



UHI Research Database pdf download summary

Modelling flight heights of Lesser Black-backed Gulls and Great Skuas from GPS: a Bayesian approach

Ross-smith, Viola H.; Thaxter, Chris B.; Masden, Elizabeth; Shamoun-baranes, Judy; Burton, Niall H.k.; Wright, Lucy J.; Rehfish, Mark M.; Johnston, Alison

Published in:
Journal of Applied Ecology

Publication date:
2016

The re-use license for this item is:
CC BY-NC-SA

The Document Version you have downloaded here is:
Peer reviewed version

The final published version is available direct from the publisher website at:
[10.1111/1365-2664.12760](https://doi.org/10.1111/1365-2664.12760)

[Link to author version on UHI Research Database](#)

Citation for published version (APA):

Ross-smith, V. H., Thaxter, C. B., Masden, E., Shamoun-baranes, J., Burton, N. H. K., Wright, L. J., Rehfish, M. M., & Johnston, A. (2016). Modelling flight heights of Lesser Black-backed Gulls and Great Skuas from GPS: a Bayesian approach. *Journal of Applied Ecology*. <https://doi.org/10.1111/1365-2664.12760>

General rights

Copyright and moral rights for the publications made accessible in the UHI Research Database are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights:

- 1) Users may download and print one copy of any publication from the UHI Research Database for the purpose of private study or research.
- 2) You may not further distribute the material or use it for any profit-making activity or commercial gain
- 3) You may freely distribute the URL identifying the publication in the UHI Research Database

Take down policy

If you believe that this document breaches copyright please contact us at RO@uhi.ac.uk providing details; we will remove access to the work immediately and investigate your claim.

A Bayesian analytical approach to modelling the flight heights of breeding Lesser Black-backed Gulls and Great Skuas from GPS tracking data

Viola H. Ross-Smith*, British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, United Kingdom. viola.ross-smith@bto.org

Chris B. Thaxter, British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, United Kingdom. chris.thaxter@bto.org

Elizabeth A. Masden, Environmental Research Institute, Centre for Energy and the Environment, North Highland College, University of the Highlands and Islands, Ormlie Road, Thurso, Caithness, KW14 7EE, United Kingdom. elizabeth.masden@uhi.ac.uk

Judy Shamoun-Baranes, Computational Geo-Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94248, 1090 GE Amsterdam, The Netherlands. shamoun@uva.nl

Niall H.K. Burton, British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, United Kingdom. niall.burton@bto.org

Lucy J. Wright, British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, United Kingdom. lucy.wright@bto.org

Mark M. Rehfisch, APEM Limited, Suite 2 Ravenscroft House, 59-61 Regent Street, Cambridge, CB2 1AB, United Kingdom. m.rehfisch@apemltd.co.uk

Alison Johnston, British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, United Kingdom. alison.johnston@bto.org

* Corresponding author

British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, United Kingdom

Tel: +44 1842 750050, Fax: +44 1842 750030

Running title: Modelling seabird flight heights from GPS

Word count: (summary = 336 words, main text = 4721 words, acknowledgements = 140 words, references = 1095 words, tables & figure legends = 704 words).

Number of figures: 6

Number of tables: 4

Summary

1. The risk of seabirds colliding with offshore wind turbines is influenced by flight height. To date, most information on flight heights has come from observers on boats, making estimates in daylight in fine weather. GPS tracking generates flight height information in a range of conditions, but the raw data has associated error. Here we present a novel analytical solution for accommodating this error.

2. We use Bayesian state-space models to describe the flight height distributions and the error in altitude measured by GPS for two seabird species, Lesser Black-backed Gull and Great Skua, 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 turbines at night, when birds' ability to detect and avoid blades 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 height above sea level swept by rotor blades for different offshore wind turbine designs. We found the highest proportion of birds at risk height 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 during daylight hours.

5. *Synthesis and applications.* Our novel modelling approach is a powerful and effective way of resolving the error associated with GPS tracks of animal movement. We demonstrate its use on GPS measurements of altitude, generating important information on how breeding seabirds use their environment; specifically, how time of day and location affect flight heights, which could inform impact assessments for offshore wind farms. This approach could be usefully adapted to calculate flight height distributions at other sites and for other species, accommodating error in estimates of altitude.

Keywords

Collision risk; Environmental Impact Assessment; MCMC; monitoring; offshore wind farm; renewable energy; 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 bird approaching a turbine, collision risk is determined by turbine dimensions and characteristics of the bird, including flight height (Johnston *et al.* 2014).

Much of our current 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 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 identification to species level (Hüppop *et al.* 2006; Schmaljohann *et al.* 2008).

An alternative to these methods is GPS tracking. Individual seabirds are fitted with small 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; Dokter *et al.* 2013; 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 potentially 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; Wade *et al.* 2014; Thaxter *et al.* 2015). 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 fly at a height that puts 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 of in terms of likelihood of collision with Scottish turbines (Furness, Wade & Masden 2013).

We use data from GPS tags to model flight heights of Lesser Black-backed Gulls and Great Skuas during the breeding season. 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 information will improve assessment of the impact of offshore wind farms by (i) providing data on bird movements in conditions missing from non-tracking datasets (e.g. variable weather conditions, and night-time) and (ii) providing flight height distributions that can contribute to turbine design to mitigate collision risks.

Materials and methods

Field methods

Twenty-five Lesser Black-backed Gulls were caught at Orford Ness, Suffolk (52°4'N, 1°33'E) during June 2010 (n = 11) and May 2011 (n = 14), while 14 Great Skuas were captured on Foula, Shetland (60°8'N, 2°5'W) in June 2010 (n = 4) and June 2011 (n = 10) and 10 on Hoy, Orkney (58°52'N, 3°24'W) in June 2011 (see Table S1 in 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. Birds were breeding adults, caught on the nest as they incubated eggs. The device plus harness weighed 21 g, < 3% of the birds' body mass (gulls: mean mass 851 g, range 710-955 g; skuas: mean 1350 g, range 1190-1490 g) (for details see Thaxter *et al.* 2014). 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), such that the data considered in this study are thought to represent normal behaviour during the breeding season.

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 located close to the colonies (for further details, see Bouten *et al.* 2013). We defined a virtual perimeter of *ca.* 200 m² around the colony to identify when birds were 'within' the colony, or away on trips. The interval between GPS measurements was chosen to optimize data capture while minimising data gaps due to insufficient memory and battery life. Devices were normally set at 30 minute intervals when birds were at the colony and five or 10 minute intervals otherwise.

GPS data for Great Skuas were only available for the year in which birds were tagged. We monitored birds' nests and analysed GPS 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 the date at which they departed each season (Table S1), because tall 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 or birds leaving the colony so tags were no longer in contact with base stations (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). We examined the extent of temporal correlation for a few individuals and based on these structures, we decided that selecting one data point per hour would 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 the bird's behaviour and location. Bird speed was used as an indication of behaviour, where $< 1 \text{ kmh}^{-1}$ was classified as sitting or standing still, $1-4 \text{ kmh}^{-1}$ as walking, swimming or floating, and $> 4 \text{ kmh}^{-1}$ 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 defined as over or on the land. 'Coastal' was defined as 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 distribution of altitudes to be log-normal, 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 log-normal 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 modelled with an additive effect on the means of the log-normal 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 log-normal 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 log-normal 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 located 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, i.e. inaccuracy in the observed altitude provided by GPS. This model failed to converge, which suggests 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:

$$obs_j \sim N(alt_j, \sigma^2_j)$$

$$\sigma^2_j = \rho + \omega \cdot DOP_j$$

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^2_j . 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 the chains, 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 $> 4 \text{ kmh}^{-1}$ (i.e. birds flying at sea), we summarise 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 $< 4 \text{ kmh}^{-1}$ were effectively at surface level regardless of location, as expected of individuals standing, sitting, walking, swimming or floating. Some slightly higher altitudes were seen for 'terrestrial' birds at $1-4 \text{ kmh}^{-1}$ (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 $> 4 \text{ kmh}^{-1}$ (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 & Fig. 2).

Lesser Black-backed Gull flight height varied with light level, with birds flying higher during the day than after dark (Table 3 & Fig. S1). 'Terrestrial' and 'coastal' flight 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. 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 $< 4 \text{ kmh}^{-1}$ (states 1 and 2) were observed at low altitudes, as expected for individuals that are not flying (Figs. 3a & 3b). Altitude was higher for birds moving at $> 4 \text{ kmh}^{-1}$ (states 3 and 4) (Figs. 3c & 3d), 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 & Fig. 4).

Great Skua flight height was not greatly affected by light levels (Table 4 & 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 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 (Fig. 5). This significant difference between day and night was true for all risk windows, with an intermediate proportion at twilight. During the day, the risk window of 22-250 m contained the highest proportion of observations, 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 day. The 22-250 m risk window contained the highest 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 the precision of altitudinal measurements. 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 assessed flight heights relative to the rotor swept area (Corman & Garthe 2014; Cleasby *et al.* 2015), and here we demonstrated 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 in bird behaviour (e.g. fast-moving birds that change altitude often might have larger modelled error than slower ones that move at a more constant height). The differences in DOP between the two species underline the importance of accounting for this factor when modelling GPS data.

The method described here is not the only solution for dealing with 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 to 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 and 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 dataset 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 of their flight time over land than over sea (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 if 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 minimising 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 and 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 minimise 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 was 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 which boat data 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 (in the case of 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 dataset 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, which might make 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 (for example, 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, environmental impact assessments 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 sample size 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 could inform environmental impact assessments and collision risk modelling. 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 datasets 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.

Acknowledgements

We were funded by the UK Department of Energy and Climate Change (DECC), and the Marine Renewable Energy and the Environment (MaREE) project (funded by Highlands and Islands Enterprise, the European Regional Development Fund, and the Scottish Funding Council). Thanks to John Hartley (Hartley Anderson), Emma Cole, Mandy King, Sophie Thomas and James Burt (DECC), the National Trust, Scottish Natural Heritage, RSPB and Natural England. Birds were ringed and tagged under licence from the British Trust for Ornithology, Scottish Natural Heritage and Natural England. Additional fieldwork was carried out by Greg Conway, Nigel Clark, Mike Marsh, Gill Stannard, Sarah Davies, Eliza Leat, Helen Wade, Bob Furness, Sheila Gear, Chris Booth and Mark Bolton. We are grateful to many others, especially Willem Bouten and Edwin Baaij at the University of Amsterdam and Aonghais Cook at the British Trust for Ornithology.

References

Bouten, W., Baaij, E.W., Shamoun-Baranes, J. & Camphuysen, K.C.J. (2013) A flexible GPS tracking system for studying bird behaviour at multiple scales. *Journal of Ornithology*, **54**, 571-580.

Camphuysen, C.J., Fox, A.D., Leopold, M.F. & Petersen, I.K. (2004) *Towards standardised seabirds at sea census techniques in connection with environmental impact assessments for offshore windfarms in the U.K.* Report commissioned by COWRIE. Koninklijk Nederlands Instituut voor Onderzoek der Zee.

Camphuysen, C.J., Shamoun-Baranes, J., Bouten, W. & Garthe, S. (2012) Identifying ecologically important marine areas for seabirds using behavioural information in combination with distribution patterns. *Biological Conservation*, **156**, 22-29.

Cleasby, I.R., Wakefield, E.D., Bearhop, S., Bodey, T.W., Votier, S.C. & Hamer, K.C. (2015) Three-dimensional tracking of a wide-ranging marine predator: flight heights and vulnerability to offshore windfarms. *Journal of Applied Ecology*, **52**, 1474-1482.

Corman, A.-M. & Garthe, S. (2014) What flight heights tell us about foraging and potential conflicts with wind farms: a case study in Lesser Black-backed Gulls (*Larus fuscus*). *Journal of Ornithology*, **155**, 1037-1043.

Dokter, A.M., Shamoun-Baranes, S., Kemp, M.U., Tijm, S., Holleman, I. (2013) High altitude bird migration at temperate latitudes: a synoptic perspective on wind assistance. *PLoS ONE*, **8**, e52300.

Dolbeer, R.A. (2006) Height distribution of birds recorded by collisions with civil aircraft. *Journal of Wildlife Management*, **70**, 1345–1350

Drewitt, A.L. & Langston, R.H.W. (2006) Assessing the impacts of wind farms on birds. *Ibis*, **148 S1**, 29–42.

Eaton, M.A., Aebischer, N.J., Brown, A F., Hearn, R.D., Lock, L., Musgrove, A.J., Noble, D.G., Stroud, D.A. & Gregory, R.D. (2015) Birds of Conservation Concern 4: the population status of birds in the United Kingdom, Channel Islands and Isle of Man. *British Birds*, **108**, 708-746.

Furness, R.W., Wade, H.M. & Masden, E.A. (2013) Assessing vulnerability of marine bird populations to offshore wind farms. *Journal of Environmental Management*, **119**, 56-66.

Garthe, S. & Hüppop, O. (2004) Scaling possible adverse effects of marine wind farms on seabirds: developing and applying a vulnerability index. *Journal of Applied Ecology*, **41**, 724-734.

Garthe, S., Guse, N., Montevecchi, W.A., Rail, J.-C. & Grégoire, F. (2014) The daily catch: Flight altitude and diving behavior of northern gannets feeding on Atlantic mackerel. *Journal of Sea Research*, **85**, 456-462.

- Gilks, W.R., Richardson, S. & Spiegelhalter, D.J. (1996) *Markov Chain Monte Carlo in practice*. Chapman & Hall/CRC.
- Hüppop, O., Dierschke, J., Exo, K.M., Fredrich, E. & Hill, R. (2006) Bird migration studies and potential collision risk with offshore wind turbines. *Ibis*, **148** S1, 90-109.
- Johnston, A., Cook, A.S.C.P, Wright, L.J., Humphreys, E.M. & Burton, N.H.K. (2014) Modelling flight heights of marine birds to more accurately assess collision risk with offshore wind turbines. *Journal of Applied Ecology*, **51**, 31-41.
- Kemp, M.U., Shamoun-Baranes, J., Dokter, A.M., van Loon, E. & Bouten, W. (2013) The influence of weather on the flight altitude of nocturnal migrants in mid-latitudes. *Ibis*, **155**, 734-749.
- King, R. (2012) A review of Bayesian state-space modelling of capture-recapture-recovery data. *Interface Focus*, **2**, 190–204.
- Krijgsveld, K. L., Akershoek, K., Schenk, F., Dijk, F., & Dirksen, S. (2009) Collision risk of birds with modern large wind turbines. *Ardea*, **97**, 357-366.
- Langley, R.B. (1999) Dilution of precision. *GPS World*, **May 1999**, 52-59.
- Lunn, D., Spiegelhalter, D., Thomas, A. & Best, N. (2009) The BUGS project: Evolution, critique, and future directions. *Statistics in Medicine*, **28**, 3049-3067.
- Mendel, B., Kotzerka, J., Sommerfeld, J., Schwemmer, H., Sontag, N. & Garthe, S. (2014) Effects of the *alpha ventus* offshore test site on distribution patterns, behaviour and flight heights of seabirds. In: Federal Maritime and Hydrographic Agency and Federal Ministry for the Environment, Nature Conservation and Nuclear Safety (eds.) *Ecological research at the offshore windfarm alpha ventus—challenges, results and perspectives*, pp. 95–110. Springer Fachmedien, Wiesbaden.
- Martin, G.R. (2011) Understanding bird collisions with man-made objects: a sensory ecology approach. *Ibis*, **153**, 239-254.

- Mateos-Rodríguez, M. & Liechti, F. (2011) How do diurnal long-distance migrants select flight altitude in relation to wind? *Behavioral Ecology*, **23**, 403-409.
- Patterson, T.A., Thomas, L., Wilcox, C., Ovaskainen, O. & Matthiopoulos, J. (2008) State-space models of individual animal movement. *Trends in Ecology and Evolution*, **23**, 87-94.
- R Core Team (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Schmaljohann, H., Liechti, F., Bachler, E., Steuri, T., & Bruderer, B. (2008) Quantification of bird migration by radar – a detection probability problem. *Ibis*, **150**, 342-355
- Shamoun-Baranes, J., van Loon, E., van Gasteren, H., van Belle, J., Bouten, W. &uurma, L. (2006) A comparative analysis of the influence of weather on the flight altitudes of birds. *Bulletin of the American Meteorological Society*, **87**, 47-61.
- Shamoun-Baranes, J. Bouten, W. & van Loon, E. (2010) Integrating meteorology into research on migration. *Integrative and Comparative Biology*, **50**, 280-292.
- Shamoun-Baranes, J., Bouten, W., Camphuysen, C.J. & Baaj, E. (2011) Riding the tide: intriguing observations of gulls resting at sea during breeding. *Ibis*, **153**, 411-415.
- Spear, L.B., Ainley, D.G., Hardesty, B.D., Howell, S.N.G. & Webb, S.W. (2004) Reducing biases affecting at-sea surveys of seabirds: use of multiple observer teams. *Marine Ornithology*, **32**, 147–157.
- Thaxter, C.B., Lascelles, B., Sugar, K., Cook, A.S.C.P., Roos, S., Bolton, M., Langston, R.H.W. & Burton, N.K.H. (2012a) Seabird foraging ranges as a preliminary tool for identifying candidate Marine Protected Areas. *Biological Conservation*, **156**, 53-61.
- Thaxter, C.B., Ross-Smith, V.H., Clark, N.A., Conway, G.J., Wade, H., Masden, E.A., Rehfish, M.M., Bouten, W. & Burton, N.H.K. (2012b) *Measuring the interaction between marine features of Special Protection Areas with offshore wind farm development zones through telemetry: second breeding season report*. BTO Research Report No. 610, BTO, Thetford.

Thaxter, C.B., Ross-Smith, V.H., Clark, J.A., Clark, N.A., Conway, G.J., Marsh, M., Leat, E.H.K. & Burton, N.H.K. (2014) A trial of three harness attachment methods and their suitability for long-term use on Lesser Black-backed Gull and Great Skua. *Ringing and Migration*, **29**, 65-76.

Thaxter, C.B., Ross-Smith, V.H., Bouten, W., Clark, N.A., Conway, G.J., Rehfisch, M.M. & Burton, N.H.K. (2015) Seabird-wind farm interactions during the breeding season vary within and between years: the case study of Lesser Black-backed Gull *Larus fuscus* in the UK. *Biological Conservation*, **186**, 347-358.

Thaxter, C.B., Ross-Smith, V.H., Clark, J.A., Clark, N.A., Conway, G.J., Masden, E.A., Wade, H.M., Leat, E.H.K., Gear, S.C., Marsh, M., Booth, C., Furness, R.W., Votier, S.C. & Burton N.H.K. (2016) Contrasting effects of GPS device and harness attachment on adult survival of Lesser Black-backed Gulls *Larus fuscus* and Great Skuas *Stercorarius skua*. *Ibis*, **158**, 279-290.

Wade, H.M., Masden, E.A., Jackson, A.C., Thaxter, C.B., Burton, N.H.K., Bouten, W. & Furness, R.W. (2014) Great Skua (*Stercorarius skua*) movements at sea in relation to marine renewable energy developments. *Marine Environmental Research*, **101**, 69-80.

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.

Table 1. Behavioural states for state-space model of Lesser Black-backed Gulls.

	Speed	< 1 kmh ⁻¹	1-4 kmh ⁻¹	> 4 kmh ⁻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 kmh ⁻¹	1-4 kmh ⁻¹	> 4 kmh ⁻¹
	Behaviour	sitting/ standing/ floating/ swimming/ walking		Flying
Location	Terrestrial	1		3
	Coastal			
	Marine	2		4

Table 3. Credible intervals for state-space model of Lesser Black-backed Gull height (m above surface level). See Table 1 for different states.

Parameter	Lower credible interval	2.5%	Median	Upper credible interval	97.5%
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

Table 4. Credible intervals for state-space model of Great Skua height (m 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

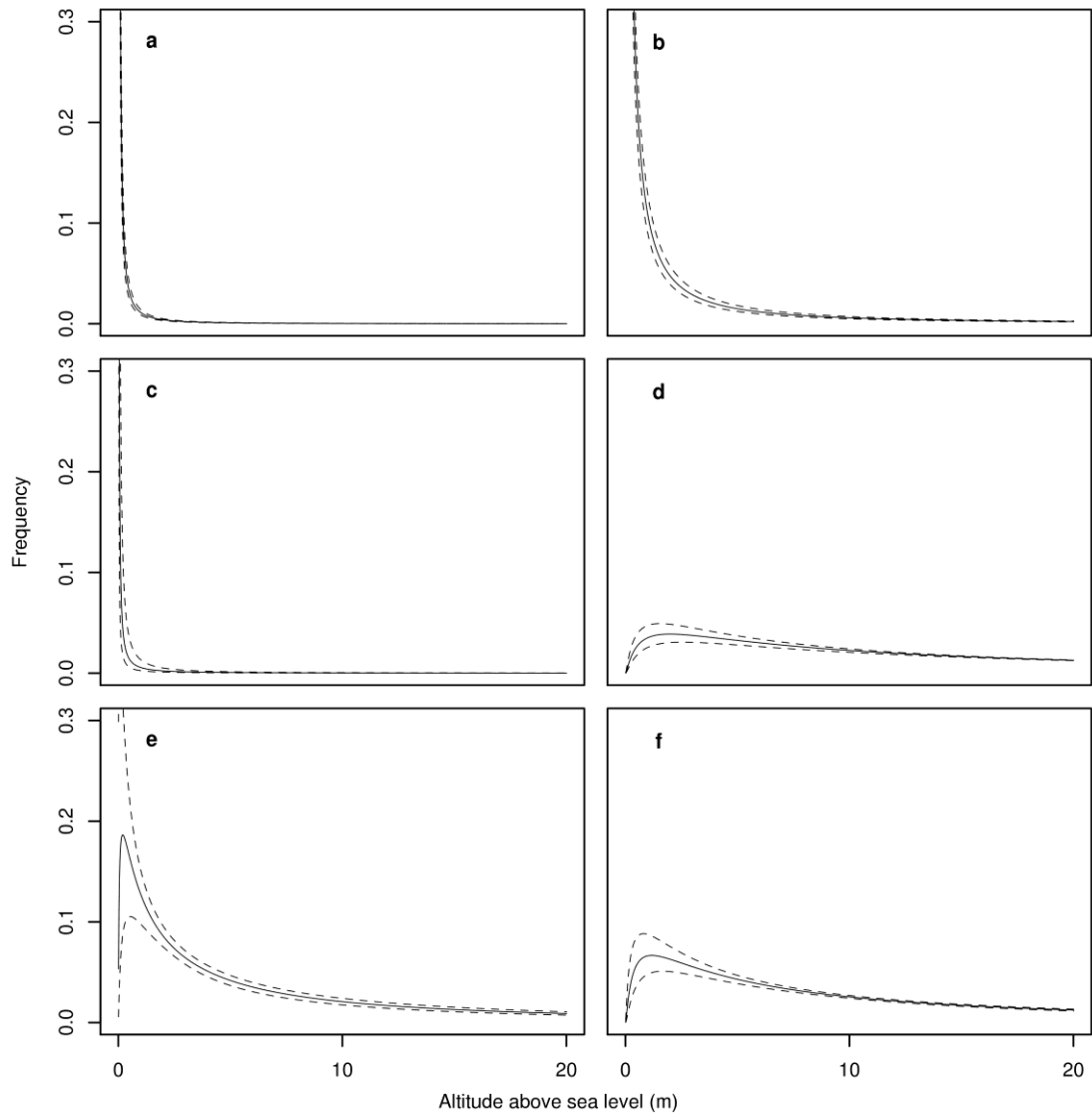


Fig. 1. Modelled heights for Lesser Black-backed Gulls during the day in (a) state 1 ($< 1 \text{ kmh}^{-1}$ 'terrestrial, coastal & marine'); (b) state 2 ($1-4 \text{ kmh}^{-1}$ 'terrestrial'); (c) state 3 ($1-4 \text{ kmh}^{-1}$ 'coastal & marine'); (d) state 4 ($> 4 \text{ kmh}^{-1}$ 'terrestrial'); (e) state 5 ($> 4 \text{ kmh}^{-1}$ 'coastal'); (f) state 6 ($> 4 \text{ kmh}^{-1}$ 'marine'). Solid lines – median; dashed lines – 2.5% & 97.5% credible intervals.

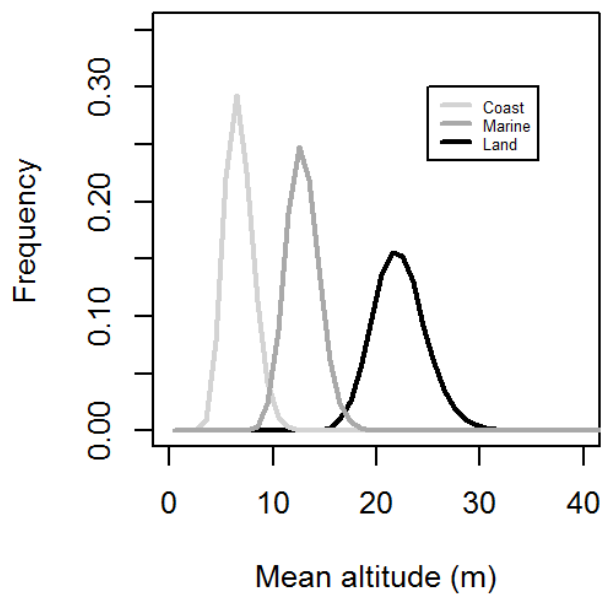


Fig. 2. Posterior distributions of mean flight height for Lesser Black-backed Gulls during the day in 'coastal' (pale grey), 'marine' (medium grey) and 'terrestrial' areas (black).

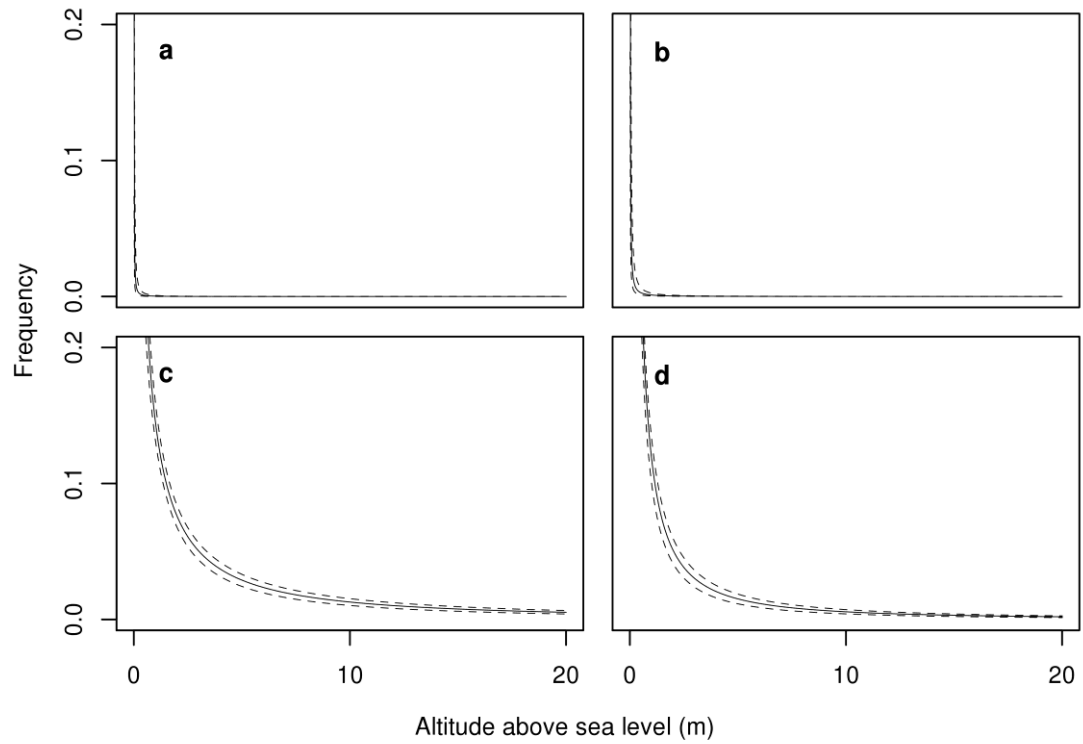


Fig. 3. Modelled heights for Great Skuas during the day in (a) state 1 ($< 4 \text{ kmh}^{-1}$ 'terrestrial'); (b) state 2 ($< 4 \text{ kmh}^{-1}$ 'coastal & marine'); (c) state 3 ($> 4 \text{ kmh}^{-1}$ 'terrestrial'); (d) state 4 ($> 4 \text{ kmh}^{-1}$ 'coastal & marine'). Solid lines – median; dashed lines – 2.5% & 97.5% credible intervals.

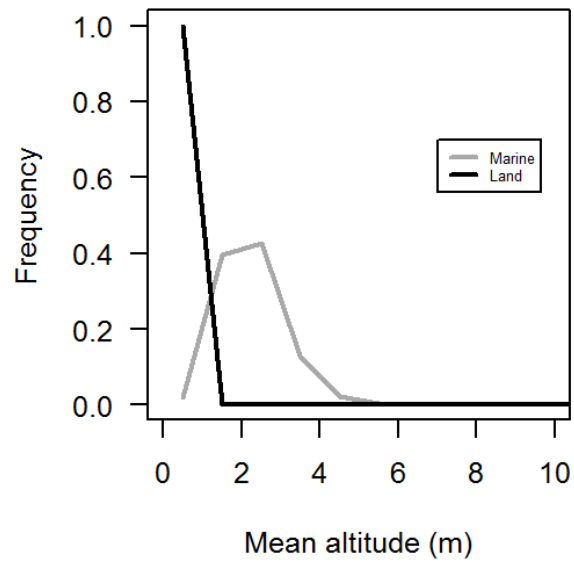


Fig. 4. Posterior distributions of mean flying altitude of Great Skuas during the day in 'coastal & marine' (grey) and 'terrestrial' areas (black).

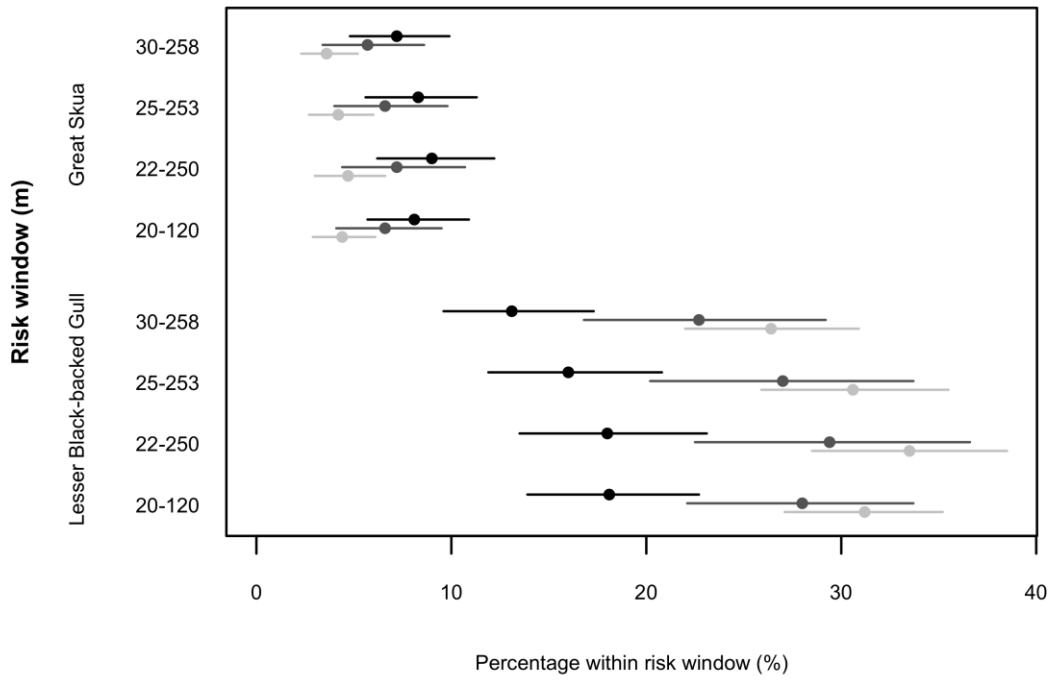
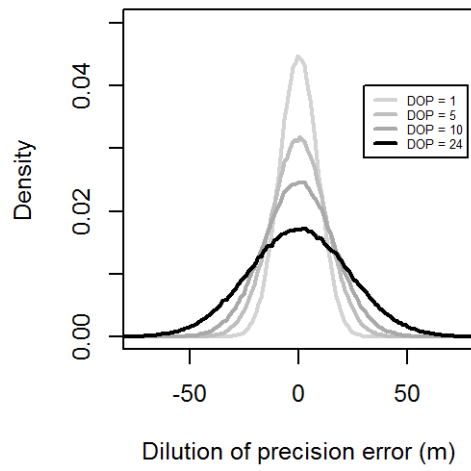


Fig. 5. Percentage of Lesser Black-backed Gull and Great Skua flight height observations within different collision risk windows. Pale grey – daylight, dark grey – twilight, black – darkness.

(a)



(b)

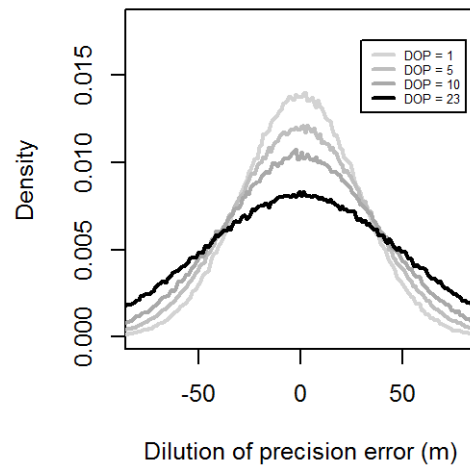


Fig. 6. Error in flight height measurements for different DOP values for (a) Lesser Black-backed Gull; (b) Great Skua. The range of errors increases as the DOP itself increases.