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Modelling flight heights of lesser black-backed gulls and great skuas from GPS: a Bayesian approach

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Summary

1. Wind energy generation is increasing globally, and associated environmental impacts must be considered. The risk of seabirds colliding with offshore wind turbines is influenced by flight height, and flight height data usually come from observers on boats, making estimates in daylight in fine weather. GPS tracking provides an alternative and generates flight height information in a range of conditions, but the raw data have associated error.

2. Here, we present a novel analytical solution for accommodating GPS error. We use Bayesian state-space models to describe the flight height distributions and the error in altitude measured by GPS for lesser black-backed gulls and great skuas, tracked throughout the breeding season. We also examine how location and light levels influence flight height.

3. Lesser black-backed gulls flew lower by night than by day, indicating that this species would be less likely to encounter turbine blades at night, when birds' ability to detect and avoid them might be reduced. Gulls flew highest over land and lowest near the coast. For great skuas, no significant relationships were found between flight height, time of day and location.

4. We consider four 'collision risk windows', corresponding to the airspace swept by rotor blades for different offshore wind turbine designs. We found the highest proportion of birds at risk for a 22–250 m turbine (up to 9% for great skuas and 34% for lesser black-backed gulls) and the lowest for a 30–258 m turbine. Our results suggest lesser black-backed gulls are at greater risk of collision than great skuas, especially by day.

5. *Synthesis and applications*. Our novel modelling approach is an effective way of resolving the error associated with GPS tracking data. We demonstrate its use on GPS measurements of altitude, generating important information on how breeding seabirds use their environment. This approach and the associated data also provide information to improve avian collision risk assessments for offshore wind farms. Our modelling approach could be applied to other GPS data sets to help manage the ecological needs of seabirds and other species at a time when the pressures on the marine environment are growing.

Key-words: collision risk, Environmental Impact Assessment, GPS tracking, great skua, lesser black-backed gull, Markov chain Monte Carlo, offshore wind farm, seabird, state-space model

Introduction

While governments worldwide are investing in offshore wind farms, detrimental effects of these developments have been reported for certain species, including seabirds (Garthe & Hüppop 2004; Furness, Wade & Masden 2013). One danger seabirds face is collision with turbine blades (Drewitt & Langston 2006), which is generally estimated using a collision risk model. For an individual approaching a turbine, collision risk is determined by turbine dimensions and characteristics of the bird, including flight height (Johnston *et al*. 2014).

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Much of our knowledge of seabird flight heights comes from observers on boats, assigning birds to height categories. These estimates can be used to generate flight height distributions (Johnston *et al.* 2014). However, as boat surveys are restricted to daylight hours and fine weather (Camphuysen *et al.* 2004), Environmental Impact Assessments (EIAs) using these data assess collision risk for only a subset of the conditions in which offshore wind farms operate. Furthermore, height estimates from boat surveys are subjective (Camphuysen *et al.* 2004) and their accuracy has not been assessed (Johnston *et al.* 2014). Information on flight heights can also be obtained using radar, digital high definition aerial surveys and rangefinders (e.g. Shamoun-Baranes *et al.* 2006; Mendel *et al.* 2014), but each also has drawbacks, for example, radar does not generally allow species identification (Hüppop *et al.* 2006; Schmaljohann *et al.* 2008).

An alternative to these methods is GPS tracking. Individual seabirds are fitted with devices that measure their position in three dimensions, assessing movements in a range of conditions that affect flight heights, such as variable weather, season and time of day (Drewitt & Langston 2006; Kemp *et al.* 2013). Sophisticated statistical techniques can be applied to GPS data, for instance Bayesian state-space models (SSMs). These deal effectively with the error inherent in location data that can bias interpretation of ecological events and processes (Patterson *et al.* 2008). In the case of GPS telemetry, error is likely to vary due to fluctuations in satellite coverage and interference (Patterson *et al.* 2008). Recent studies have used pressure loggers in conjunction with GPS tracking to reduce the error associated with GPS measurements of seabird flight heights (Garthe *et al.* 2014; Cleasby *et al.* 2015). Our study presents an alternative analytical solution to this problem, applying SSMs to GPS data from seabirds.

Lesser black-backed gull *Larus fuscus* (Linnaeus) and great skua *Stercorarius skua* (Brünnich) have breeding distributions and foraging ranges that suggest a high probability of interactions with UK offshore wind farms (Thaxter *et al.* 2012a, 2015; Wade *et al.* 2014). Both species are of conservation concern in the UK (Eaton *et al.* 2015), and their potential to be adversely affected by offshore wind farms has been considered in several assessments for proposed developments. Previous studies, including with GPS for lesser black-backed gulls (Corman & Garthe 2014), have indicated that these species' flight heights put them at risk of collision with offshore wind turbine blades (Garthe & Hüppop 2004; Johnston *et al.* 2014), and a review of 38 marine bird species ranked lesser black-backed gull and great skua as third and ninth, respectively, for likelihood of collision with Scottish turbines (Furness, Wade & Masden 2013).

We use data from GPS tags to model flight heights of breeding lesser black-backed gulls and great skuas. Our SSMs provide estimated flight height distributions and information on how these vary according to a bird's location and between day and night. This approach will improve impact assessments for offshore wind farms by (i) providing data on bird movements in conditions missing from non-tracking data sets (e.g. variable weather conditions and night-time), and (ii) providing flight height distributions that are directly applicable to existing collision risk models (Masden & Cook 2015).

Materials and methods

FIELD METHODS

Twenty-five lesser black-backed gulls were caught at Orford Ness, Suffolk (52°04′ N, 1°33′ E), during June 2010 ($n = 11$) and May 2011 ($n = 14$), while 14 great skuas were captured on Foula, Shetland (60°06′ N, 2°03′ W), in June 2010 ($n = 4$) and June 2011 ($n = 10$) and 10 on Hoy, Orkney (58°51′ N, 3°18′ W), in June 2011 (see Table S1, Supporting Information). Each bird was fitted with a University of Amsterdam Bird Tracking System (UvA-BiTS) GPS device (Bouten *et al.* 2013) attached with a Teflon harness, weighing a total of 21 g, <3% of body mass (gulls: mean 851 g, range 710–955 g; skuas: mean 1350 g, range 1190–1490 g; for details, see Thaxter *et al.* 2014). Birds were breeding adults and were captured while incubating eggs. We found no impact of capture and tagging on productivity or nest attendance for either species during the period of data collection (Thaxter *et al.* 2016), so the data in this study are thought to represent normal breeding season behaviour.

GPS DEVICES AND DATA COLLECTION

Our GPS devices were solar-powered. They recorded geographical position, altitude above mean sea level, ground speed and dilution of precision (DOP). The tags downloaded time-stamped GPS data to base stations near the colonies (for details, see Bouten *et al.* 2013). We defined a virtual perimeter of *ca.* 200 m^2 around the colony to identify when birds were 'within' it, or away on trips. Devices were normally set to take GPS measurements every 30 min when birds were at the colony and every five or 10 min otherwise. These intervals optimized data capture while minimizing gaps due to insufficient memory and battery life.

GPS data for great skuas were only available for the year in which birds were tagged. We monitored birds' nests and analysed data collected when they were known to be actively breeding (incubating eggs or rearing young; Table S1). For lesser black-backed gulls, we analysed all GPS data from the time individuals were first recorded at the breeding colony until their departure each season (Table S1), because vegetation obscuring nests, and chick mobility, meant we could not tell when birds were actively breeding. We collected up to four breeding seasons' data per bird for this species. For both species, the amount of GPS data available for each individual varied due to tag wear, failure and birds leaving the colony (Table S1). We modelled 99 245 height measurements for lesser black-backed gulls and 63 755 for great skuas (Table S1).

DATA ANALYSIS

Data processing was carried out in R (R Core Team 2015) and ARCGIS (ESRI, Redlands, CA, USA). We examined the extent of temporal correlation for a few individuals and based on these structures, we selected one data point per hour for gulls to remove most of the temporal autocorrelation (gaps in tag transmission meant there were some hours for which no data were available). We converted altitude measurements to altitude above land/sea using tidal data and land surface elevation data. Tidal data were from the British Oceanographic Data Centre (https://www.bodc.ac.uk/data/online_delivery/ntslf/), using the nearest tide gauges for each breeding colony (Harwich ~30 km from Orford Ness, Lerwick ~50 km from Foula and Wick ~45 km from Hoy). Surface elevation was obtained from the Shuttle Radar Topography Mission 90 m digital elevation data (http://srtm.csi.cgiar.org/), aggregated at the 1 km square level.

GPS tags record altitude with error (Bouten *et al.* 2013), and we found unrealistic readings, like birds recorded below sea level (Appendix S1). We therefore could not use the flight height measurements directly from the tags. Instead, we treated each recorded flight height as an observation with error. The SSM explicitly models the underlying flight height distribution and the process of observation with error. SSMs are particularly appropriate when the data have significant or non-uniform error, due to the separation of the biological and error processes (King 2012).

FLIGHT HEIGHT DISTRIBUTION MODEL

The first of these two processes is the true distribution of flight height. We expected the distribution of flight height to be determined by behaviour and location, so we estimated a different distribution for several 'states'. The states were assigned to birds at each data point, based on their behaviour and location. Bird speed was used as an indication of behaviour, where <1 km h^{-1} was classified as sitting or standing still, 1–4 km h^{-1} as walking, swimming or floating and >4 km h^{-1} as flying, after Shamoun-Baranes *et al.* (2011). We also defined states based on location, as habitat differences are likely to influence flight height; for example, food at sea is more likely to be ephemeral than terrestrial food, so best captured by remaining close to the surface (Corman & Garthe 2014). We defined three location states: 'terrestrial', 'coastal' and 'marine'. 'Terrestrial' locations were those on or over the land. 'Coastal' was for observations at sea, but within 200 m of land, and 'marine' was at sea and further than 200 m from land. The three behavioural and three location categories were combined to produce nine distinct 'states'. However, data were too few for us to fit nine distributions for each species, so we combined them based on some assumptions about distributions; for example, height distributions of birds floating/swimming will be the same for birds in coastal and marine habitats. In total, we considered six states for lesser black-backed gulls (Table 1) and four for great skuas (Table 2).

Within each state, we assumed the distribution of altitudes to be lognormal, enabling a variety of distribution shapes. This was supported by previous analysis of flight distributions based on boat survey data (Johnston *et al.* 2014). The lognormal distributions were defined by a mean and a standard deviation on the natural log scale, and these parameters were estimated in the modelling process. A random effect on the mean was incorporated for each bird, allowing individual-specific height preferences. We included information on light levels as a covariate for flying states only, with each data point categorized as 'day', 'night' or 'twilight' (half an hour before and after sunrise or sunset, for each measured location). This categorical variable was

Table 1. Behavioural states for state-space model of lesser black-backed gulls

	Speed	<1 km h^{-1}	1–4 km h^{-1}	>4 km h^{-1}
	Behaviour	Sitting/ standing/ floating	Swimming/ walking	Flying
Location	Terrestrial	1	2	4
	Coastal		3	5
	Marine			6

Table 2. Behavioural states for state-space model of great skuas

	Speed	<1 km h^{-1}	1-4 km h^{-1}	>4 km h^{-1}
	Behaviour	Sitting/standing/floating/ swimming/walking		Flying
Location	Terrestrial	1		3
	Coastal	2		4
	Marine			

modelled with an additive effect on the means of the lognormal distributions. The flight height distribution model was therefore

$$\log(\text{alt}_{i,k,l}) \sim N(\mu_{i,k,l}, \sigma_k^2)$$

defining the altitude, $\text{alt}_{i,k,l}$, for individual i in state k and in light level l, where

$$\mu_{i,k,l} = \alpha_k + \beta_{k,l} + \gamma_i.$$

The mean of the lognormal distribution, $\mu_{i,k,l}$, was determined by a state-specific intercept, α_k, an effect of light-level category which varied by state, $\beta_{k,l}$, and an individual random effect, $\gamma_i \sim N(0, \tau^2)$. The variance of the lognormal distribution (σ_k^2) was also state-specific, but did not vary with light level or individual.

OBSERVATION MODEL OF GPS ERROR

The second of the two processes estimated with the SSM was the observation error. We expected GPS tag error to vary with the number and position of satellites, which is captured by DOP. This quantifies the multiplicative effect of satellite geometry on the precision of positional measurements. The lower the DOP value, the better the positional precision, which occurs when satellites are far apart in the sky (Langley 1999).

We assumed the error in altitudinal measurements was normally distributed around the true altitude. The standard deviation of the normal distribution was linearly related to the DOP of each observation. We also ran an alternative model that additionally considered a term accounting for the potential bias between observed altitude and true altitude, that is inaccuracy in the observed altitude provided by GPS. This model failed to converge, suggesting that the bias between observed altitude and true altitude is small. It could also mean the bias, or inaccuracy, might be correlated with the error, or precision, of GPS estimates and hence might be reflected in confidence limits.

Our observation model was defined as

$$\text{obs}_j \sim N(\text{alt}_j, \sigma_j^2)$$

$$\sigma_j^2 = \rho + \omega \cdot \text{DOP}_j$$

where obs_j is the altitude recorded by the GPS tag for each observation, j. We assumed obs_j to be distributed according to a normal distribution around the true altitude, alt_j, with variance, σ_j^2. The variance of the observation distribution was determined by the intercept, ρ, and a linear effect of DOP_j, ω. The flight height distribution model and observation model structures were the same for both species, although we modelled a different number of states for the two.

MODEL FITTING

We used a Markov chain Monte Carlo (MCMC) approach to fit our models (Gilks, Richardson & Spiegelhalter 1996) using OPENBUGS 3.2.2 (Lunn *et al.* 2009) with vague prior distributions (Table S2). Initial values were randomly generated from the prior distributions. We ran three chains and assessed convergence by examining mixing within them, Brooks–Gelman–Rubin statistics and Monte Carlo error estimates. We discarded the first 40 000 iterations in each chain and used the next 200 000 iterations.

COLLISION RISK

We examined four 'collision risk windows' for flight height, corresponding to the height swept by the rotor blades for offshore wind turbine designs. These were 20–120 m above sea level (to enable comparison with previous studies) and 22–250 m, 25–253 m and 30–258 m to reflect turbine heights at consented wind farms (http://www.4coffshore.com/windfarms/). For birds in the 'marine' state at speeds of >4 km h^{-1} (i.e. birds flying at sea), we summarize the percentage of measurements within these collision risk windows.

Results

FLIGHT HEIGHT

Lesser black-backed gull

Estimated mean altitude varied significantly with behavioural state (Table 3). Gulls moving at <4 km h^{-1} were effectively at surface level regardless of location, as expected standing, sitting, walking, swimming or floating behaviour. Some slightly higher altitudes were seen for 'terrestrial' birds at 1–4 km h^{-1} (state 2), which could represent small vertical movements or inaccuracies in the digital elevation model (Fig. 1b).

Lesser black-backed gull altitude was highest for birds moving at >4 km h^{-1} (Fig. 1d), as expected for flight. Flight height over land was higher than over sea (Fig. 2). During the day, 50% of 'terrestrial' observations (state 4) were within 22·1 m of ground level, whereas 50% of 'marine' observations (state 6) were within 12·8 m of sea level. 'Coastal' measurements (state 5) had the lowest height distribution (50% of observations within 6·7 m of sea level; Fig. 2). The difference between the log mean altitudes of 'terrestrial' observations and 'coastal' observations was significant, as was the difference between 'terrestrial' and 'marine' measurements. (Table 3 and Fig. 2).

Lesser black-backed gull flight height varied with light level; birds flew higher during the day than after dark (Table 3 and Fig. S1). 'Terrestrial' and 'coastal' flight

Table 3. Credible intervals for state-space model of lesser black-backed gull height (metres above surface level). See Table 1 for different states

Parameter	Lower 2·5% credible interval	Median	Upper 97·5% credible interval
State 1 mean ln height (daylight)	−10·16	−8·88	−7·89
State 2 mean ln height (daylight)	−2·32	−1·64	−1·04
State 3 mean ln height (daylight)	−25·26	−15·75	−9·42
State 4 mean ln flight height (daylight)	2·86	3·10	3·32
State 5 mean ln flight height (daylight)	1·47	1·89	2·27
State 6 mean ln flight height (daylight)	2·30	2·55	2·79
State 4 mean ln flight height (twilight)	2·18	2·48	2·79
State 5 mean ln flight height (twilight)	−0·27	0·94	1·92
State 6 mean ln flight height (twilight)	1·98	2·34	2·70
State 4 mean ln flight height (darkness)	2·38	2·64	2·90
State 5 mean ln flight height (darkness)	1·11	1·70	2·23
State 6 mean ln flight height (darkness)	1·41	1·72	2·02
State 1 variance of ln height	15·51	18·68	23·08
State 2 variance of ln height	8·40	10·59	13·49
State 3 variance of ln height	23·85	54·86	125·60
State 4 variance of ln flight height	2·29	2·41	2·53
State 5 variance of ln flight height	2·71	3·52	4·67
State 6 variance of ln flight height	2·14	2·39	2·66
Intercept of variance of observation error	56·97	59·33	61·70
Coefficient of DOP for variance of observation error	19·28	20·04	20·80
Variance of individual random effect	0·15	0·28	0·57

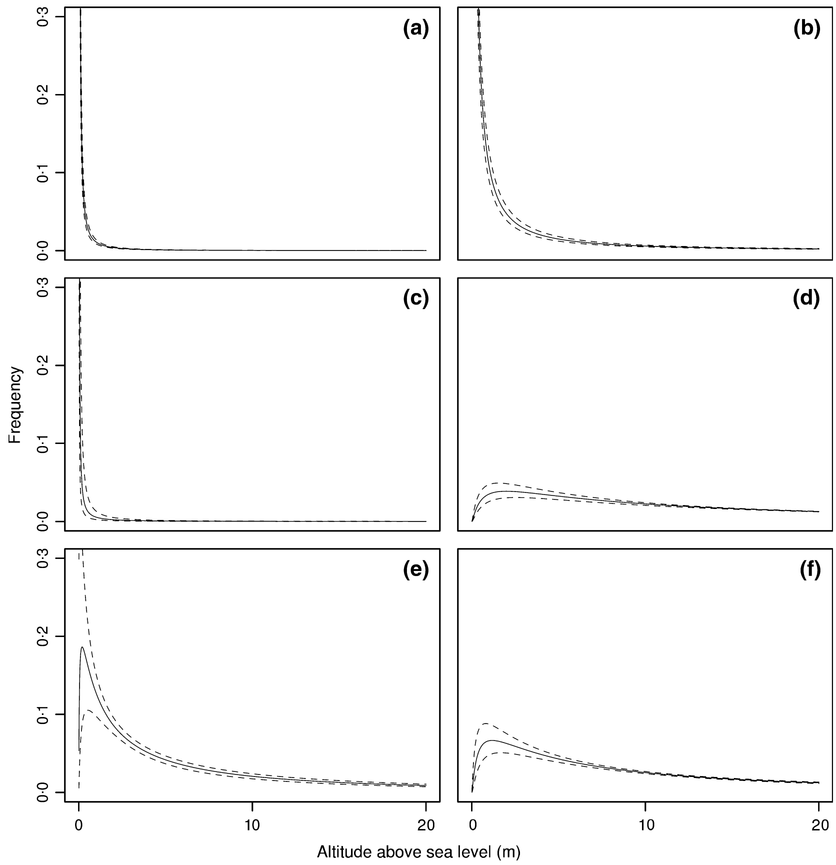

Fig. 1. Modelled heights for lesser black-backed gulls during the day in (a) state 1 (<1 km h^{-1} 'terrestrial, coastal and marine'); (b) state 2 (1–4 km h^{-1} 'terrestrial'); (c) state 3 (1–4 km h^{-1} 'coastal and marine'); (d) state 4 (>4 km h^{-1} 'terrestrial'); (e) state 5 (>4 km h^{-1} 'coastal'); and (f) state 6 (>4 km h^{-1} 'marine'). Solid lines – median; dashed lines – 2·5% and 97·5% credible intervals.

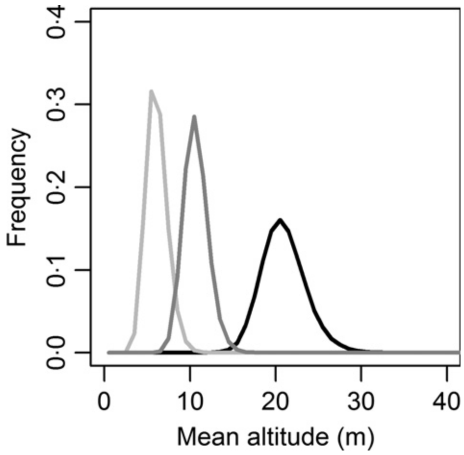

Fig. 2. Posterior distributions of mean flight height for lesser black-backed gulls during the day in 'coastal' (pale grey), 'marine' (medium grey) and 'terrestrial' areas (black).

heights were lowest at twilight, whereas 'marine' flight heights were lowest after dark. Half the observations for 'terrestrial' gulls were within 14·0 m of ground level after dark, compared to half within 12·0 m at twilight. For 'coastal' habitats, 50% of observations fell within 5·4 m of sea level after dark, compared to 2·5 m at twilight. About 50% of 'marine' measurements fell within 5·6 m of sea level after dark, versus 50% within 10·4 m at twilight.

Great skua

Great skuas travelling at <4 km h^{-1} (states 1 and 2) were observed at low altitudes, as expected for individuals that are not flying (Fig. 3a,b). Altitude was higher for birds moving at >4 km h^{-1} (states 3 and 4; Fig. 3c,d), but the difference was less marked than for lesser black-backed gulls. During daylight, 50% of 'terrestrial' observations (state 3) were within 2·2 m of ground level, and 50% of 'marine & coastal' measurements (state 4) were within 0·2 m of sea level. Flight height over land was therefore higher than that over sea (Fig. 4), but the difference between the log mean altitudes was not quite significant (Table 4 and Fig. 4).

Great skua flight height was not greatly affected by light levels (Table 4 and Fig. S2). Estimated heights in 'terrestrial' habitats were higher during daylight than at twilight, or at night (Fig. 4). While 50% of observations were within 2·2 m of the ground in daylight, the corresponding heights for twilight and darkness were 0·6 m and 1·1 m, respectively. Flight over 'coastal & marine' areas occurred at very low heights regardless of light level. During the day, 50% of observations were within 0·2 m of sea level, while at twilight, this figure was 0·4 m, and in darkness, it was 0·6 m.

FLIGHT AT COLLISION RISK HEIGHT

The risk window of 30–258 m encompassed the lowest proportion of lesser black-backed gull flight at sea in all

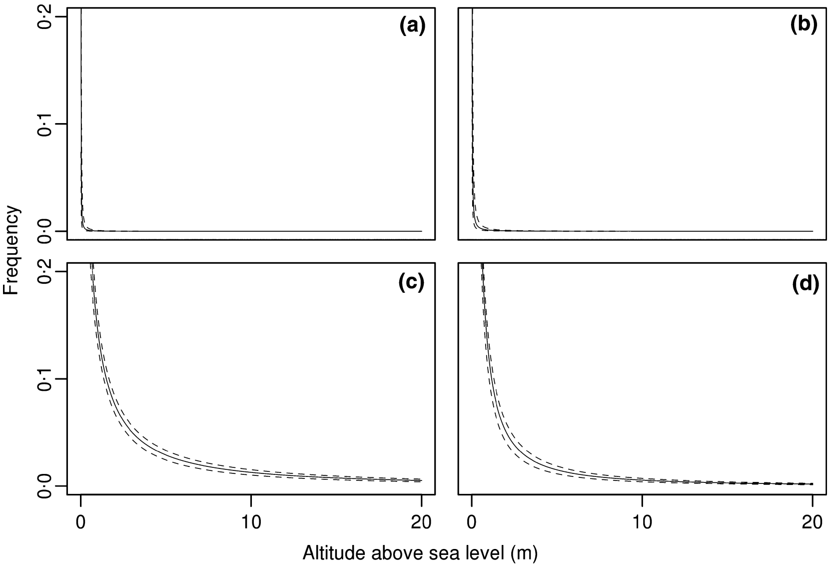

Fig. 3. Modelled heights for great skuas during the day in (a) state 1 (<4 km h^{-1} 'terrestrial'); (b) state 2 (<4 km h^{-1} 'coastal & marine'); (c) state 3 (>4 km h^{-1} 'terrestrial'); and (d) state 4 (>4 km h^{-1} 'coastal & marine'). Solid lines – median; dashed lines –2·5% and 97·5% credible intervals.

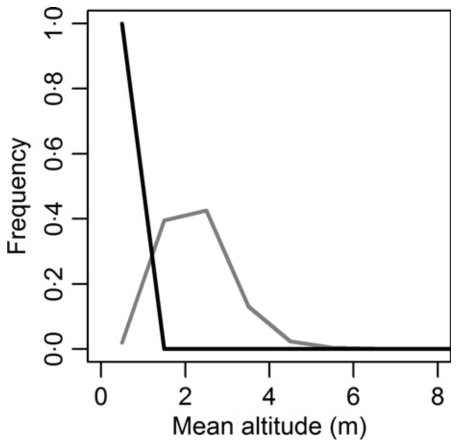

Fig. 4. Posterior distributions of mean flying altitude of great skuas during the day in 'coastal and marine' (grey) and 'terrestrial' areas (black).

light levels (26·4% by day, 22·7% at twilight, 13·1% after dark) and a significantly lower proportion fell within this risk window after dark than by day (identified by the non-overlapping credible intervals in Fig. 5). This significant difference between day and night was true for all risk windows, with an intermediate proportion at twilight. The risk window of 22–250 m contained the highest proportion of observations by day, at 33·5%. This risk window was also highest for twilight (29·4%), but after dark, the window of 20–120 m held the highest percentage of observations (18·1%).

The proportion of flying great skuas at risk was considerably lower than lesser black-backed gulls for all risk windows, but the 30–258 m risk window also had the lowest percentage at risk (Fig. 5) holding 3·6% of flight height observations by day, 5·7% at twilight and 7·2% after dark. The 22–250 m risk window contained the highest

Table 4. Credible intervals for state-space model of great skua height (metres above surface level). See Table 2 for different states

Parameter	Lower 2·5% credible interval	Median	Upper 97·5% credible interval
State 1 mean ln height (daylight)	−27·18	−19·55	−14·94
State 2 mean ln height (daylight)	−29·44	−20·50	−14·43
State 3 mean ln flight height (daylight)	0·05	0·76	1·41
State 4 mean ln flight height (daylight)	−2·25	−1·56	−0·96
State 3 mean ln flight height (twilight)	−13·47	−0·44	1·77
State 4 mean ln flight height (twilight)	−1·69	−0·86	−0·11
State 3 mean ln flight height (darkness)	−1·34	0·06	1·25
State 4 mean ln flight height (darkness)	−1·17	−0·46	0·18
State 1 variance of ln height	21·44	35·24	65·75
State 2 variance of ln height	30·00	53·69	101·50
State 3 variance of ln flight height	5·50	6·78	8·45
State 4 variance of ln flight height	7·54	8·36	9·29
Intercept of variance of observation error	721·90	754·50	787·00
Coefficient of DOP for variance of observation error	63·24	72·47	81·91
Variance of individual random effect	0·64	1·31	3·12

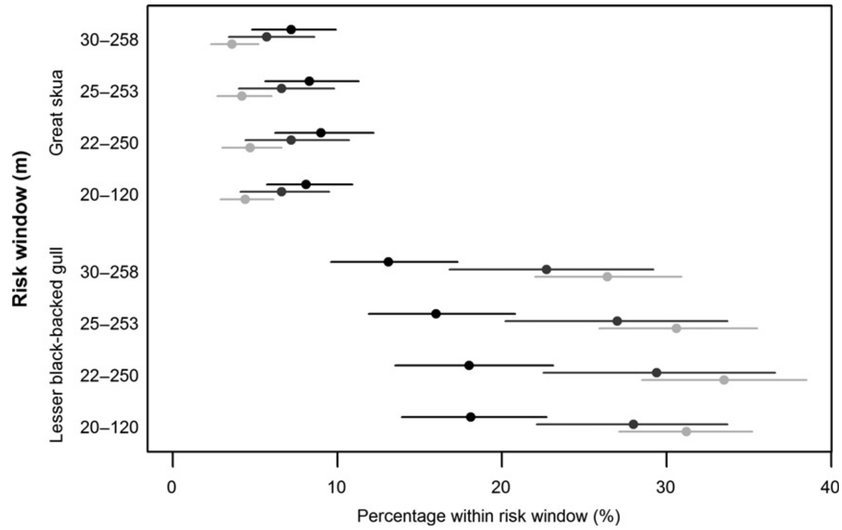

Fig. 5. Percentage (and 95% credible interval) of lesser black-backed gull and great skua flight height observations within different collision risk windows. Pale grey – daylight, dark grey – twilight, black – darkness.

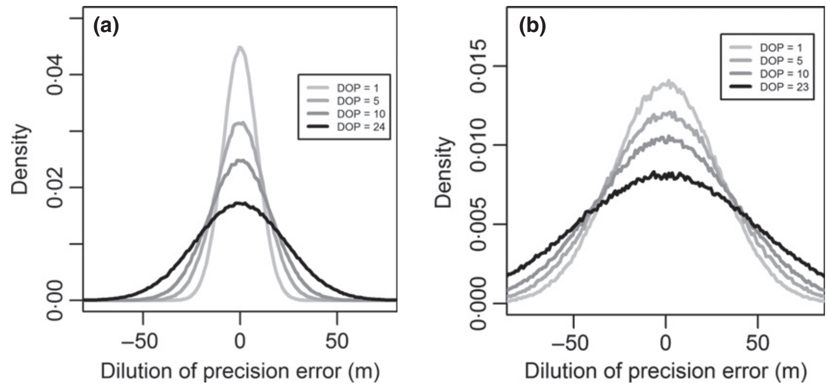

Fig. 6. Error in flight height measurements for different DOP values for (a) lesser black-backed gull; (b) great skua. The range of errors increases as the DOP itself increases.

proportion of observations (4·7% by day, 5·7% at twilight, 9·0% by night). Daytime observations had the lowest proportion at risk height of all light levels for all risk windows, followed by twilight and then darkness, although there was less distinction between different light levels for great skuas than for lesser black-backed gulls.

OBSERVATION ERROR IN RECORDED FLIGHT HEIGHTS

The mean DOP was 3·3 (SD = 1·6) for lesser black-backed gulls and 3·7 (SD = 1·6) for great skuas. A higher DOP value resulted in a higher standard deviation and therefore a wider error distribution and less precise flight height estimates. For lesser black-backed gulls, the standard deviation of the error distribution was 8·9 m for DOP = 1, rising to 16·1 m for DOP = 10. For great skuas, the standard deviation of the error distribution was 28·8 m for DOP = 1, rising to 38·5 m for DOP = 10 (Fig. 6).

Discussion

This study is the first application of SSMs to altitude data from GPS tracks of animal movement. Our distributions of seabird flight heights at different light levels account for error in altitude measurements and variation in their precision. We show that breeding adult lesser black-backed gull and great skua flight height varied with location and light level, and both species flew at heights corresponding to the area swept by offshore wind turbine blades for a variety of turbine designs regardless of light level. Other studies using GPS to assess seabird flight heights have also examined flight heights relative to the rotor swept area (Corman & Garthe 2014; Cleasby *et al.* 2015), but here we demonstrate how the error associated with GPS measurements of flight height can be accommodated analytically.

ACCOUNTING FOR ERROR IN GPS DATA WITH THE BAYESIAN MODELLING APPROACH

Our SSMs are a powerful way of exploring seabird flight heights while accounting for the error inherent in GPS altitude measurements. We demonstrate that DOP is strongly related to the degree of error in observations of altitude. This error was larger for great skuas than for lesser black-backed gulls, possibly due to differences bird behaviour (e.g. fast-moving birds that change altitude often might have larger modelled error than slower ones moving at a more constant height). The differences in DOP between the two species underline the importance of accounting for this when modelling GPS data.

The method described here is not the only solution for accommodating the error in GPS measurements of altitude. Recent studies have effectively used pressure loggers to correct for this (Garthe *et al.* 2014; Cleasby *et al.* 2015). However, tests show that precision declines as the length of flights increases (Cleasby *et al.* 2015), and our analytical approach is not affected by this. Both techniques are likely to be useful, depending on the nature of the study. For example, our SSMs are computationally intensive, so ecological questions that require a fast answer might be best addressed by the deployment of pressure loggers.

FLIGHT HEIGHTS IN COMPARISON WITH PREVIOUS STUDIES AND IMPLICATIONS FOR COLLISION RISK

We show that breeding adult lesser black-backed gulls fly higher over land than over sea. This result supports that of Corman & Garthe (2014), who used GPS to record eight breeding lesser black-backed gulls flying higher over land than at sea during part of May/June 2013. Our study extends this finding to another breeding colony, as well as incorporating a larger data set of a bigger sample of birds tracked over a longer time period, suggesting it could be generally applicable to breeding lesser black-backed gulls across their range. As our tagged lesser black-backed gulls flew higher over land than over sea and spent more flight time over land (Appendix S2), these individuals could be at higher risk of collision with onshore wind turbines and other human structures than with developments offshore. Other gull species have been found to collide with onshore wind turbines (Krijgsveld *et al.* 2009). We also found that lesser black-backed gulls flew lower nearer the coast than further out at sea. It would be useful to investigate whether such locational differences exist for this species (and others) more generally, as if this finding is replicated, it might suggest that optimal turbine heights for minimizing bird collisions vary in different marine areas.

Both species mostly flew at low heights; 61·4% of lesser black-backed gull flight at sea was below 20 m (the lowest height swept by turbine blades in our collision risk windows). This altitude is lower than that recorded in boat surveys (e.g. Garthe & Hüppop 2004) and with rangefinders (Mendel *et al.* 2014), but higher than that documented by Corman & Garthe (2014), who found that 89% of GPS fixes from breeding lesser black-backed gulls (over land and sea) were below 20 m. Great skua flight height at sea was lower still, with 94·2% below 20 m. This is also lower than that recorded in boat surveys (e.g. Garthe & Hüppop 2004). Taken together, our results support previous studies (e.g. Furness, Wade & Masden 2013) in suggesting that great skuas are at lower risk of collision with offshore wind turbines than lesser black-backed gulls. Our results also support those of Cleasby *et al.* (2015), who proposed raising the height of offshore wind turbine blades to 30 m above sea level to minimize seabird collisions, as our 30–258 m risk window was the safest for both species.

Modelled observations from boat surveys estimated that 28·2% (95% confidence interval: 20·3–43·1%) of lesser black-backed gulls and 5·9% (3·5–17·9%) of great skuas flew within a collision risk window of 20–120 m (Johnston *et al.* 2014). The figures from our study are similar and fall within these confidence limits; 31·2% of daytime flight at sea by lesser black-backed gulls and 4·4% by great skuas were in this height band, providing a useful validation of boat survey data. The reasons for the differences between the two studies could include the inaccuracy of flight height estimates from boat surveys and the more restricted weather conditions they represent, as well as the possibility that birds altered their flight behaviour in the presence of boats (e.g. Spear *et al.* 2004), or different assumptions involved in the two modelling processes. Our GPS data are higher quality than boat data, since they are more accurate, span the breeding season, were collected in various conditions and (for lesser black-backed gulls) over several years. GPS also gives information for individuals over a broader geographical range than the snapshot provided by single boat surveys – lesser black-backed gulls in our data set travelled up to 159 km from their colonies (Thaxter *et al.* 2015), while great skuas from Foula had a maximum foraging range of 265 km (Thaxter *et al.* 2012b).

FLIGHT HEIGHTS BY NIGHT AND DAY

Previous research has indicated that flying birds might be more at risk of collision with man-made structures at night than by day (e.g. Dolbeer 2006; Furness, Wade & Masden 2013). The results of this study show lesser black-backed gulls fly lower, especially over sea, at night than during the day. This apparent reduction in collision risk due to lower night flight height could be offset by poor visibility, making turbine blades, or even masts, harder to detect and avoid. However, gulls spent relatively little time flying at night (only 0·03% of their total time, Appendix S2), suggesting that the risk of interacting with offshore developments after dark is small and that collisions at night are less probable than during the day.

Great skuas in our study consistently flew close to the land/sea surface regardless of light level. However, a higher proportion of great skua flight was found to be within the possible height bands swept by offshore wind turbine blades after dark than in daylight. Great skuas spent approximately 8% of their time flying at night (a higher proportion than lesser black-backed gulls, Appendix S2) so collision with turbines could be a danger if this species' night vision and/or ability to detect objects in front of them is poor. It should be noted, however, that during mid-summer, hours of darkness are short and there is often still some light in the sky after sunset at the northern latitudes frequented by the great skuas in our study. Birds might encounter turbines in darker conditions than those modelled here at other times of the year and at different latitudes (e.g. wind farms in the southern North Sea on migration), and flight behaviour could differ accordingly.

The ability of birds to detect and avoid wind turbines and other structures in different conditions must be influenced by constraints on their visual system that are not yet well understood (Martin 2011). However, EIAs for offshore wind farms currently use limited, or even no, data on flight behaviour and collision risk at night, so our results help fill an important knowledge gap.

FUTURE USE OF GPS TRACKING

GPS tracking data could be used alongside records from boat and aerial surveys for impact assessments, in a complementary approach similar to that suggested for the identification of ecologically important areas for seabirds (Camphuysen *et al.* 2012). The long-term, detailed and accurate GPS data for known individuals from a small number of colonies could be combined with the large samples assessed in boat and aerial surveys, representing birds from several colonies, and encompassing breeding and non-breeding individuals that might behave differently because of differing foraging needs. Together, these survey techniques could provide high-quality, cost-effective and accurate information on seabirds' three dimensional use of their environment for impact assessments.

CONCLUSIONS

We demonstrate a novel and powerful approach for modelling GPS measurements of flight heights. The data we modelled are among the best available on lesser black-backed gull and great skua flight heights, and the distributions produced are directly applicable to existing collision risk models (e.g. Band 2012). This study focused on birds associated with their breeding colony. In future, our method could be adapted to study flight heights throughout the annual cycle, as optimal flight modes might differ across the year. Migrating birds, for example, face variable atmospheric conditions and use different flight strategies to those favoured during the breeding season (Shamoun-Baranes, Bouten & van Loon 2010; Mateos-Rodríguez & Liechti 2011). The application of our modelling approach to other GPS data sets could help define and manage the ecological needs of lesser black-backed gulls, great skuas and other species at a time when the pressures on the marine environment are growing.

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Data accessibility

GPS tracks from this project can be viewed at http://www.uva-bits.nl/project/seabird-windfarm-interactions/ and http://www.uva-bits.nl/project/seabird-windfarm-interactions-2/. The data we used are available via the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.dp2ms (Ross-Smith *et al.* 2016).

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Supporting Information

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

Fig. S1. Modelled flight heights of tagged lesser black-backed gulls at different light levels.

Fig. S2. Modelled flight heights of tagged great skuas at different light levels.

Table S1. Data availability and measurements modelled per tagged individual.

Table S2. Parameters estimated in state-space models and associated prior distributions.

Appendix S1. Histograms of data modelled in state-space models.

Appendix S2. Amount of time GPS-tagged individuals spent in different states.