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Influence of wind on kittiwake *Rissa tridactyla* flight and offshore wind turbine collision risk

Jacob G. Davies¹ · Philipp H. Boersch-Supan² · Gary D. Clewley¹ · Elizabeth M. Humphreys¹ · Nina J. O'Hanlon¹ · Judy Shamoun-Baranes³ · Chris B. Thaxter² · Ewan Weston⁴ · Aonghais S. C. P. Cook²

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Abstract

Offshore windfarms are a potential threat to seabirds, partly due to collision risk with turbine blades. Wind influences the mode, height and speed of seabird flight, and therefore the risk of collision with turbines. We investigated how wind influences the flight of black-legged kittiwakes *Rissa tridactyla*, a gull of conservation concern, in order to incorporate these findings into collision risk estimates and identify mitigation measures. We used GPS telemetry data (23rd June to 10th August 2021) from 20 kittiwakes breeding in Aberdeenshire, UK (57.385°N, 1.868°W) to estimate the effect of wind on behavioural state, proportion of flight at collision risk height, probability of collision when within the rotor-swept zone, and overall collision risk. We found that as windspeed increased, kittiwakes commuted less and rested more. With increasing windspeed, kittiwakes spent a considerably smaller proportion of their flight time in the rotor-swept zone, but had a slightly higher probability of collision while in it. Uncertainty was high for most relationships between windspeed and kittiwake flight metrics. The overall effect of increasing windspeed on collision risk was negative, although we did not model avoidance rate. Effects of windspeed on collision risk were largely mediated through effects on commuting flight, and contingent on wind direction. Collision risk estimates incorporating the effects of windspeed may have greater precision and accuracy, but considerable uncertainty in windspeed-flight parameter relationships remains. Therefore although kittiwake collision risk may be mitigated by raising the 'cut-in' windspeed above which wind turbines generate power, the magnitude of this effect is uncertain.

Keywords Behavioural ecology · Telemetry · Seabird · GPS error · Offshore windfarm · Renewable energy

Introduction

Offshore windfarms are being developed rapidly in order to reduce greenhouse gas emissions and thus mitigate climate change (IEA 2024). However, offshore windfarms pose an emerging threat to seabirds and other marine wildlife through a range of mechanisms, including displacement and

collision with turbine blades (Drewitt and Langston 2006; Schuster et al. 2015; Dias et al. 2019). One seabird species that is potentially threatened by the current proliferation of offshore windfarms is the black-legged kittiwake *Rissa tridactyla* (hereafter 'kittiwake'), which spends a relatively high proportion of time flying at the height of wind turbine blades and thus at risk of collision (Furness et al. 2013). The global kittiwake population has declined by ~40% since 1975, and the species is currently evaluated on the IUCN Red List as 'Vulnerable' (Birdlife International 2023). In the UK, kittiwakes are on the Birds of Conservation Concern Red List due to a severe long-term decline in breeding population size (Stanbury et al. 2021). Kittiwakes are chiefly threatened by declines in prey availability due to climate change and overfishing (Burthe et al. 2012; Paredes et al. 2014; Wanless et al. 2018). Offshore windfarm developers must assess whether a proposed windfarm will adversely affect Natura 2000 sites, for example Special Protection

Responsible Editor: T. Clay.

✉ Jacob G. Davies
jacob.davies@bto.org

- 1 British Trust for Ornithology Scotland, Stirling, UK
- 2 British Trust for Ornithology, Thetford, UK
- 3 Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, The Netherlands
- 4 Comers Wood Croft, Midmar, UK

Areas designated for their breeding kittiwake populations. Therefore kittiwake collision risk is a key concern to industry; residual uncertainty around kittiwake collision risk impedes decision-making around offshore windfarm development, representing a potential barrier to meeting obligations to develop renewable energy to mitigate climate change (Black et al. 2019). Environmental conditions such as weather, food availability, time of day and season can influence seabird behaviour and therefore, potentially, collision risk (Marques et al. 2014; Ainley et al. 2015; Thaxter et al. 2015).

For seabirds, wind alters the energetic costs of movement in the marine environment (Gabrielsen et al. 1987; Elliott et al. 2014), and modifies the ease of detecting and catching prey (Finney et al. 1999). By altering their behavioural state (hereafter referring to the states of rest, commuting or foraging) or flight speed (hereafter referring to ground speed), mode or height, seabirds have some capacity to reduce the energetic costs presented by wind, or to exploit the opportunities presented by wind (McLaren et al. 2016; Lane et al. 2019; Ventura et al. 2020). The relationship between wind-speed and flight behaviour varies considerably between species, apparently being strongly influenced by flight mode. For example, the relationship between windspeed and flight height is typically positive for diving shearwaters and large alcids, whereas for gulls, skuas and phalaropes this relationship is typically negative (Ainley et al. 2015). This relationship is also strongly contingent on wind direction: for example, lesser black-backed gull *Larus fuscus* flight height in the North Sea decreases with absolute windspeed, but increases with tailwind speed (Vanermen et al. 2018). Seabirds fly more slowly in headwinds than in crosswinds or tailwinds (Spear and Ainley 1997). By increasing their wingbeat strength (but not wingbeat frequency), kittiwakes can increase their airspeed to partially, but not completely, compensate for headwinds (Elliott et al. 2014; Collins et al. 2020).

Although the effects of wind on seabird flight metrics are well known for some species (Elliott et al. 2014; Collins et al. 2020), explicit investigations of the effects of wind on components of seabird collision risk itself are rare. For example, Ainley et al. (2015) investigated the effect of wind on proportion of flight at risk height by seabird species group, but not the effect of wind on behavioural state, avoidance rate or probability of collision. Opportunities are therefore being missed to mitigate collision risk, or to reduce its uncertainty. Also, although new technologies are increasingly informing flight height distributions, most collision risk models still use data derived from visual observations during low wind conditions (Johnston et al. 2014). The full environmental variation that seabirds experience is therefore not being incorporated into collision risk estimates,

potentially leading to bias. The recent proliferation of seabird telemetry data, used with freely-available high resolution weather data, could help inform the investigation of the effects of windspeed on collision risk.

Environmental authorities and developers use collision risk estimates to help estimate the potential impact of proposed offshore wind farms on seabird populations. Collision risk models seek to estimate two main quantities: (i) the number of birds exposed to potential collision; (ii) the probability that a bird exposed to potential collision actually collides. A range of collision risk models exists, with models differing mainly in their specification of factors such as probability of collision, bird shape or angle of approach, and in how they incorporate uncertainty (Masden and Cook 2016). In collision risk models which do not have a stochastic component, for example the extended Band model which is commonly used in the UK (Band 2012), flight height and speed are typically considered to be invariant to environmental conditions (Masden and Cook 2016). Non-stochastic collision risk models that take into account the effects of wind (Desholm 2006; Holmstrom et al. 2011) are more rarely used (Masden and Cook 2016), and focus solely on wind's effects on flight speed, rather than behavioural state or flight height. The magnitude of the risk of a flying bird colliding with a given wind turbine is influenced by the bird's behavioural state, its flight height (determining the proportion of flight at collision risk height) and its flight speed (determining the probability of collision for flights in the rotor-swept zone (the area swept by turbine blades); Masden et al. 2021); all of these aspects of flight may be influenced by environmental factors (Marques et al. 2014). Environmentally-driven variation in seabird flight represents unknown but potentially important variation in seabird collision risk that is currently not accounted for in collision risk modelling. Reducing uncertainty in seabird collision risk, for example by quantifying the influence of environmental conditions on flight activity, is a priority to allow offshore wind farm development for the mitigation of climate change (Searle et al. 2023).

In this study, we use GPS telemetry data and weather data to estimate the effects of wind on components of kittiwake collision risk. Firstly, we aim to estimate the relationships between kittiwake flight speed and height and behavioural state and windspeed. In order to better understand these relationships between kittiwake flight and windspeed (hereafter referring to absolute windspeed, i.e. as a scalar rather than as a vector), we also estimate the relationships between kittiwake flight and tailwind and crosswind speed. Using the fitted relationships between windspeed and kittiwake flight height and speed, we then describe how windspeed influences proportion of flight at collision risk height, probability of collision and (by estimating the probability of different

behavioural states with windspeed) overall collision risk. We estimate these components of collision risk – behavioural state, proportion of flight at risk height, probability of collision while in rotor-swept zone – at a range of potential windspeeds and turbine sizes, to inform how best to reduce kittiwake mortality arising from collision with offshore wind turbines.

Materials and methods

Study site and tagging

21 breeding adult kittiwakes were fitted with UvA-BiTS GPS tags (Bouten et al. 2013) near Whinnyfold, Aberdeenshire, UK (57.385°N, 1.868°W) between 23rd and 26th June 2021 (O’Hanlon et al. 2024). This kittiwake colony is close to several operational and planned offshore wind-farms. Tags were fitted by trimming an area of feathers in the centre of the bird’s back, and then supergluing the tag (which itself had been superglued to a muslin base) onto this area. The total mass of the GPS device, attachment material and additional identifying marks summed to 10.03 ± 0.06 g (mean \pm SD), representing 2.25 to 2.73% of the body mass of the tagged kittiwakes (<3% of body mass is the guideline for avoiding negative tag effects; Phillips et al. 2003). All tagging activities were approved by the Special Methods Technical Panel, part of the British Trust for Ornithology Ringing Committee; see O’Hanlon et al. (2024) for details of monitoring for adverse tag effects. Tags remained attached until they fell off naturally between 13th July 2021 and 10th August 2021. Tags recorded data every 10 min, or every 10 s if within windfarms and if the battery level was sufficient. Due to the failure of one device, data were available for 20 of the 21 deployed tags.

Behavioural classification

Behavioural state was used to aid estimation of true flight height from raw flight height (see Flight Height Estimation), and in order to investigate whether the relationship between wind and kittiwake flight (and therefore collision risk) varies by behaviour. After resampling to one fix every 10 min and removing fixes within a polygon of the UK coastline (to focus on at-sea behaviour), kittiwake fixes were classified into four behavioural states on the basis of distance moved between fixes (‘step length’) and angle between consecutive track segments (‘turning angle’) using a Hidden Markov Model (HMM; for full details see O’Hanlon et al. 2024). These behavioural states were: 1, ‘resting/bathing’ (short step lengths, low turning angles); 2, ‘resting/foraging’ (short step lengths, high turning angles); 3, ‘foraging flight/

searching’ (long step lengths, high turning angles); 4, ‘commuting’ (long step lengths, low turning angles).

Flight height estimation

Error in triangulated GPS altitude estimates arises from various potential sources, and can be considerable in magnitude (Péron et al. 2020; Lato et al. 2022). The median altitude above mean sea level of fixes for kittiwakes in HMM behavioural states 1 or 2 (resting/bathing and resting/foraging) was zero metres, so there was no systematic bias in altitudes needing correction. However, as for many studies (Péron et al. 2020), there was random error in GPS altitudes. The GPS altitude distribution was very fat-tailed: 95% of altitudes were between -8 m and 58 m (Online Resource Fig. S1a), but there were 15 fixes above 1,000 m and the highest fix was at 38,166 m. Altitude errors were probably generated by multiple stochastic processes: at least one process producing very high altitudes (on the order of 10,000 m), possibly caused by receiver errors, and at least one process producing relatively minor deviations from true altitude (on the order of 10–100 m; including negative altitudes), likely related to more commonly considered sources of GPS positioning such as satellite geometry and atmospheric effects (Karaim et al. 2018). We addressed these assumed sources of error respectively in two separate ways: by removing fixes of implausibly high altitude, and by application of a GPS altitude error model (Ross-Smith et al. 2016; Péron et al. 2020).

Fixes with implausibly high altitudes were identified in the tracking dataset; then the corresponding fixes from the post-HMM tracking dataset were removed. Fixes were considered to be of implausibly high altitude if they implied biologically extreme rates of ascent or descent for several hundred metres. For this we used three criteria: (a) if they were above 500 m in altitude (representing 0.02% of fixes) and were both followed and preceded by fixes of less than 100 m in altitude; (b) if they were above 500 m in altitude and followed an ascent whose rate was greater than the 95th percentile of kittiwake instantaneous ascent speeds (6.41ms^{-1}); (c) if they were above 500 m in altitude and were followed by a descent whose rate was greater than the 95th percentile of kittiwake instantaneous descent speeds (6.57ms^{-1}), or were consecutively above 500 m in altitude before such a fix. Thus 18 fixes (out of 224,467) of implausibly high GPS altitude were identified in the tracking dataset, leading to the removal of three fixes from the post-HMM tracking dataset. After data preparation and cleaning the tracking dataset consisted of 2,214 fixes from 80 trips from 20 kittiwakes (Online Resource Fig. S2); most of the loss of fixes arose from subsampling to 1 fix every 10 min.

We adapted the approach of Ross-Smith et al. (2016) to estimate GPS error using a hierarchical model separating observation error from process error, allowing the estimation of true altitude (altitudes before and after application of GPS error model presented in Online Resource Fig. S1). Briefly, this approach assumes true flight heights originate from a log-normal distribution, but are observed imperfectly by the GPS tag. GPS observation errors are modelled as arising from a normal distribution around the true flight height whose standard deviation scales with the number of satellites used in the location of a particular fix. Because the aim was to estimate true altitude, rather than estimate flight height distribution for various categories, we discretised by behavioural state only (rather than by behavioural state, colony, location and light level, as in Ross-Smith et al. 2016). We used the number of satellites visible (specifically, the number of satellites visible for a given fix subtracted from 13, the maximum number of satellites visible for any fix) as a covariate of observation error. The tracking dataset was subsampled to 1 fix per 2.5 h before fitting the GPS error model, both in order to speed up fitting of this model and to minimize temporal autocorrelation in altitude or flight speed for later analyses. Parameter estimation for the GPS error model was implemented in JAGS (Plummer 2003), accessed using the runjags package (Denwood 2016) in R (R Core Team 2024). Markov Chain Monte Carlo (MCMC) chains were run for 3000 iterations, with the first 1000 discarded as warm-up. Convergence was considered to have been achieved if the Gelman-Rubin statistic was less than 1.1 for all parameters.

In the GPS error model, the estimated intercept of the altitude observation error standard deviation (SD) was 0.232 (95% credible interval (CI) 0.000, 0.932) and the estimated slope of its relationship with negative number of satellites (the number of satellites visible for a given fix subtracted from 13, the maximum number of satellites visible for any fix) was 2.080 (95% CI 1.957, 2.187). This meant that with the minimum number of satellites used (four), estimated altitude observation error SD was 18.987 m (95% CI 18.293, 19.768); while with the maximum number of satellites used (13), estimated altitude observation error SD was 0.232 m (95% CI 0.000, 0.932). Our estimates of the SD of the error distribution, with different numbers of satellites used, are similar in magnitude to the estimated error from field tests of these devices (Bouten et al. 2013).

Wind data

Wind data were derived from the ERA5 reanalysis dataset (Hersbach et al. 2023), which combines European Centre for Medium-Range Weather Forecasts (ECMWF) model data with weather observations (Hersbach et al. 2023).

Gridded eastward and northward windspeed components at 10 m altitude, at 0.25° spatial and hourly temporal resolution, were acquired over a rectangle containing all offshore kittiwake location fixes during the study. The speed and direction (hereafter referring to the direction towards which the air is moving) of the wind at 10 m altitude were calculated from these two wind components. The windspeed and direction at a given kittiwake GPS fix was taken to be the windspeed and direction for the 0.25° grid cell the fix was in, at the nearest hour to the time of the fix. Although some studies use windspeed on land as a proxy of the windspeed experienced by seabirds (e.g. Christensen-Dalsgaard et al. 2018), the average windspeed at the fix locations in our study was significantly higher than the windspeed at the colony (where the windspeed at the colony was that of the grid cell containing the colony, at the same hour as the corresponding fix; t-test; mean difference = 0.443 ms⁻¹, t = 19.0, df = 2213, p < 0.001; Online Resource Fig. S3).

We defined the tailwind and crosswind components (the components of the wind velocity vector that are respectively aligned with and perpendicular to the direction of travel of the kittiwake; Collins et al. 2020) for every fix (Online Resource Fig. S4). Where θ is the difference in bearing between the wind direction and the kittiwake direction of travel (i.e. heading),

$$\text{tailwind} = \cos\theta \times \text{windspeed}$$

$$\text{crosswind} = \sin\theta \times \text{windspeed}$$

Relationships between windspeed, kittiwake flight and collision risk

Two variables were used to describe kittiwake flight: estimated flight height above mean sea level (the output from the GPS error model) and instantaneous 2D flight speed. Preliminary analyses showed that the relationships between wind variables and bird flight variables was nonlinear, and differed between individuals; therefore these relationships were estimated using a generalized additive mixed model (GAMM) with an individual random intercept. For the models for flight height and speed, four models were fitted, comprising all combinations of: the response variables - either flight height or flight speed (modelled as lognormal responses); and explanatory variables - either just windspeed, or both tailwind speed and crosswind speed. Models including the combined effects of tailwind speed and crosswind speed (no interaction) on flight height or speed were fitted in order to understand how effects of windspeed arise. For the model for kittiwake flight behavioural state, the response variable was behavioural state category (modelled

as a categorical response) and the explanatory variable was windspeed. Models were Bayesian and were fitted using the R package brms (Bürkner 2018). Default priors were used: improper flat priors for population-level (fixed) parameters, and half Student-t priors with 3 degrees of freedom for variance parameters. MCMC chains were run for 2000 iterations, with the first 1000 discarded as warm-up. Convergence was considered to have been achieved if the Gelman-Rubin statistic was less than 1.1 for all parameters (Kéry and Schaub 2011). Model fit was assessed using Bayesian R^2 (using 'bayes_R2' in the brms package; Gelman et al. 2019).

For analyses of flight height and speed, we restricted the dataset to fixes that were likely to have been made in flight. Although the slightly higher step length for resting/foraging kittiwakes (O'Hanlon et al. 2024) allows the inclusion of fixes from when kittiwakes are in flight, it almost certainly also includes many fixes from when kittiwakes were genuinely static on the sea surface: the median GPS altitude for fixes in this behavioural state was zero metres. Therefore fixes were omitted from the dataset if they had been classified as resting/bathing or resting/foraging; this may mean that some fixes for which kittiwakes were genuinely in flight have been omitted from the analysis. Models for the effect of windspeed on flight height and speed were fitted once for each remaining behavioural state (commuting; foraging/searching), because seabirds' responses to wind are likely to vary with their behavioural state.

Using the estimated relationships between windspeed and flight height or speed, components of collision risk (proportion at risk height and average probability of collision) were estimated at given windspeeds and for given turbine sizes. Wind turbines have a 'cut-in' windspeed, below which the turbine does not rotate. Turbine cut-in windspeeds are typically 3 or 4 ms^{-1} (NREL 2023); although we estimated windspeed-flight relationships across all windspeeds, we computed components of collision risk over the interval 2.5–7.5 ms^{-1} to estimate the effect of potentially acceptable increases in cut-in speeds. A plausible range of turbine sizes was used (Table 1; Burton et al. 2013). To create heatmaps of the effects of windspeed on collision risk, collision risk

was calculated for all combinations of windspeed and turbine size within the intervals.

Estimating proportion at risk height

First, using the fitted relationship between windspeed and flight height, the proportion of flight activity at risk height at different windspeeds and turbine sizes was calculated. At a given windspeed, the estimated value of μ for that windspeed and the total estimated SD (square root of the sum of squared σ and squared individual random effect SD) was taken. Then, the cumulative distribution function of the lognormal distribution with those parameters, at a given height of the lower limit of the rotor-swept zone, was subtracted from 1 (this assumes that a negligible proportion of the kittiwake flight height distribution is above the upper limit of the rotor-swept zone). This process was carried out over the windspeed interval and the turbine height interval (Table 1). Proportion of flight at risk height (for each windspeed and turbine size) h was calculated for 500 draws from the posterior distribution of the two parameters (μ and total estimated standard deviation) of the lognormal flight height distribution; from this, the mean and 95% CI of proportion of flight at risk height was calculated. This calculation was carried out separately for commuting flight and for foraging/searching flight.

Estimating probability of collision

Second, using the fitted relationship between windspeed and flight speed, the probability of collision for a single transit of the rotor-swept zone was estimated for both behavioural states at different windspeeds. For a given draw d from the posterior distribution of the fitted windspeed-flight speed model, turbine size t and windspeed w , the probability of collision p was then estimated (Eq. 1).

$$p_{d,t,w} = \sum_{i=1}^{101} c(s_i, t) f_{d,w}(s_i) \quad (1)$$

Here, c is the average probability of collision for a given flight speed $s \{0, 1, \dots, 100\}$ and turbine size t (rotor speed, rotor radius and blade width were drawn from Table 1; bird length = 0.39 m; wingspan = 1.08 m; proportion of flights upwind = 0.5; correction for flapping/gliding birds = 1; blade pitch angle = 0.262 rad; number of blades = 3), using the function 'get_avg_prob_collision()' from the R package stochLAB (Caneco et al. 2022). This function applies a stochastic version of the extended Band collision risk model (Band 2012; Masden 2015). $f_{w,d}$ is the probability density of a given flight speed for a given windspeed (ms^{-1}) w , for a lognormal flight speed distribution whose parameters (μ and total estimated standard deviation) are drawn d from the

Table 1 Turbine specifications used in modelling of components of collision risk

	Turbine size	
	Minimum	Maximum
Hub height (m above mean sea level)	105.5	142.5
Rotor radius (m)	83.5	112.5
Lower limit of rotor-swept zone (m above mean sea level)	22	30
Blade width (m)	5.5	6.7
Rotation speed (revolutions min^{-1})	8.84	6.85

posterior distribution from the fitted windspeed-flight speed model. Probability of collision for a given turbine size and windspeed was then summarized by taking the mean and 95% CI of p across 500 draws d from the posterior distribution. This calculation was carried out once for commuting flight and once for foraging/searching flight.

Estimating combined collision risk

The effect of windspeed and turbine size on ‘combined’ collision risk was estimated. We defined ‘combined collision risk’ as total collision risk excluding the potential effect of wind on turbine and/or wind-farm avoidance rate (proportion of birds avoiding a turbine or wind-farm), which was beyond the scope of this study to estimate. Combined collision risk was estimated by multiplying estimates of behavioural state, proportion at risk height, and probability of collision across the intervals of windspeed and turbine size, and then summing these quantities across behavioural states. For a given behavioural state b (only for the two states ‘commuting’ and ‘foraging/searching’), draw d , turbine size t and windspeed w , the combined collision risk r was estimated (Eqs. 2 & 3).

$$r_{b,d,t,w} = \prod g_{b,d,w} h_{b,d,t,w} p_{b,d,t,w} \quad (2)$$

$$r_{d,t,w} = \sum_b r_{b,d,t,w} \quad (3)$$

Here, g is the probability density of a given behavioural state b for a given draw d and windspeed w ; h and p are proportion at risk height and collision probability respectively (see

previous sections). This gave 500 estimates of combined collision risk; the mean and 95% CI of these was taken to summarise combined collision risk for a given turbine size t and windspeed w . Multiplying posterior draws between independent models in this way assumes that errors are uncorrelated; however, this is unlikely to be the case (e.g. flight speed may not be independent of flight height, for a given behavioural state). Therefore our estimated CIs for combined collision risk are likely to be conservative.

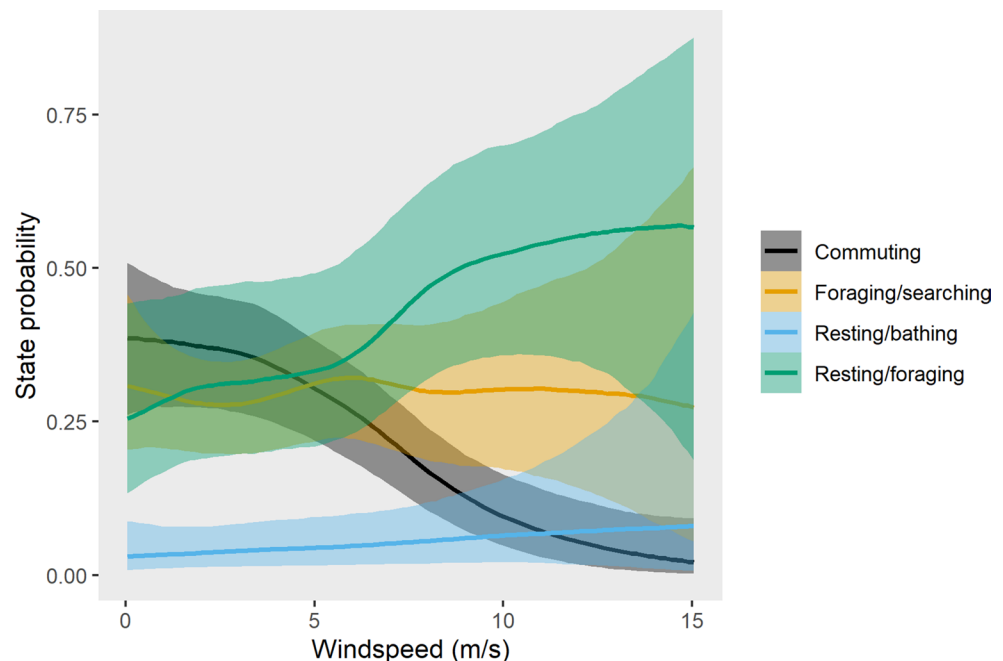
All analyses were carried out in R 4.2.1 (R Core Team 2024).

Results

Effect of wind on kittiwake behavioural state

Based on model predictions, at 2.5ms^{-1} windspeed (the lower limit of the windspeed interval over which we estimated components of collision risk), the behavioural state with the highest probability was commuting (0.359) and the lowest was resting/bathing (0.048). As windspeed increased, probability of commuting decreased while probability of resting/foraging increased (Fig. 1), as did resting/bathing (which was relatively low at all windspeeds, and for which uncertainty increased greatly at higher windspeeds). Over the interval from 2.5ms^{-1} to 7.5ms^{-1} windspeed, the probability of commuting decreased by 49.4%, while the probability of foraging/searching increased by just 7.8%. At 7.5ms^{-1} windspeed the highest probability state was resting/foraging (0.458) and the lowest was resting/bathing (0.058). Above 11ms^{-1} windspeed, commuting was the

Fig. 1 Modelled relationship between windspeed (ms^{-1}) and kittiwake behavioural state



lowest probability behavioural state. Probability of foraging/searching was relatively unaffected by windspeed.

Effect of wind on kittiwake flight height

Windspeed explained a very low proportion of variation in kittiwake flight height: for commuting flight, Bayesian $R^2=0.018$; for foraging/searching flight, Bayesian $R^2=0.041$. At zero wind, mean flight height was 16.1 m (95% CI 3.66 m, 47.1 m) for commuting flight and 9.0 m (95% CI 1.85 m, 27.8 m) for foraging/searching flight. For both commuting and foraging/searching flight, flight height decreased slightly with increasing windspeed; this relationship was steeper for commuting flight (Fig. 2a & b). A moderate proportion of the error variance was attributed to the individual random effect for commuting flight (18.4%) and for foraging/searching flight (23.4%).

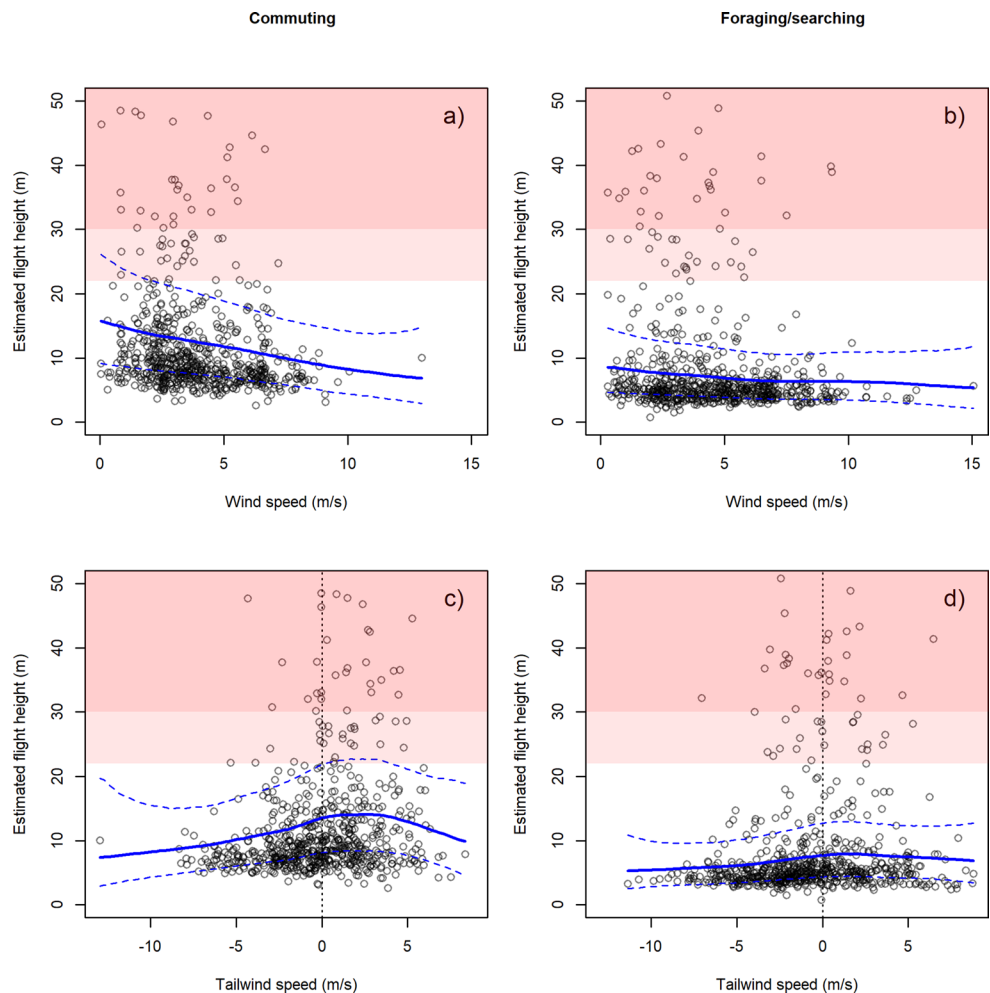
Tailwind and crosswind speed explained a low proportion of variation in kittiwake flight height: for commuting flight, Bayesian $R^2=0.020$; for foraging/searching flight, Bayesian $R^2=0.043$. For both behavioural states there was a hump-shaped relationship between tailwind speed and flight

height (Fig. 2c & d), and median peak flight height was at a positive tailwind speed (for commuting flight, 2.18 (95% CI 0.32, 5.33) ms^{-1} tailwind; for foraging/searching flight, 1.62 (95% CI -0.28, 6.42) ms^{-1} tailwind; to avoid maxima where smooths were uncertain at very low/high tailwind speed, smooths were truncated to 95% CI of observed tailwind speed for a given behavioural state). Crosswind speed had a slight negative effect on flight height for commuting flight, but no effect for foraging/searching flight (Online Resource Fig. S5).

Effect of wind on kittiwake flight speed

Windspeed explained a low proportion of variation in kittiwake flight speed: for commuting flight, Bayesian $R^2=0.068$; for foraging/searching flight, Bayesian $R^2=0.102$. At zero wind, mean flight speed was 13.41 ms^{-1} (95% CI 3.75 ms^{-1} , 35.76 ms^{-1}) for commuting flight and 14.63 ms^{-1} (0.74 ms^{-1} , 73.62 ms^{-1}) for foraging/searching flight. Commuting flight speed decreased slightly with windspeed (Fig. 3a). The slightly negative relationship between windspeed and foraging/searching flight speed was

Fig. 2 Modelled relationship (blue line) between windspeed and kittiwake flight height: **a**) & **b**) windspeed; **c**) & **d**) tailwind speed; **a**) & **c**) commuting flight; **b**) & **d**) foraging/searching flight. For clarity, y-axis is limited to [0,50]: this interval omits 3.6% of fixes for commuting flight, and 1.2% of fixes for foraging/searching flight. Shaded area shows minimum and maximum lower limits to rotor-swept zone used in collision risk calculations (see Table 1 for turbine sizes): light, > 22 m; dark, > 30 m



very uncertain (Fig. 3b). A very low proportion of the error variance was attributed to the individual random effect for commuting flight (0.4%) and for foraging/searching flight (0.7%).

Tailwind and crosswind speed explained a moderate proportion of variation in kittiwake flight speed: for commuting flight, Bayesian $R^2=0.419$; for foraging/searching flight, Bayesian $R^2=0.270$. For both commuting and foraging/searching flight, flight speed increased with tailwind speed; this relationship was more nonlinear and more uncertain for foraging/searching flight (Fig. 3c & d). Crosswind speed had a slight negative effect on flight speed for commuting flight, but no clear effect for foraging/searching flight (Online Resource Fig. S6).

Effect of windspeed on proportion of kittiwake flight at risk height

For both behavioural states, projected proportion of kittiwake flight in the rotor-swept zone (using the fitted relationship between windspeed and flight height) was lowest at high windspeeds and at high turbine size (Fig. 4). Across

behavioural states, windspeeds and turbine sizes, mean projected proportion of kittiwake flight in the rotor-swept zone varied from 0.007 to 0.160.

For commuting flight, projected proportion of kittiwake flights in the rotor-swept zone decreased considerably with windspeed (Fig. 4a & S7a, c). For a small turbine (lower limit of rotor-swept zone = 22 m), mean projected proportion of kittiwake flights at rotor-swept height decreased by 53.5% over the windspeed interval 2.5 to 7.5 ms^{-1} : from 0.160 (95% CI 0.112, 0.229) to 0.074 (95% CI 0.042, 0.129). For a large turbine (lower limit of rotor-swept zone = 30 m), mean projected proportion of kittiwake flights at rotor-swept height decreased by 60.7% over the same windspeed interval: from 0.073 (95% CI 0.045, 0.119) to 0.029 (95% CI 0.014, 0.058).

For foraging/searching flight, mean projected proportion of kittiwake flights in the rotor-swept zone was lower than for commuting flight, due to the lower flight heights (meaning that kittiwakes fly beneath the rotor) in this behavioural category. For foraging/searching flight, mean projected proportion of kittiwake flights in the rotor-swept zone decreased considerably with windspeed (Fig. 4b & S7b, d).

Fig. 3 Modelled relationship (blue line) between windspeed and kittiwake flight speed: **a**) & **b**) windspeed; **c**) & **d**) tailwind speed; **a**) & **c**) commuting flight; **b**) & **d**) foraging/searching flight

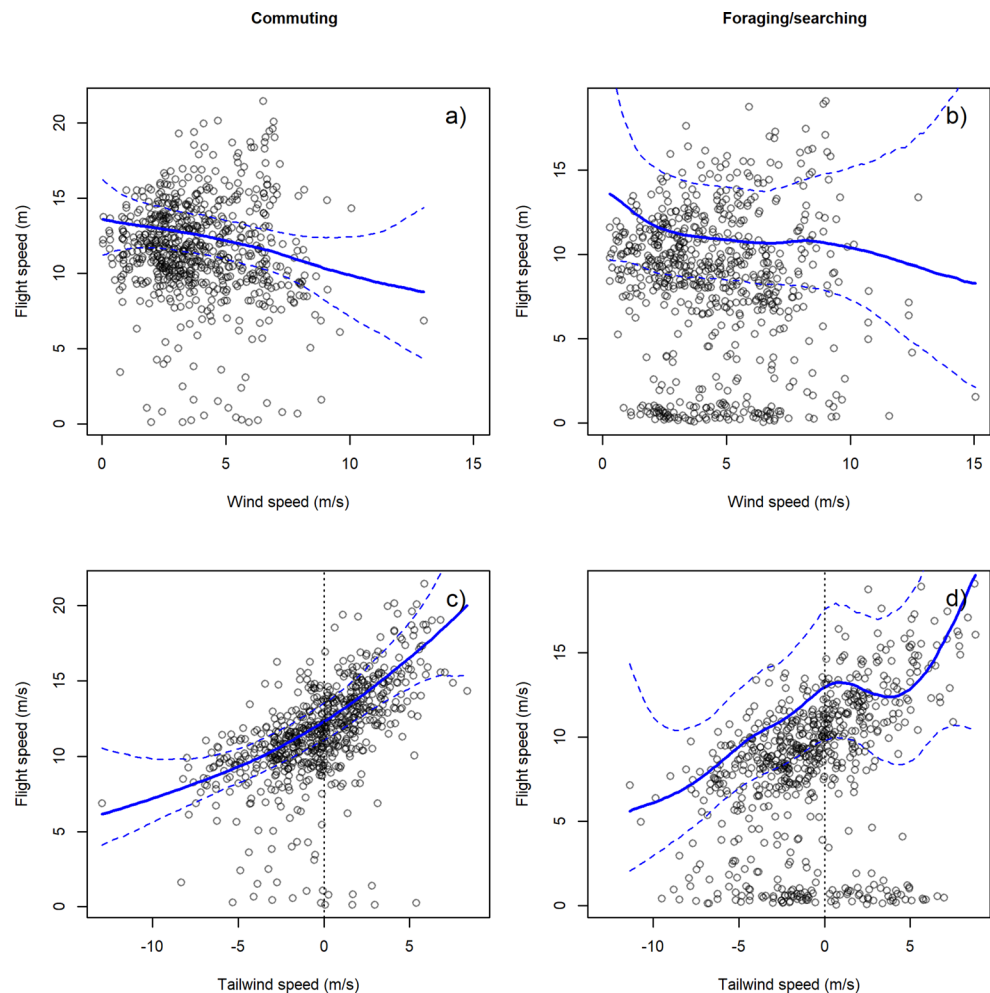


Fig. 4 Effects of windspeed and the lower limit of rotor-swept height (RSH) on mean projected proportion of flight at risk height (PRH): **a**) commuting flight; **b**) foraging/searching flight. NB colour scale differs between panels; proportion of flight at risk height is much lower overall for foraging/searching flight than for commuting flight

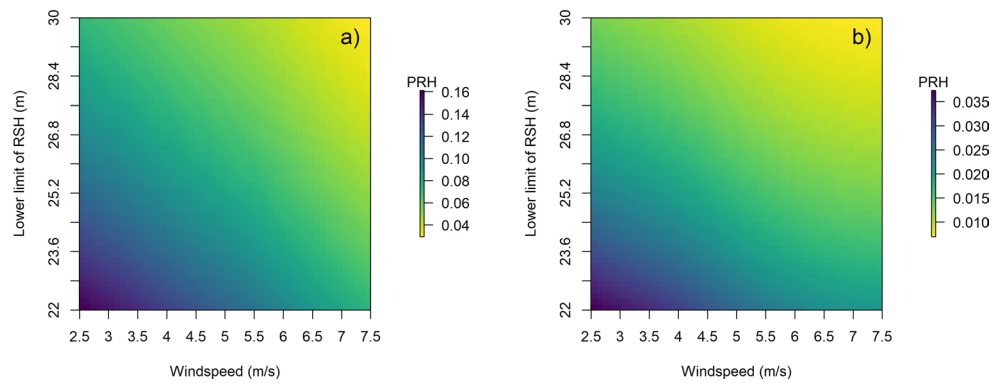
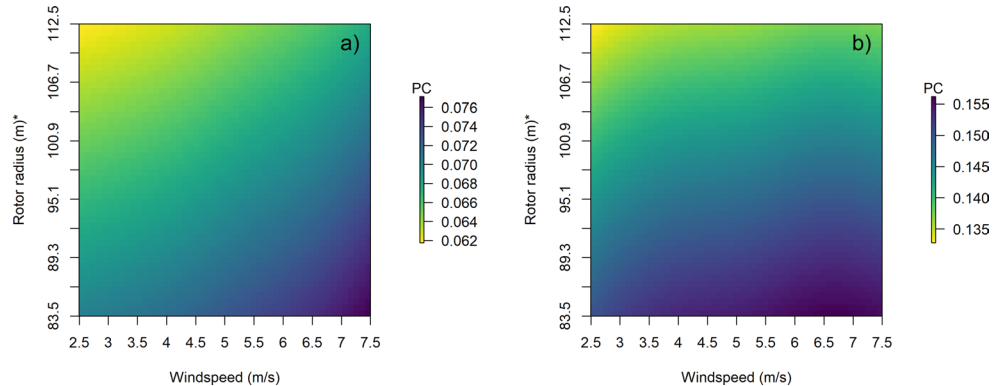


Fig. 5 Effects of windspeed and turbine size on mean probability of collision (PC): **a**) commuting flight; **b**) foraging/searching flight. * blade width and rotation speed also vary with rotor radius (Table 1). NB colour scale differs between panels; probability of collision is much higher overall for foraging/searching flight than for commuting flight



This relationship was more uncertain than for commuting flight. For a small turbine, mean projected proportion of kittiwake flights at rotor-swept height decreased by 43.3% over the windspeed interval 2.5 to 7.5 ms^{-1} : from 0.039 (95% CI 0.021, 0.069) to 0.022 (95% CI 0.010, 0.042). For a large turbine, mean projected proportion of kittiwake flights at rotor-swept height decreased by 48.2% over the same windspeed interval: from 0.014 (95% CI 0.006, 0.030) to 0.007 (95% CI 0.003, 0.016).

Effects of windspeed on kittiwake probability of collision

For both behavioural states, estimated kittiwake probability of collision given presence in the rotor-swept zone (using the fitted relationship between windspeed and flight speed) was lowest at low windspeeds and at large turbine size (Fig. 5). Across behavioural states, windspeeds and turbine sizes, mean probability of collision in the rotor-swept zone varied from 0.062 to 0.156.

For commuting flight, estimated kittiwake probability of collision increased slightly with windspeed (Fig. 5a & S8a, c). For a small turbine (rotor radius=83.5 m; blade width=5.5 m; rotation speed=8.84 $\text{revolutions min}^{-1}$), mean probability of collision increased by 9.9% over the windspeed interval 2.5 to 7.5 ms^{-1} : from 0.071 (95% CI 0.068, 0.073) to 0.078 (95% CI 0.073, 0.084). For a large turbine (rotor radius=112.5 m; blade width=6.7 m;

rotation speed=6.85 $\text{revolutions min}^{-1}$), mean probability of collision increased by 10.2% over the windspeed interval 2.5 to 7.5 ms^{-1} : from 0.062 (95% CI 0.060, 0.064) to 0.068 (95% CI 0.064, 0.074).

For foraging/searching flight, estimated kittiwake probability of collision was greater than for commuting flight (because of the generally lower flight speeds), and increases slightly with windspeed (Fig. 5b & S8b, d). This relationship was more uncertain for foraging/searching flight than for commuting flight. For a small turbine, mean probability of collision increased by 3.5% over the windspeed interval 2.5 to 7.5 ms^{-1} : from 0.150 (95% CI 0.138, 0.164) to 0.156 (95% CI 0.140, 0.172). For a large turbine, mean probability of collision increased by 3.5% over the same windspeed interval: from 0.133 (95% CI 0.122, 0.145) to 0.138 (95% CI 0.124, 0.152).

Effects of windspeed on combined collision risk

The net effect of windspeed on combined collision risk was negative (Fig. 6 & S9). For a small turbine (as specified above), mean combined collision risk decreased by 62.1% over the windspeed interval 2.5 to 7.5 ms^{-1} : from 0.006 (95% CI 0.004, 0.008) to 0.002 (95% CI 0.001, 0.004). For a large turbine, mean combined collision risk decreased by 68.2% over the windspeed interval 2.5 to 7.5 ms^{-1} : from 0.002 (95% CI 0.001, 0.004) to 0.001 (95% CI 0.000, 0.001).

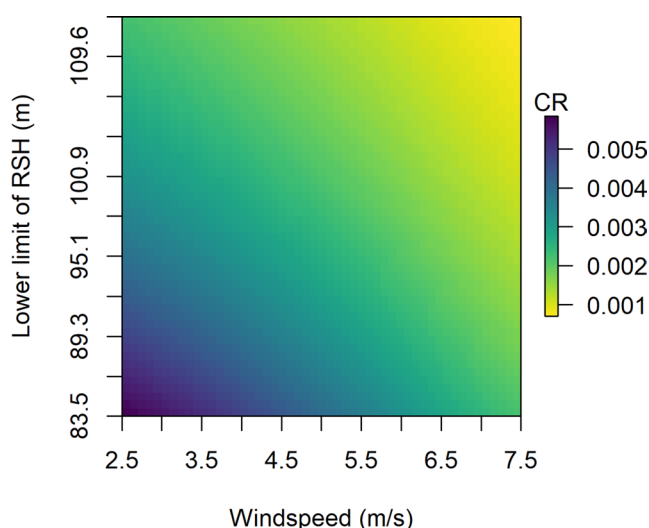


Fig. 6 Effects of windspeed and turbine size (RSH=rotor-swept height) on mean combined collision risk (CR)

Discussion

Our study is, to our knowledge, the first to investigate the effect of wind on multiple components of seabird collision risk. As with other studies (Elliott et al. 2014; Christensen-Dalsgaard et al. 2018), we found that kittiwakes respond to the variable aerial environment in a flexible way. This flexibility means that wind generates important and opposing variation in components of kittiwake collision risk with offshore wind turbines.

We found that kittiwake behavioural state is modulated by windspeed, with commuting behaviour becoming less common and resting behaviour becoming more common with increasing windspeeds. Given that kittiwakes are typically on the water (and therefore not susceptible to collision with turbine blades) during resting, bathing or foraging, this relationship serves to reduce one aspect of collision risk (proportion of flight time at risk height) at higher windspeeds. The effect of windspeed on commuting behaviour is likely to be particularly influential on collision risk, because kittiwakes are at greater risk of collision while commuting than while foraging/searching. The behavioural response to wind of kittiwakes in our study area in north-east Scotland is different to that of kittiwakes in mid-north Norway (Christensen-Dalsgaard et al. 2018): there, the proportion of time commuting and foraging generally increased with windspeed, while resting behaviour decreased with windspeed. It is possible that the differing relationships arose from methodological differences between the studies: e.g. Christensen-Dalsgaard et al. (2018) used windspeed values at the colony location, while we used windspeed values at the tag location. However, the relationships Christensen-Dalsgaard et al. (2018) found between wind and kittiwake

flight differed between colonies and according to whether birds were over the continental shelf, suggesting that the differences with our findings could likewise be genuine. This shows that the effects of wind on seabird flight behaviour are likely to vary geographically, demonstrating the importance of local studies or studies with geographically varying parameters when investigating the effects of environmental conditions on collision risk.

As has been observed for other gull species (Ainley et al. 2015; McLaren et al. 2016), kittiwakes in our study reduced their flight height with increasing windspeed. The slope of this negative relationship was steeper for commuting flight than for foraging/searching flight. Kittiwakes' flight height distribution lies on the lower edge of the rotor-swept zone, and so the relatively shallow negative relationship between windspeed and kittiwake flight height drives a decline in proportion of flight at risk height (>50% decline for commuting flight; >40% decline for foraging/searching flight) even over the small windspeed interval examined. However, for both behavioural states, the amount of variation in flight height explained by windspeed was very low, and so there remains considerable uncertainty in the proportion of flight at risk height at all windspeeds.

The overall relationships between kittiwake flight height/speed and windspeed emerge from the relationships between flight height/speed and tailwind/crosswind speed, integrated across all wind directions experienced by the kittiwakes. As for other species (Vanermen et al. 2018), the effect of windspeed on kittiwake flight height and speed is contingent on direction: it differs between windspeed and tailwind speed. Therefore if (as is likely) wind direction at a windfarm is unevenly distributed, or if kittiwake flight direction is also unevenly distributed, or varies temporally, then the effects of windspeed on collision risk might differ considerably from our overall relationships. Furthermore, probability of collision varies with angle-of-approach (Holmstrom et al. 2011), and thus will vary in complex ways with crosswind speed. We found that at high crosswinds, kittiwakes fly more slowly; this positive effect on probability of collision is likely to be enhanced by the longer time kittiwakes spend in the rotor-swept zone as the turbines turn side-on to bird flight during crosswinds (Holmstrom et al. 2011).

Overall, windspeed explains a relatively small proportion of variation in flight height and speed. Even this relatively low proportion of variation is probably an overestimate, because we do not propagate uncertainty from the HMM, GPS error model, ERA5 windspeed, or the probability of collision into our uncertainty estimates. For flight height, the apparently weak relationship with windspeed may be genuine: many other intrinsic (Clay et al. 2020) or environmental (Cook et al. 2018; Becciu et al. 2021; Coleman et al. 2022) factors are known to influence seabird flight, and could be

investigated for their effects on kittiwake flight height. Interestingly, the proportion of the error variance attributed to the individual random effect was greater for flight height than for flight speed, suggesting that individual variation is much more important for flight height than for flight speed. By contrast, the apparently weak effect of overall windspeed on flight speed appears to be because this effect is contingent on wind direction: the relationship between tailwind speed and flight speed is strong, but is muddled by the variability of wind direction.

We found that although windspeed had opposing effects on different components of kittiwake collision risk, the net effect of windspeed on collision risk was negative and substantial: for a large turbine, mean combined collision risk decreased (albeit from an already low level) by two-thirds over the windspeed interval 2.5 to 7.5 ms^{-1} . This was largely driven by effects of wind on behavioural state and proportion at risk height: the negative effect of windspeed on combined collision risk through commuting probability and proportion of flight time at risk height was of considerably greater magnitude than the positive effect of windspeed on combined collision risk through probability of collision. These effects were largely passed on through commuting flight: the magnitude of the reduction in commuting probability was much greater than the increase in foraging/searching probability over the windspeed interval, and kittiwakes in foraging/searching flight are at lower altitude and thus lower risk of collision.

We did not investigate the effects of wind on all aspects of collision risk in our study. Firstly, because we only used at-sea fixes in our analyses, our estimates of collision risk were conditioned on already being at sea. However, we might expect windspeed to exert an additional negative influence on collision risk through propensity to go to sea (and thus baseline exposure), because Christensen-Dalsgaard et al. (2018) found that kittiwakes are less likely to make trips to the ocean in high winds. Secondly, we did not estimate the effects of windspeed on avoidance rate, which can be the most important aspect of collision risk (Masden et al. 2021). If kittiwake avoidance rate decreases with windspeed (e.g. if maneuverability decreases with windspeed; e.g. Shepard et al. 2019), then the overall effect of windspeed on total collision risk may be less negative or even positive. Future investigation of the relationship between windspeed and avoidance rate will improve understanding of the role of avoidance rate in kittiwake collision risk. Thirdly, turbine rotation speed increases with increasing windspeed, increasing blade strike probability, partly due to the reduced visibility of the turbine blade to the bird (Marques et al. 2014); we did not have sufficient information on these processes to incorporate them in our model. Therefore, we may have underestimated the potential for

positive effects of windspeed on probability of collision to compensate for the negative effects of windspeed on proportion of flight at risk height. Finally, seabirds may change their space use to make the most efficient use of wind conditions (Christensen-Dalsgaard et al. 2018; De Pascalis et al. 2020; Ventura et al. 2020); we did not investigate the possibility that during periods of high winds, kittiwakes might respond by moving to less windy areas.

Seabird behaviour and associated collision risk can vary considerably both within and between seasons (Thaxter et al. 2015; Clewley et al. 2023). We do not know whether our inferences on the relationship between wind and kittiwake flight, gleaned from just a few weeks during the chick-rearing phase of the breeding season, generalise to the rest of the breeding season. For example, during the incubation phase, adults are under less pressure to forage, and so it is possible that under high winds during this phase they might be less likely to maintain higher flight height or speed, or to forage at all, than during the chick-rearing phase. Additionally during the non-breeding season kittiwake flight metrics may in turn have a different relationship with wind, not least because average windspeed is considerably higher. Ascertaining the temporal generality of the relationships we found will require year-round attachment of telemetry tags; for now, finding a suitable long-term tag attachment method for kittiwake remains a challenge (Clewley et al. 2021). At a larger temporal scale, global windspeed is changing (Dunn et al. 2022), but it is unclear how windspeed will change in the future (Lowe et al. 2018). Until projections of future windspeed are more precise and until a more holistic understanding of the effect of windspeed on kittiwake collision risk is achieved, it is difficult to predict how climate change will affect kittiwake collision risk in the future.

Environmental variation is not typically taken into account when estimating seabird collision risk with wind turbines (Masden and Cook 2016). However, there is a growing understanding that the way that seabirds interact with offshore windfarms varies temporally and spatially (Thaxter et al. 2015; van Erp et al. 2021); accounting for environmental variation in collision risk estimates may improve their precision and accuracy. In the present study we have demonstrated that kittiwake collision risk is likely to vary with windspeed and direction; therefore, incorporating expected windspeed for a given windfarm into kittiwake collision risk estimates may help improve their precision. However, this improvement may be only slight, due to the remaining uncertainty in the relationship between windspeed and kittiwake flight behaviour, height and speed. Relatedly, collision risk estimates are sometimes potentially biased by being based on flight height and speed estimates that are gathered in benign conditions (i.e. sea state ≤ 4 , likely windspeeds $\leq 10 \text{ ms}^{-1}$). Based on our results, kittiwake

collision risk may be overestimated if based on behavioural probabilities, flight heights and speeds associated with low wind conditions. Therefore for kittiwake and other seabird species for which flight metrics vary with windspeed, collision risk estimates that integrate across environmental conditions, for example those based on telemetry, are likely to be of greater accuracy.

Better understanding of how environmental parameters influence windfarm collision risk helps in the identification of effective mitigation measures (Marques et al. 2014). Various wind turbine features (e.g. turbine height; Johnston et al. 2014; Cleasby et al. 2015) can be altered to reduce seabird collision risk. The negative relationship between windspeed and kittiwake collision risk suggests another tool for mitigating collision risk for this species. Raising turbine cut-in speed has been effective for the reduction of bat collision fatalities, by reducing collision risk during low-wind periods, when bat feeding activity is higher (Martin et al. 2017). Because windspeed has a considerable negative effect on collision risk for kittiwakes over the windspeed interval 2.5 to 7.5 ms⁻¹, an increase in cut-in speed at offshore windfarms may help reduce total collision risk for kittiwakes. However, amongst all seabirds, gulls have an unusually negative relationship between windspeed and flight height (Ainley et al. 2015), and so this mitigation approach may not reduce collision risk for all seabirds. Also, this mitigation approach may not necessarily be effective in other regions as the behavioural response of kittiwakes to wind in our study area is the opposite of that found in mid-north Norway (Christensen-Dalsgaard et al. 2018).

Future work to reduce the remaining uncertainty in kittiwake collision risk would be aided by investigating other potential intrinsic and environmental drivers of kittiwake collision risk, particularly components of collision risk that we did not investigate (such as avoidance rate). Furthermore, it is important to identify the extent to which the relationship between windspeed and kittiwake collision risk varies geographically and with phase of the annual cycle; the generality of this relationship will determine whether it needs to be estimated for each offshore wind farm planning assessment. Uncertainty in collision risk contributes importantly to uncertainty in ornithological impact assessments of offshore wind developments (Searle et al. 2023). Our study demonstrates that environmental conditions drive important variation in kittiwake collision risk; future offshore wind farm planning assessments can take this into account to reduce uncertainty. Given our findings, it may be valuable to investigate the effects of environmental conditions on offshore wind turbine collision risk in other contexts, for example the effects of other environmental conditions such as fog, or the effects on collision risk in other avian taxa such as other seabirds or migrating terrestrial birds.

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Author contributions Aonghais Cook, Elizabeth Humphreys, Philipp Boersch-Supan & Chris Thaxter designed the study. Gary Clewley, Jacob Davies, Nina O'Hanlon and Ewan Weston carried out the tagging and monitoring. Jacob Davies carried out the data analysis and wrote the first draft of the manuscript. Judy Shamoun-Baranes contributed to data collection and interpretation. All authors contributed critically to and approved the manuscript as submitted.

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Data availability The kittiwake tracking dataset analysed during the current study are available at Movebank (www.movebank.org) in the study "BTO - Whinnyfold 2021 - Kittiwake" (Movebank Study ID 4447816442). ERA5 reanalysis data are available from the Copernicus Climate Data Store (<https://doi.org/10.24381/cds.adbb2d47>).

Declarations

Ethical approval The authors have no relevant financial or non-financial interests to disclose. All kittiwake capture, marking and tagging was approved by the Special Methods Technical Panel of the British Trust for Ornithology.

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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