this method, at least in temperate regions or for species that range widely.

The data presented here were all obtained in relatively calm periods, during mid-summer, in years of near-average prey availability (inferred from relative foraging distances; median ± IQR = 175 ± 70 km in 2010, 109 ± 110 km in 2011, 160 ± 145 km in 2012, compared

Table 1. Generalized additive model of gannet flight height (*n* = 12989 locations from 54 foraging trips by 16 birds)

Variable	Estimate	Lower 95% CI	Upper 95% CI	P-value	ΔAICc
Fixed effects					
Intercept	3·02	2·80	3·24	<0·001	NA
Isotropic smooths					
s (Lon, Lat)	d.f. = 21·98			<0·001	+508
Random effects					
Trip ID	0·36	0·23	0·57		+640
Bird ID	0·38	0·30	0·48		+1360
Variance functions					
Time elapsed since P_0 measured	−0·001	−0·004	0·004		−136

ΔAICc is the change in the Akaike Information Criterion (corrected for finite sample sizes) associated with deleting a term from the best fitting model; +ΔAICc indicates that the model fit is worse after deleting a term; ΔAICc <2 indicates that removing the term has little effect on the model. d.f., estimated degrees of freedom for the isotropic smooth, reflecting sinuosity.
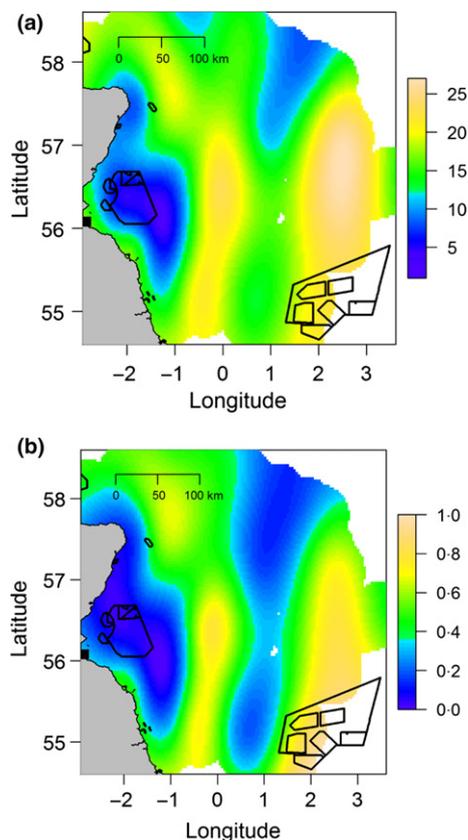
Fig. 6. Variation in (a) mean flight height (m) and (b) the probability of flying within a collision-risk envelope of 30–160 m, across the sampled foraging distribution of gannets breeding at Bass Rock (black square). Locations of proposed wind farms within the foraging range are also shown.

Table 3. Predicted potential collisions per month with wind turbines at two recently consented offshore wind farms, for gannets rearing chicks at Bass Rock

| Model | Flight-height data | | | Avoidance rate | |
	Type	Recording method	Source	98·5%	99%
Basic	Categorical*	Ship-/shore-based observers and radar	Cook et al. (2012)	80	**53**
	Continuous	Pressure loggers	This study	467	**311**
Extended	Continuous	Ship-based observers	Johnston et al. (2014)	**26**	16
	Continuous	Pressure loggers	This study	**304**	203

Figures in bold indicate rates considered most appropriate based on data in Cook et al. (2014).
*Taking the proportion of flights within the modelled collision-risk envelope (29–159 m asl) to be 5%; estimated from height distribution of survey data (figure 3·6 in Cook et al. 2012).

to long-term average of 155 km, range of annual medians = 105 ± 133–238 ± 193 km; Hamer et al. 2007; Wakefield et al. 2015). The foraging ranges of gannets vary with population size and per capita prey availability (Hamer et al. 2007; Wakefield et al. 2013), and their foraging behaviour also varies in relation to weather conditions and feeding opportunities including potential prey species (Amélineau et al. 2014; Cleasby et al. 2015b). Hence, the potential occurrence of gannets in the turbine envelope of different proposed wind farm sites will also vary with these factors resulting in both spatial and temporal variability in collision risk. Moreover, foraging ranges of breeding birds are frequently longer during incubation than chick-rearing, and the movement patterns of juvenile and immature birds, non-breeding adults and failed breeders are only poorly understood but could also encompass much larger foraging areas than those of breeding birds (Votier et al. 2011). Foraging ranges and behaviour also differ between males and females (Cleasby et al. 2015b), potentially resulting in an asymmetry in male–female collision risks. In addition, we found that flight heights varied significantly among individuals, in keeping with consistent individual variation in foraging locations, movements, diets and diving behaviour (Patrick et al. 2015; Wakefield et al. 2015), producing likely marked differences among individuals in collision risk. Further data are needed on all of these factors in order to make a full assessment of the collision risks posed to gannets and other potentially vulnerable species by offshore wind farm developments.

FORAGING AREAS AND FLIGHT HEIGHTS

Using high-resolution (1 Hz) data, we estimated that gannets flew at a median height of 12 m whilst commuting and 27 m during foraging bouts, which corresponds reasonably well with a previous estimate of 37 m whilst foraging (Garthe et al. 2014). In contrast, flight heights estimated from ship-based surveys are much lower, with fewer than 10% of flights exceeding 20 m (Cook et al. 2012). This discrepancy may partly reflect a high proportion of survey data from sites in the southern North Sea where gannets are mainly seen during migration, when they may spend little time foraging. Radar-based estimates were also low (mean height c. 10 m; Parnell et al. 2005), probably because they were site-specific with a maximum range within c. 6 km of land, meaning that these estimates are likely to represent a high proportion of birds commuting along the coast.

In keeping with spatial density estimates from ship-based surveys, areas with the highest density of gannets at sea were close to the colony (Camphuysen et al. 2012) and overlapped proposed wind farm sites close to the Firth of Forth. Many of these birds were apparently commuting to or from foraging areas further from the colony, at heights typically below 15 m, resulting in a relatively low probability of flying at 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 a large number of potential collisions within proposed wind farm sites despite a low average flight height. Further from the colony, average heights were greater as a result of relatively little commuting flight in the distal sections of trips, probably combined with spatial variation in foraging behaviour; birds rely on momentum to attain depth during V-shaped dives and these were significantly deeper in stratified water offshore than in mixed inshore waters close to the colony (Cleasby *et al.* 2015b), suggesting that birds were diving from greater heights offshore.

POTENTIAL POPULATION-LEVEL EFFECTS

Using our data on flight heights, the basic Band (2012) collision-risk model with 99% avoidance and the extended model with 98·5% avoidance yielded very similar estimates for the two sites in our analysis, predicting that during chick-rearing, 311 and 304 breeding adults, respectively, could be killed each month. There is great uncertainty over actual avoidance rates (Cook *et al.* 2014), but taking a figure of ~300 collisions per month and assuming similar foraging behaviour during incubation and chick-rearing, the cumulative predicted mortality during the breeding season (mid-April to mid-September) each year would be ~1500 adults.

To put these data into perspective, a population model for gannets at Bass Rock, based on a population of 48 000 breeding pairs in 2004, suggested that additional mortality of 2000 birds per year, estimated to comprise 1400 adults and 600 immature birds, would be sufficient to cause a sustained decrease in breeding population size (WWT Consulting 2012). This threshold may have been underestimated, since the breeding population at Bass Rock has apparently increased by an average of 2700 pairs per year since then (Murray, Harris & Wanless 2015). Nonetheless, our estimate of predicted adult mortality due to collision with turbines is sufficiently high to cause concern. Moreover, it may be conservative: adults are present at the colony for 9 months each year (Nelson 2002), they may be killed at other proposed wind farms not considered in our study, and we assume a minimum blade clearance of 30 m, whereas this may be to be up to 8 m lower (Marine Scotland 2014). Hence, there is an urgent need for further data, both for gannets and for other high-priority species such as large gulls, to refine collision-risk estimates and mortality thresholds for long-term population viability, and for strategic monitoring at key sites to determine whether predicted collision mortality is realized and has significant effects on population trajectories. We also strongly recommend that, at sites with high potential collision risk, the minimum permitted clearance of turbine blades should be raised from 22 to 30 m above sea level.

Data accessibility

GPS logger and barometric logger data are available free of charge via Birdlife International's Seabird Tracking Database (http://seabirdtracking.org/mapper/contributor.php?contributor_id=204) and the Dryad Digital Repository doi: 10.5061/dryad.1ds1q (Cleasby *et al.* 2015a).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Validation of barometric altitude estimates.

Appendix S2. Discrimination of foraging and commuting behaviour.

Appendix S3. Statistical comparison of foraging and commuting flight heights.

Appendix S4. Statistical comparison of flight heights calculated using high-resolution and standard-resolution data.

Appendix S5. Modelling collision risk.

Table S1. Data used in mechanistic collision-risk models.

Fig. S1. Precision of height estimates based on pressure recorded at the Bass Rock vs. interval between pressure observations.