Understanding seabird behaviour at sea part 2: improved estimates of collision risk model parameters

October 2023

Scottish Government
Riaghaltas na h-Alba

Understanding seabird behaviour at sea part 2: improved estimates of collision risk model parameters

Aonghais S. C. P. Cook, Chris B. Thaxter, Jacob Davies, Ros M. W. Green, Saskia Wischnewski, Philipp Boersch-Supan

June 2023

While every effort has been made to make this publication accessible to all, some sections may remain inaccessible due to the nature of the content. If you are unable to access any content you require, please contact ScotMER@gov.scot

Executive Summary

Collision risk models form a key part of the environmental impact assessments for offshore wind farms. These models require inputs on species behaviour including flight speed, flight heights and nocturnal activity rates. At present, these are largely based on generic estimates from the literature, some of which are largely qualitative rather than quantitative. However, the rapid expansion of GPS tracking offers a valuable source of data for information on these parameters.

We collated GPS data from gannet, kittiwake and lesser black-backed gull, three species of key concern in relation to collision risk, from across multiple colonies. As a first step, we use Expectation-Maximisation Binary Clustering (EMbC) to classify GPS tracks as relating to foraging or commuting behaviour. These data were used to estimate the proportion of time birds were active during the night (e.g., classified as foraging or commuting) relative to the proportion of time birds were active during the day in order to quantify nocturnal activity rates. This parameter is difficult to estimate using other methods for collecting collision risk model parameter information, e.g. visual records. For all three species, nocturnal activity levels (e.g., the proportion of time birds were active at night, relative to the proportion of time birds were active during the day) varied between sites and years. However, the proportion of time birds were active during the night remained relatively constant, suggesting that this variation was driven by activity levels during the day.

Flight speeds were estimated separately for foraging and commuting flight. We used two different approaches to estimate flight speed – instantaneous speeds measured directly by the GPS tags using the Doppler effect, and trajectory speeds based on the distance travelled between fixes. In both cases, data were highly autocorrelated and had to be sub-sampled to one point every hour. Trajectory and instantaneous speeds were highly correlated with one another; however, the trajectory speeds were consistently an underestimate, compared with instantaneous speeds, an effect which became more pronounced as the sampling interval of the tags increased. Regardless of the approach used, foraging flight speeds were consistently lower than commuting flight speeds, and all speeds were lower than the current generic estimates of flight speeds recommended for use in the Band Collision Risk Model.

Flight heights were also estimated separately for foraging and commuting flight. Of the species considered, lesser black-backed gulls typically flew higher, and spent a greater proportion of time at collision risk height, than was the case for either gannets or kittiwakes. Commuting flights typically took place at greater heights than foraging flights. For lesser black-backed gulls, whilst there was consistency in foraging flight heights, there was evidence of differences in commuting flight heights among colonies.

GPS tracking provides a valuable source of data for parameterising collision risk models. However, there are clear differences in flight heights and speeds between areas used for foraging and commuting behaviour, which are likely to have implications for collision risk. The greater heights and faster speeds of commuting birds are likely to lead to greater estimates of collision risk than is the case for foraging birds. Furthermore, colony-specific

differences in both nocturnal activity rates and flight heights suggest that some degree of site-specific data may be required for reliable parameterisation of collision risk models in ornithological impact assessments.

Contents

1. Introduction

Offshore wind farm developments play a key role in strategies to reduce our reliance on energy generated using fossil fuels (Toke 2011). However, there are also concerns about the potential for offshore wind farms to negatively impact the environment, with the risk to seabirds receiving particular attention (Furness *et al.* 2013). Consequently, Environmental Impact Assessments (EIAs) must be carried out as part of the consenting process for proposed offshore wind farms. In relation to seabird populations, the key potential effects are perceived to be collisions with turbines, the loss of habitat as a result of displacement and barrier effects resulting in elevated energy expenditure costs.

Collision risk is assessed as part of the EIA process using a Collision Risk Model (CRM) such as the Band model (Band et al., 2007). The Band (2007) model was originally developed for use onshore, but refined in order to better reflect data collection methodologies in the offshore environment (Band, 2012). In common with most CRMs, the Band (2012) model requires reliable estimates of behavioural parameters, including estimates of species-specific flight heights, flight speeds and levels of nocturnal activity (Masden & Cook, 2016). However, these parameters are subject to significant uncertainty and variability, and how this is accounted for within the Band (2012) model has not always been clear. Consequently, Masden (2015) updated the Band (2012) model to incorporate stochasticity by enabling users to input parameters as distributions rather than point estimates. This was subsequently updated and made available as a more user-friendly web application (McGregor et al., 2018).

At present, estimates of species flight heights have typically been based on boat or digital aerial survey data (Johnston & Cook, 2016; Johnston *et al.* 2014). Similarly, estimates of other key parameters such as flight speed and levels of nocturnal activity have been drawn from studies with limited sample sizes or have been based on reviews inferred from our understanding of the ecology of the species concerned (Alerstam *et al.* 2007; Garthe & Huppop, 2004). However, ongoing analyses have highlighted how using data in this way may give a mis-leading impression of collision risk (Masden et al., 2021). Analysis of Lesser Black-backed Gull flight heights has shown that they differ between day and night (Ross-Smith et al., 2016). Other recent analysis of bird flight speeds and nocturnal activity also reveal disparities with the generic values incorporated in collision risk models (Fijn & Gyimesi, 2018; Furness et al., 2018). These parameters may also be influenced by other factors including wind speed and direction, time of day and distance from the breeding colony (Thaxter et al., 2019). Given the sensitivity of collision risk models to these parameters (Masden, 2015), getting better estimates for these parameters and an improved understanding of factors influencing their spatial and temporal variation will be a key step for reducing the uncertainty associated with assessments of collision risk.

We collate GPS tracking data collected from lesser black-backed gull *Larus fuscus*, kittiwake *Rissa tridactyla* and gannet *Morus bassanus* and analyse these to generate estimates of flight height, flight speed and nocturnal activity for these species. Drawing on previous analyses (Thaxter et al., 2019), we investigate how flight height and speed vary between foraging and commuting behaviours. For lesser black-backed gull we also consider how levels of nocturnal activity vary over the course of the breeding season. Finally, we consider the implications of our results for the assessment of collision risk.

2. Methods

2.1. Data sets

Building on the analyses carried out in Thaxter et al. (2019), we estimate nocturnal activity, defined as the period from sunrise to sunset as per Band (2000) and Forsythe et al. (1995), from GPS tagging data, and estimate behaviour-specific flight heights and flight speeds. In addition to the data considered in Thaxter et al. (2019), data were also available for 36 kittiwakes and 10 gannets fitted with University of Amsterdam (UvA) GPS tags by RSPB within the Flamborough Head and Bempton Cliffs SPA. Analysis of nocturnal activity levels considered data collected using both IGotU GT-120 (Mobile Action Technology, Taipei, Taiwan) and UvA GPS tags (Table 1).

Given the data recording capabilities of the different tags, analyses of flight height and flight speed were restricted to the UvA tags (Table 1). For lesser black-backed gulls, analyses of flight heights were based on GPS estimates, for gannets and kittiwakes flight height estimates were based on altimeter data analysed by RSPB as part of ongoing work (Babcock et al., 2018). A summary of the data sets and analyses considered in this report is presented in Table 1.

Table 1 Species and colonies for which data relating to nocturnal activity, flight speed and flight height were analysed as part of this project.

Species	Colony	Tag	Sample Size	Nocturnal Activity	Flight Speed	Flight Height
Kittiwake	**Isle of May**	**IGotU**	**50**	✓		
	Orkney	**IGotU**	**86**	✓		
	Colonsay	**IGotU**	**84**	✓		
	Bempton Cliffs	**IGotU**	**104**	✓		
	Bempton Cliffs	**UvA**	**16**	✓	✓*	✓**
Lesser Black-backed Gull	**Walney**	**UvA**	**37**	✓	✓	✓
	Orfordness	**UvA**	**24**	✓	✓	✓
	Skokholm	**UvA**	**24**	✓	✓	✓
Gannet	**Bass Rock**	**IGotU**	**133**	✓		
	Alderney	**IGotU**	**61**	✓		
	Bempton Cliffs	**UvA**	**10**	✓	✓*	✓**

*Analyses undertaken by RSPB as part of ongoing work prior to award of contract;
**Analysis of altimeter data undertaken by RSPB as part of ongoing work.

Initially, we hoped to carry out similar analyses for herring gulls. However, examination of available GPS tracking data for this species suggested that, due to movements largely being restricted to onshore areas, there were insufficient data for analysis of offshore behaviour (e.g., Figure 1).

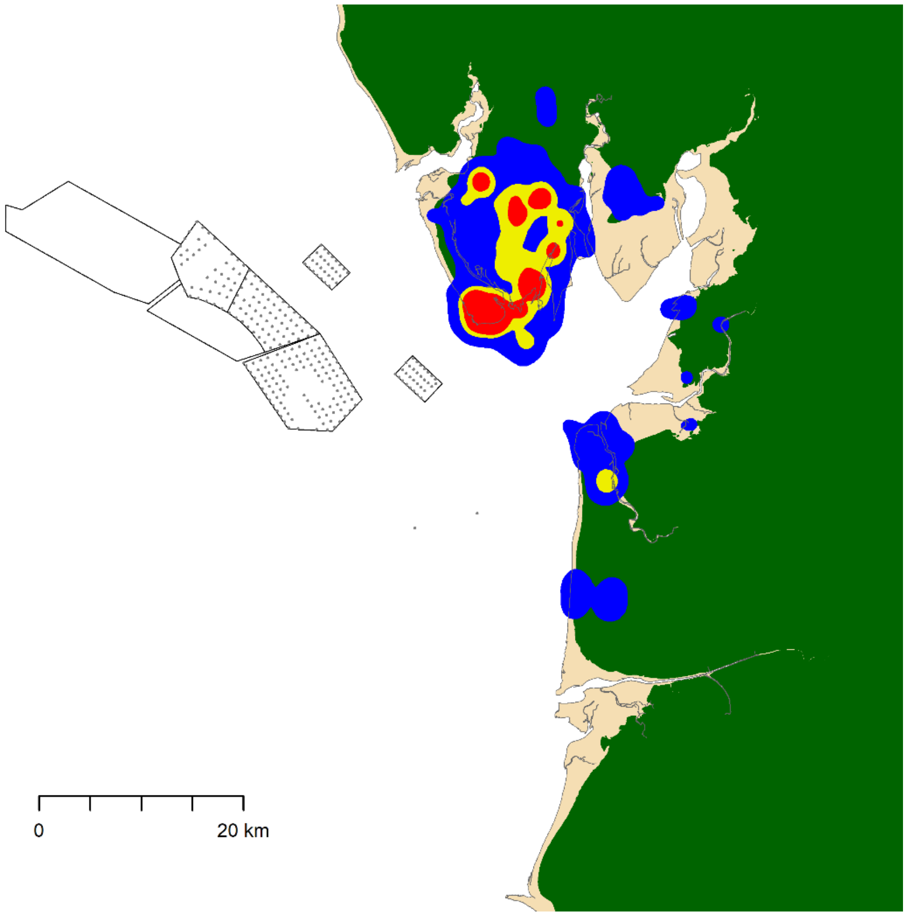


Figure 1 Example of area use by Herring Gulls from Walney with 95% (blue), 75% (yellow) and 50% (red) usage kernels indicated.

2.2. Behavioural classification

Previous analyses were based on Hidden Markov Models (HMMs) (Thaxter et al., 2019). A Hidden Markov Model (HMM) is a state-space continuous time movement approach that includes a ‘hidden’ component modelled as a Markov process, that allows states to be estimated informed by the relationships to an ‘observed component’ of the model (in this case, based on the step length between GPS fixes and turning angle). As a pre-requisite, this analysis required that time steps between consecutive GPS fixes were at a constant ‘regularised’ sampling rate, such that time steps were precisely the same for all points. Data were regularised to a constant spatial and temporal spacing using R packages ‘crawl’ (Johnson et al., 2008) and ‘momentuHMM’ (McClintock & Michelot, 2018). The ‘crawl’ model was used to fit a correlated random walk-through locations (Johnson et al., 2008), and further allowed interpolative prediction of points at five-minute intervals. Initial analyses suggested that this approach posed particular problems for the analysis of nocturnal activity.

The HMM analyses (Thaxter et al., 2019) classified points as floating, foraging or commuting behaviour, with an additional perching classification for lesser black-backed gull. In assessing activity levels, it is necessary to consider the proportion of time spent foraging and commuting in relation to the proportion of time spent perching or floating. However, these classifications are based on data collected away from the breeding colonies. Consequently, it is necessary to account for time spent at the colony in addition to time spent in perching or floating behaviour when classifying birds as not active. However, for a number of reasons, there may be biases associated with GPS points recorded when birds are at their colony. These include the use of GPS fences to preserve battery life by recording data at a lower temporal resolution when birds are at their breeding colonies, and the potential for the surrounding habitat (e.g., cliffs) to impair the ability of GPS tags to communicate with satellites and/or, in the case of the UvA tags, for solar panels to receive sufficient light to recharge tag batteries. Regardless of the cause, if birds spend more time at the colonies at night than during the day, as seems likely, these biases are likely to produce an over-estimate of nocturnal activity levels. The need for regularised time steps in HMMs means that adding time spent at colonies back into the data, in order to overcome these biases, is not straightforward.

A second approach was also used to identify the same four-level behavioural states described above for the HMM. Expectation-Maximisation Binary Clustering (EMbC) is a further state-space approach that uses a Gaussian mixture model (see Garriga et al., 2016 for more details). Unlike the HMM, the EMbC approach does not strictly need a regularised interpolated dataset, as it is based on GPS speed and turning angle, rather than distance within a constant time period. The EMbC model by default allows classification of four states grouped by: low speed, low turn ('LL', = floating); low speed, high turn ('LH' = stopped); high speed, low turn ('HL' = commuting); and high speed, high turn ('HH' = potential foraging/searching) (Figure 2). Whilst the definitions of most of these categories are fairly clear, the LH category is less obvious. The low speed indicates that birds are not altering their locations, while the high turning angle indicates birds are altering their orientation regularly, implying that they are active. This category is likely to reflect a combination of maintenance behaviour and foraging from the sea surface. For simplicity, in this report the behaviour is referred to as "stopped" however, it is important to acknowledge that it may also include aspects of foraging behaviour.

By using the expectation maximisation algorithm, the EMbC approach seeks the most optimised split in the data but does not require prior information for perceived delineations for each category as with HMMs above. The EMbC approach can handle temporal data "gaps" in the dataset. However, it is generally best applied on a reasonably regular dataset, i.e., without excessively variable sampling resolutions, and so the data were filtered to a rate of five minutes, for a comparable assessment to the HMMs above. The resulting classifications of foraging and commuting behaviour were broadly consistent with those obtained from HMM.

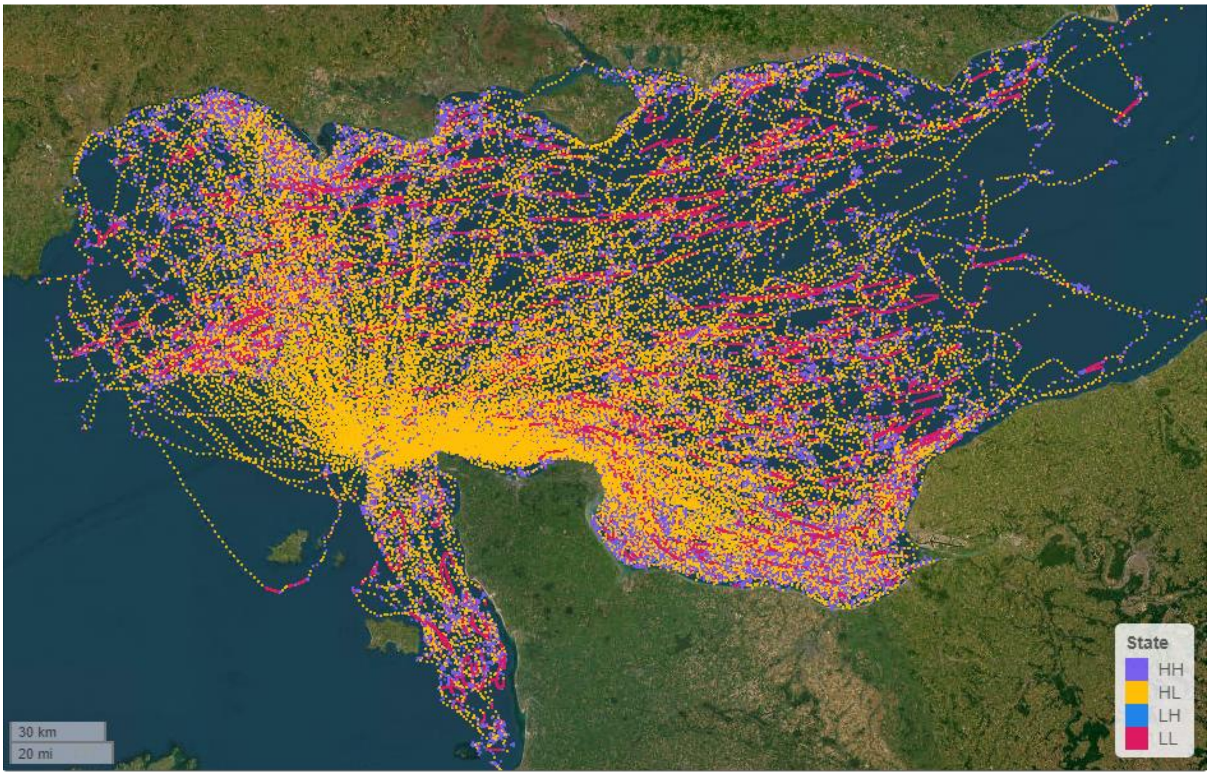


Figure 2 EMbC classification of behavioural states for Gannets from Alderney, states indicate high speed, high turning angle (HH), high speed, low turning angle (HL), low speed, high turning angle (LH) and low speed, low turning angle (LL).

2.3. Nocturnal activity

We follow the approach of (Furness et al., 2018) in assigning the timing of GPS points to dawn, daylight, dusk and night using the *'sunriset'* and '*crepuscule'* functions in the R package "maptools" (Bivand & Lewin-Koh, 2021). We then analyse activity levels using a Generalized Linear Mixed Model (GLMM) with a binomial error distribution and a logit-link. Using this approach, we analyse the proportion of time active (behavioural states HL and HH) in relation to the light level classifications above. For each species and colony combination, we fitted a model for each year in which data were collected. For our models, we include light levels (dawn, day, dusk, night) as a categorical fixed effect and, bird identification as a random effect. The model was parameterised as follows:

Activity ~ light level + (1|TagID) [1]

The outputs from these models are used to quantify the proportion of time birds are active in relation to each light level. For the purposes of collision risk modelling, nocturnal activity levels are the proportion of time birds are active at night relative to their activity during the day. Consequently, to estimate nocturnal activity levels for use in collision risk models, we divided the proportion of time active at night by the proportion of time active during the day. We then compared nocturnal activity levels between species, sites, and colonies.

2.4. Flight speed

2.4.1. Instantaneous speed estimates for foraging and commuting flight

In Thaxter et al. (2019), estimates of flight speed were obtained for foraging and commuting flight based on the straight line distance travelled between sampling intervals. However, concern was raised that the temporal resolution of the fixes meant that estimates based on this approach may under-estimate true speed if birds were not travelling in a straight line at the time. However, UvA tags also collect vector-based instantaneous speed measures, taken over a short period for each GPS fix, resulting in x, y, and z speeds in m/s. These can be combined into a "3D" vector-based instantaneous speed for each GPS fix (*i*) through the following equation:

$$\text{speed\_3d}_i = \text{sqrt}\,(\text{x\_speed}_i\text{\^{}}2 + \text{y\_speed}_i\text{\^{}}2 + \text{z\_speed}_i\text{\^{}}2) \quad [2]$$

Using the EMbC classifications of behaviour, these speeds were then summarised for points classified as foraging and commuting flight for lesser black-backed gull, gannet and kittiwake.

2.4.2. Comparison of instantaneous and trajectory speed

The EMbC model was assessed for each species at a 300 s rate (*t*), reflecting the overall "base" rate of GPS sampling protocols for each project (Table 1). A trajectory speed was also estimated, based on the distance travelled (*d*) between sampling intervals, measured as:

$$\text{traj\_speed}_i = d_{i\rightarrow i+1} \,/\, t_{i\rightarrow i+1} \quad [3]$$

For the lesser black-backed gull data from Walney, Skokholm and Orfordness, instantaneous and trajectory speeds were considered in more detail. The subsampling regime removed often faster rates (up to 5s) that had been collected for finer-scale investigations into movements within wind farms. Thus, although trajectory speeds were sometimes available for these "bursts" of activity, the ones used for comparison to instantaneous speeds were the sub-sampled re-calculated ones at the base rates described above, enabling a fairer comparison across the rest of the dataset.

Point estimates of bird flight speeds are likely to be correlated with the immediately preceding estimates. These correlations can introduce bias into any subsequent analysis that influence the resulting parameter estimates. To avoid unduly biasing parameter estimates, an initial investigation was made into the autocorrelation within the data for both instantaneous and trajectory speed parameters. These assessments were carried out at the individual bird level through Auto-Correlation Function (ACF) plots, examining the ACF for the five-minute rate used in the EMbC, and subsequent data degradation to coarser rates of 600s, 900s, 1200s, 1800s and 3600s, with the ACF re-examined for each sub-sampling rate level, and examined for each bird in each breeding season year.

We then used both simple linear regression to compare the pairwise point-level data for each speed type, and further fitted a Generalized Linear Mixed Effects Model to compare differences in the relationships between speed types over behavioural states; a model was therefore specified as:

$$\text{speed} \sim \text{speed\_type*state*offshore} + (1 \mid \text{year} \mid \text{TagID}) + \varepsilon \quad [4]$$

Given the focus of the work, a further model investigating just offshore was therefore considered further for behavioural states, simplifying the above model to remove the offshore three-way interaction, for which results are presented:

$$\text{speed offshore} \sim \text{speed\_type*state} + (1 \mid \text{year} \mid \text{TagID}) + \varepsilon \quad [5]$$

where speed_type is a factor of instantaneous or trajectory, offshore a factor of onshore or offshore, and random effects if TagID nested within year were specified and the error distribution (ε) being a log-transformed gaussian distribution (which gave superior residuals and quickest model run time). This model was specified using R package glmmTMB (Brooks et al., 2017) and further tests of autocorrelation were carried out with R package DHARMa(Hartig, 2022). The slope and significance of the relationship was then examined for each interaction for all factor levels of state. Estimates from the above model were examined using estimated marginal means (R package emmeans, Lenth, 2022).

For each EMbC state (1-4), we further visualised the two types of speed measures. The approach for comparison was one of a distribution comparison and summary of basic statistics of error around the measures, being histograms, and non-parametric boxplot statistics.

2.5. Flight Heights

2.5.1. Bias in GPS altitudes

For lesser black-backed gull at Orfordness (but not Skokholm or Walney), and gannet and kittiwake at Flamborough Head and Bempton Cliffs, the bulk of the distribution of raw GPS altitudes was negative (Fig. 3). This suggests that the GPS altitude measurements are negatively biased in the southern North Sea. An ecological cause for this bias was explored: that birds are preferentially going out at low tide. If this was a cause of the altitude bias, it was not the sole cause: lesser black-backed gull altitude while stopped on land was also biased below the Digital Elevation Model (DEM) for birds tagged at Orfordness (not shown), and the bulk of GPS altitudes from a test tag left at the shoreline at Orfordness in 2011 were negative (Fig. 3f).

It could instead be that there was error in the calculation of altitude over mean sea level from altitude over the ellipsoid: perhaps due to spatially variable error in the geoid. There was some evidence that the altitude bias varied smoothly across the study areas, suggesting there are issues with the model of mean sea level used. Furthermore, a recent test tag at Havergate (near Orfordness) had no altitude bias. However, the error in the height of true mean sea level relative to the geoid is almost entirely less than 1m, considerably less than the average bias in our dataset. Whilst the bulk of the GPS altitude distribution is below zero, the modal GPS altitude for kittiwake and gannet is zero. Consequently, the cause of the altitude bias is unclear.

We applied a correction to account for this based on the median altitude estimate of birds classified as floating on the sea surface. Assuming that instances of floating behaviour are distributed evenly across the tidal cycle, the median estimated flight height should reflect sea-level, and this value can be subtracted from GPS estimated flight heights to correct for biases in these estimates. This will only be an informal solution to the problem, for two reasons. Firstly, the altitude bias varied smoothly within the study areas: so, the median altitude of birds floating on water is only a useful estimate of altitude bias *on average* at a colony, and any uncertainty in the average bias is not propagated into the remainder of the analysis. Secondly, although the bulk of the GPS altitudes for kittiwake, gannet and Orfordness lesser black-backed gulls are below zero, an unknown process in the data-generating process results in the modal GPS altitude for kittiwake and gannet being zero; after adjustment this is above zero. If the zero-metre mode of the GPS altitudes has an ecological cause (rather than being caused by observation processes), then this aspect of the distribution is distorted by our adjustment.

Where a high proportion of GPS altitudes are negatively biased, this may influence flight height distributions because the lognormal distribution used to model imperfectly observed true flight heights only has support over the set of positive numbers. Any negative flight height observations will be classified as measurement errors by the model and may lead to estimates of very small positive true altitudes (highly negative values on the log scale). Even after corrections based on measurements of birds classified as floating on the sea surface, a high proportion of altitude measurements for kittiwake and gannet remained below zero. Consequently, GPS measurements of flight heights from gannet and kittiwake were not considered as part of further analyses.

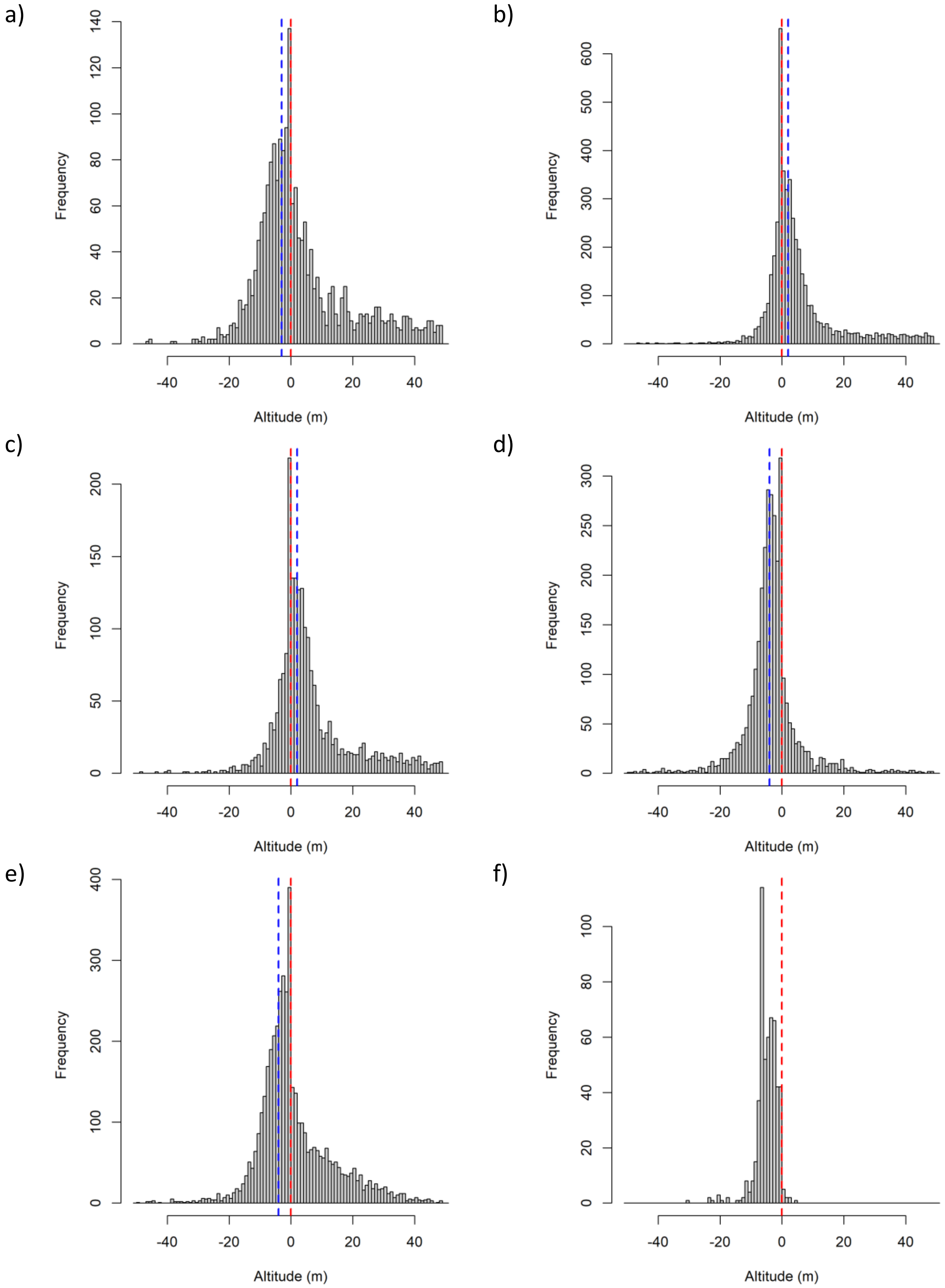


Figure 3 Raw GPS altitudes (only shown between -50m and 50m) for: lesser black-backed gulls at a) Orfordness, b) Skokholm, and c) Walney; d) gannets at Bempton; e) kittiwakes at Bempton; f) test tag at Orfordness. Red dashed line shows zero. Blue dashed line (a-e only) shows median GPS altitude of birds classified as floating on the sea surface by the behavioural model.

2.5.2. Lesser black-backed gull

GPS altitude measurements are subject to error arising from various processes (Péron et al. 2020). The hierarchical model framework, separating observation error from process error, is ideal for properly accounting for GPS error when estimating species' flight height distributions. Here we adapt a hierarchical model developed by Ross-Smith et al. (2016) to estimate the flight height distributions of lesser black-backed gulls.

Analyses were restricted to GPS points classified by EMbC as commuting or foraging. Points with uncertain classification (probability < 0.9) were excluded from analysis. To account for autocorrelation, and following Ross-Smith et al. (2016), data were sub-sampled to one point every 60 minutes. To focus solely on flight height over sea, onshore fixes were removed. After cleaning this left a dataset of 10,461 altitude measurements for lesser black-backed gulls.

The model structure we use for our two research questions is simpler than that of Ross-Smith et al. (2016), in that we do not discretize flight height by 'location' (terrestrial/coastal/marine) or by light-level. For the first research question, we discretize flight height by behaviour; for the second we discretize flight height by behaviour and colony. To help separate observation error from process error, we used the number of satellites associated with each flight height measurement (specifically, the number of satellites used for a given fix subtracted from 14, the maximum number of satellites used for any fix) as a covariate of observation error.

We assume that the observed altitude data *obs* are drawn from a normal distribution with mean *alt* and variance γ^2. *alt* represents the true unobserved altitude, and γ is the sum of an intercept δ and a linear effect (slope θ) of the number of satellites *nsat* (see above). For observation i,

$$obs_i \sim N(alt_i, \gamma_i^2) \qquad [6]$$

$$\gamma_i = \delta + \theta \cdot nsat_i \qquad [7]$$

On the log scale, we assume that the logarithm of the latent true altitude *alt* is drawn from a normal distribution with mean μ and variance σ^2. μ is the sum of an intercept α and an individual random effect β. In the first models α and σ are estimated separately for each behavioural state. In the second model α and σ are estimated separately for each behavioural state and by colony. For observation *i* and individual *j* (structure of first model only),

$$\log(alt_{i,j}) \sim N(\mu_{i,j}, \sigma^2_{state_{i,j}}) \quad [8]$$

$$\mu_{i,j} \sim \alpha_{state_{i,j}} + \beta_j \qquad [9]$$

Model parameters were estimated in a Bayesian framework using Markov Chain Monte Carlo (MCMC) sampling for inference and with vague priors. Parameter estimation was implemented in “Just Another Gibbs Sampler” (JAGS) (Plummer 2003), accessed using the runjags package (Denwood 2016) in R (R Core Team 2020). To minimize autocorrelation in the chains only one in every 10 iterations was retained. The first 30,000 iterations were discarded as burn-in, and the following 200,000 iterations were used for estimating the posterior probability distributions of the parameters.

Model convergence was assessed by visual inspection of MCMC trace plots and the Gelman-Rubin statistic R-hat. Models were considered to have converged on the posterior probability distribution if the MCMC chain plots were well-mixed and if R-hat was less than 1.1, for all parameters. Correlation between the MCMC traces was also examined to give indications of interdependencies among parameters.

2.5.3. Kittiwake and Gannet

As the GPS estimates of flight height for kittiwake and gannet were not considered reliable for the purposes of these analyses, we considered estimates that were collected using altimeters deployed concurrently with the GPS tags. These data were collected and analysed by RSPB as part of ongoing work (Wischnewski, McCluskie, et al., in prep.; Wischnewski, Sansom, et al., in prep.).

Atmospheric pressure declines with altitude and, consequently, the pressure measurements recorded using altimeters can be used as a proxy for the flight altitude of birds. This requires a baseline estimate of local atmospheric pressure at a known altitude. This can be compared to the pressure recorded by the altimeter which is then converted into an estimate of flight altitude using established relationships between air pressure and altitude. For the purposes of this study, estimates of air pressure were obtained from a local weather station in Bridlington, close to the study site.

The data considered in these analyses were collected from 10 gannets and 16 kittiwakes. As above, GPS data collected alongside the altimeter data were used to partition points into resting, stopped, foraging, and commuting behaviour using EMbC with sampling intervals of 5 minutes. The altimeter estimates of flight altitude for foraging and commuting birds were then compared. In contrast to the flight heights estimated using GPS, the observation error process for altimeter flight height estimates has not been modelled as this is part of ongoing work. Consequently, a small proportion of flight height estimates for both species are below sea level.

3. Results

3.1. Nocturnal activity

3.1.1. Lesser Black-backed Gull

Nocturnal activity levels in lesser black-backed gulls were assessed using data from UvA GPS tags deployed across the breeding season as a whole at Walney, Skokholm and Orfordness (Figure 4). There was substantial variation in activity levels both between years and between colonies. Nocturnal activity levels were greatest at Walney, where they ranged from 28 – 40% of daytime activity, and lowest at Skokholm, where they ranged from 5 – 17% of daytime activity (Tables 2-4). This in part reflects differences in daytime activity levels between colonies, potentially as a result of differences in foraging behaviour between colonies. Whilst birds were active for less than 5% of the time at night, birds were active for 6-19% of the time during the day (Figure 5).

In contrast to gannets and kittiwakes, the attachment methodology used for lesser black-backed gulls meant data were collected across the breeding season as a whole. However, there were no clear trends in nocturnal activity over the course of the breeding season.

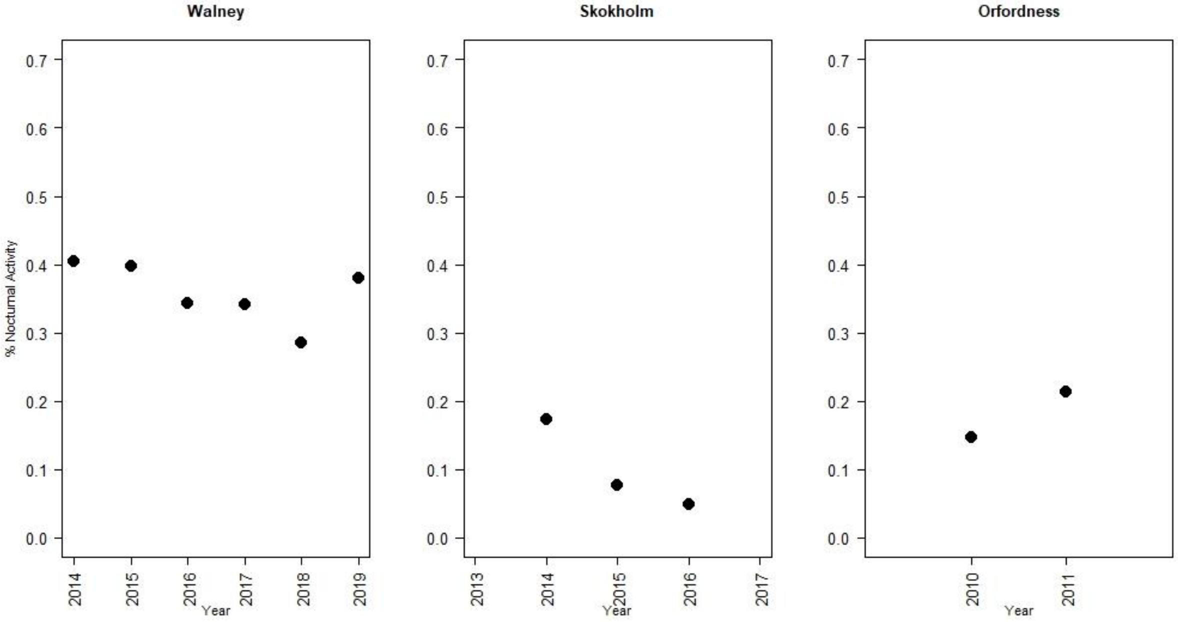


Figure 4 Estimated nocturnal activity levels in lesser black-backed gulls at Walney, Skokholm and Orfordness

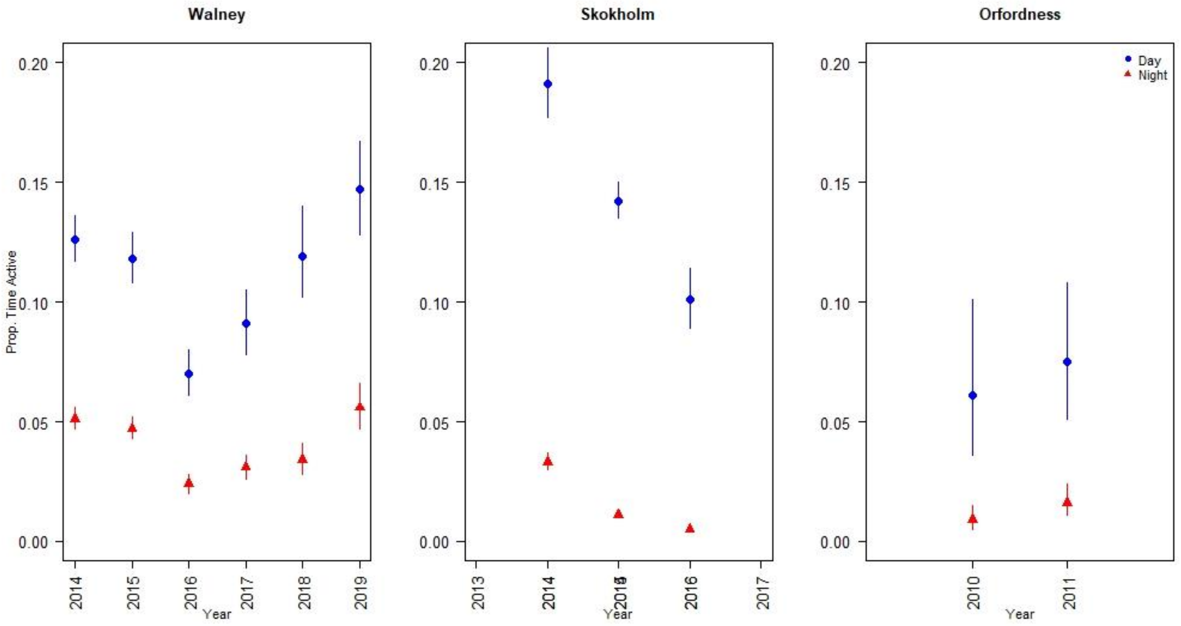


Figure 5 Day and night activity levels, as a proportion of time available, for Lesser Black-backed Gulls at Walney, Skokholm and Orfordness

Table 2 Activity levels at dawn, during daylight (sunrise – sunset), dusk and at night (sunset-sunrise) in lesser black-backed gulls at Walney between 2014 & 2019 recorded using University of Amsterdam tags. Nocturnal activity is defined as activity at night as a proportion of activity during daylight (i.e., Night/Day, note calculations may not match due to rounding).

Year	**Month**	**Dawn**	**Day**	**Dusk**	**Night**	**Nocturnal activity**
2014	**All**	0.19 (0.17 - 0.21)	0.13 (0.12 - 0.14)	0.11 (0.10 - 0.118)	0.05 (0.05 - 0.056)	0.41 (0.40 - 0.41)
	5	0.07 (0.06 - 0.09)	0.05 (0.04 - 0.06)	0.04 (0.03 - 0.05)	0.03 (0.02 - 0.03)	0.48 (0.47 - 0.49)
	6	0.21 (0.18 - 0.23)	0.15 (0.14 - 0.16)	0.10 (0.09 - 0.12)	0.04 (0.04 - 0.05)	0.28 (0.27 - 0.29)
	7	0.22 (0.2-0 - 0.25)	0.14 (0.12 - 0.14)	0.16 (0.14 - 0.18)	0.08 (0.07 - 0.09)	0.57 (0.56 - 0.58)
	8	0.22 (0.16 - 0.30)	0.10 (0.07 - 0.13)	0.11 (0.07 - 0.16)	0.05 (0.04 - 0.07)	0.52 (0.50 - 0.54)
2015	**All**	0.236 (0.216 - 0.258)	0.12 (0.11 - 0.13)	0.09 (0.08 - 0.11)	0.05 (0.04 - 0.05)	0.40 (0.39 - 0.40)
	3	0.043 (0.02 - 0.10)	0.03(0.01 - 0.07)	0.01 (0.00- 0.03)	0.02 (0.01 - 0.05)	0.61 (0.60 - 0.62)
	4	0.08 (0.06 - 0.11)	0.05 (0.04 - 0.07)	0.02 (0.02 - 0.03)	0.03 (0.03 - 0.04)	0.63 (0.62 - 0.64)

Year	Month	Dawn	Day	Dusk	Night	Nocturnal activity
	5	0.16 (0.14 - 0.19)	0.09 (0.08 - 0.10)	0.06 (0.05 - 0.07)	0.01 (0.01 - 0.01)	0.13 (0.12 - 0.13)
	6	0.28 (0.25 - 0.31)	0.14 (0.13 - 0.16)	0.11 (0.10 - 0.131)	0.04 (0.04 - 0.05)	0.28 (0.27 - 0.29)
	7	0.36 (0.32 - 0.39)	0.14 (0.13 - 0.16)	0.18 (0.16 - 0.21)	0.11 (0.10 - 0.12)	0.78 (0.77 - 0.79)
2016	**All**	0.12 (0.10 - 0.14)	0.07 (0.06 - 0.08)	0.05 (0.04 - 0.06)	0.02 (0.02 - 0.03)	0.34 (0.34 - 0.34)
	5	0.13 (0.10 - 0.16)	0.07 (0.06 - 0.09)	0.05 (0.04 - 0.07)	0.02 (0.02 - 0.03)	0.28 (0.28 - 0.29)
	6	0.12 (0.10 - 0.15)	0.07 (0.06 - 0.09)	0.06 (0.05 - 0.08)	0.03 (0.02 - 0.03)	0.38 (0.37 - 0.38)
	7	0.03 (0.02 - 0.04)	0.01(0.01 - 0.02)	0.01 (0.00 - 0.01)	0.01 (0.00 - 0.01)	0.42 (0.41 - 0.42)
2017	**All**	0.16 (0.14 - 0.19)	0.09 (0.08 - 0.11)	0.08 (0.07 - 0.09)	0.03 (0.03 - 0.04)	0.34 (0.34 - 0.35)
	4	0.08 (0.05 - 0.12)	0.05 (0.03 - 0.08)	0.04 (0.02 - 0.06)	0.01 (0.01 - 0.02)	0.25 (0.25 - 0.26)
	5	0.14 (0.12 - 0.16)	0.08 (0.07 - 0.093)	0.05 (0.04 - 0.07)	0.02 (0.02 - 0.03)	0.29 (0.28 - 0.29)
	6	0.22 (0.19 - 0.26)	0.11 (0.10 - 0.13)	0.13 (0.11 - 0.16)	0.06 (0.05 - 0.07)	0.50 (0.48 - 0.51)
	8	0.14 (0.12 - 0.19)	0.09 (0.07 - 0.12)	0.07 (0.05 - 0.10)	0.03 (0.02 - 0.04)	0.28 (0.27 - 0.30)
2018	**All**	0.19 (0.16 - 0.22)	0.12 (0.10 - 0.14)	0.09 (0.07 - 0.11)	0.03 (0.03 - 0.04)	0.29 (0.28 - 0.29)
	5	0.14 (0.10 - 0.19)	0.09 (0.07 - 0.12)	0.07 (0.05 - 0.10)	0.03 (0.02 - 0.04)	0.28 (0.27 - 0.30)
	6	0.25 (0.21 - 0.30)	0.17(0.14 - 0.20)	0.12 (0.09 - 0.15)	0.05 (0.04 - 0.07)	0.31 (0.29 - 0.32)
	7	0.50 (0.43 - 0.57)	0.33 (0.31 - 0.35)	0.14 (0.09 - 0.20)	0.05 (0.04 - 0.07)	0.15 (0.12 - 0.19)
2019	**All**	0.28 (0.24 - 0.33)	0.15 (0.13 - 0.17)	0.12 (0.105 - 0.15)	0.06 (0.05 - 0.07)	0.38 (0.37 - 0.39)
	5	0.25 (0.20 - 0.31)	0.15 (0.13 - 0.18)	0.13 (0.10 - 0.16)	0.05 (0.04 - 0.06)	0.34 (0.32 - 0.35)
	6	0.32 (0.26 - 0.39)	0.12 (0.10 - 0.15)	0.10(0.07 - 0.14)	0.06 (0.05 - 0.08)	0.49 (0.46 - 0.52)

Table 3 Activity levels at dawn, during daylight (sunrise – sunset), dusk and at night (sunset-sunrise) in lesser black-backed gulls at Skokholm between 2014 & 2019 recorded using University of Amsterdam tags. Nocturnal activity is defined as activity at night as a proportion of activity during daylight (i.e., Night/Day, note calculations may not match due to rounding).

Year	Month	Dawn	Day	Dusk	Night	Nocturnal activity
2014	**All**	0.21 (0.19 - 0.23)	0.19(0.18 - 0.21)	0.13 (0.12 - 0.15)	0.03 (0.03 - 0.04)	0.17 (0.17 - 0.18)
	5	0.15 (0.13 - 0.18)	0.14 (0.13 - 0.15)	0.09 (0.08 - 0.11)	0.01 (0.01 - 0.01)	0.08 (0.07 - 0.08)
	6	0.28 (0.25 - 0.32)	0.24 (0.22 - 0.27)	0.17 (0.15 - 0.19)	0.05 (0.04 - 0.06)	0.21 (0.20 - 0.22)
	7	0.11 (0.10 - 0.13)	0.14 (0.13 - 0.15)	0.09 (0.08 - 0.11)	0.03 (0.03 - 0.03)	0.21 (0.21 - 0.22)
	8	0.11 (0.08 - 0.16)	0.14 (0.11 - 0.17)	0.08 (0.05 - 0.11)	0.02 (0.01-0.02)	0.11 (0.10 - 0.12)
2015	**All**	0.18 (0.17 - 0.19)	0.14 (0.14 - 0.15)	0.10 (0.09 - 0.11)	0.01 (0.01 - 0.01)	0.07 (0.07 - 0.08)
	5	0.13 (0.11 - 0.15)	0.12 (0.11 - 0.13)	0.09 (0.08 - 0.11)	0.01 (0.01 - 0.01)	0.07 (0.06 - 0.07)
	6	0.26 (0.23 - 0.30)	0.17 (0.15 - 0.20)	0.16 (0.14 - 0.19)	0.04 (0.03 - 0.04)	0.21 (0.20 - 0.22)
	7	0.20 (0.18 - 0.23)	0.16 (0.15 - 0.18)	0.14 (0.12 - 0.17)	0.02 (0.01 - 0.02)	0.10 (0.01 - 0.11)
2016	**All**	0.10 (0.09 - 0.12)	0.10 (0.09 - 0.11)	0.07 (0.06 - 0.09)	0.01 (0.00 - 0.01)	0.05 (0.05 - 0.05)
	5	0.16 (0.13 - 0.19)	0.15 (0.13 - 0.16)	0.14 (0.12 - 0.17)	0.0216 (0.01 - 0.02)	0.11 (0.01 - 0.11)
	6	0.21 (0.18 - 0.26)	0.15 (0.13 - 0.17)	0.18 (0.15 - 0.23)	0.02 (0.02 - 0.03)	0.16 (0.15 - 0.18)

Table 4 Activity levels at dawn, during daylight (sunrise – sunset), dusk and at night (sunset-sunrise) in lesser black-backed gulls at Orford in 2010 & 2011 recorded using University of Amsterdam tags. Nocturnal activity is defined as activity at night as a proportion of activity during daylight (i.e., Night/Day, note calculations may not match due to rounding).

Year	**Month**	**Dawn**	**Day**	**Dusk**	**Night**	**Nocturnal activity**
2010	**All**	0.06 (0.04 - 0.11)	0.06 (0.04 - 0.10)	0.04 (0.022 - 0.07)	0.01 (0.01 - 0.02)	0.14 (0.14 - 0.15)
	6	0.05 (0.02 - 0.09)	0.04 (0.02 - 0.08)	0.03 (0.01 - 0.06)	0.01 (0.00 - 0.01)	0.15 (0.14 - 0.15)
	7	0.14 (0.10 - 0.21)	0.16 (0.12 - 0.20)	0.08 (0.05 - 0.13)	0.02 (0.01 - 0.03)	0.13 (0.12 - 0.16)
2011	**All**	0.09 (0.07 - 0.14)	0.08 (0.05 - 0.11)	0.05 (0.03 - 0.07)	0.02 (0.01 - 0.02)	0.22 (0.21 - 0.22)
	5	0.04 (0.03 - 0.05)	0.04 (0.03 - 0.06)	0.03 (0.02 - 0.04)	0.01 (0.01 - 0.01)	0.20 (0.19 - 0.20)
	6	0.13 (0.09 - 0.19)	0.11 (0.08 - 0.16)	0.08 (0.05 - 0.11)	0.03 (0.02 - 0.04)	0.23 (0.22 - 0.24)
	7	0.12 (0.08 - 0.18)	0.07 (0.05 - 0.10)	0.04 (0.03 - 0.07)	0.01 (0.01 - 0.02)	0.20 (0.19 - 0.21)

3.1.2. Kittiwake

Nocturnal activity in kittiwakes was collected using IGotU GPS tags deployed on birds at Colonsay, Isle of May, Orkney, Flamborough Head and Bempton Cliffs, and from UvA tags deployed birds at Flamborough Head and Bempton Cliffs. Levels of nocturnal activity showed substantial variation between colonies and years, from 27 – 63 % of daytime activity (Figure 6, Tables 5 & 6). However, understanding these differences is challenging due to the different tag types used. The longer-term deployment of the UvA tags means it is possible to get a clearer picture of nocturnal activity over the breeding season as a whole, in comparison to the IGotU tags which were shorter term deployments, typically focussed on the period around early chick rearing. Possibly reflecting this, overall activity levels estimated from the UvA tags were lower than those estimated using IGotU tags (Figure 7). However, estimates of nocturnal activity as a proportion of daytime activity obtained from UvA tags also showed variation between years, at 20% in 2017 and 33% in 2018 (Table 6).

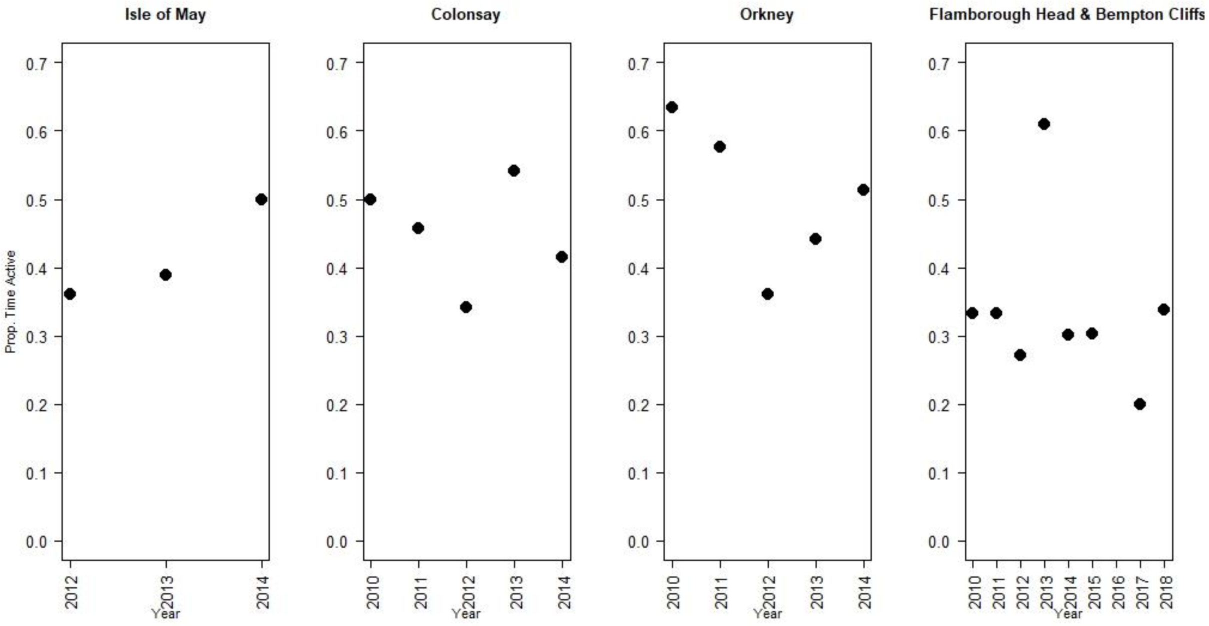


Figure 6 Estimated nocturnal activity levels in kittiwake at Isle of May, Flamborough Head and Bempton Cliffs, Colonsay and Orkney.

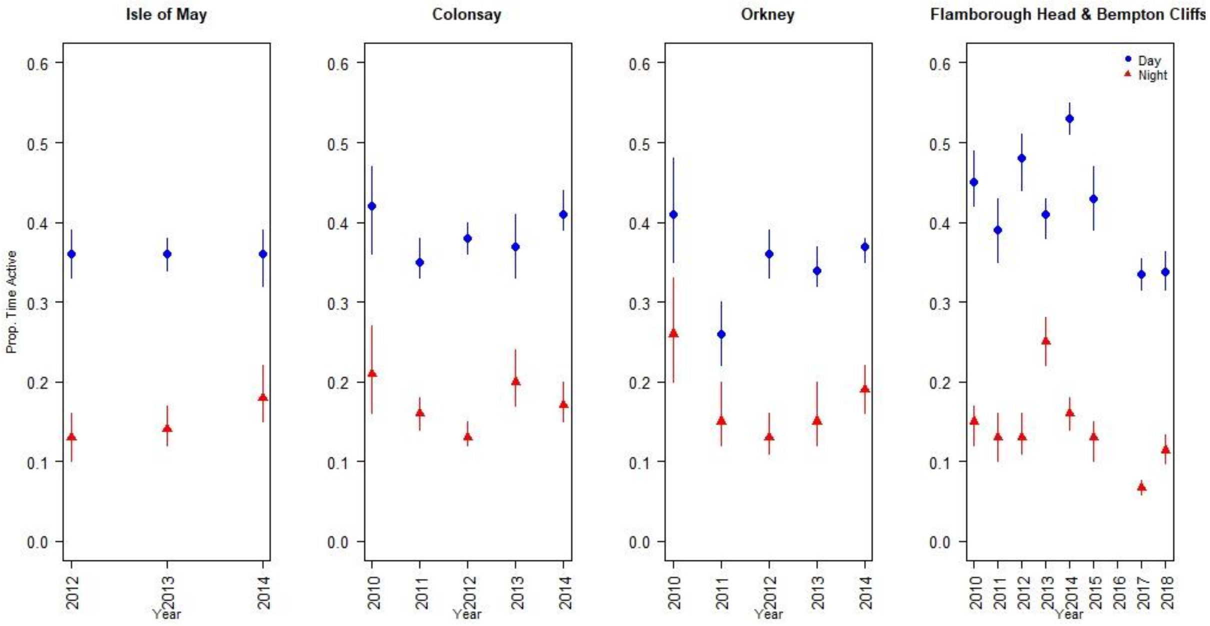


Figure 7 Day and night activity levels for Kittiwake at the Isle of May, Colonsay, Orkney and Flamborough Head and Bempton Cliffs.

Table 5 Activity levels at dawn, during daylight (sunrise – sunset), dusk and at night (sunset-sunrise) in kittiwake recorded using IGotU. Nocturnal activity is defined as activity at night as a proportion of activity during daylight (i.e., Night/Day, note calculations may not match due to rounding).

Site	**Year**	**Dawn**	**Day**	**Dusk**	**Night**	**Nocturnal Activity**
Isle of May	2012	0.10 (0.06 - 0.16)	0.36 (0.33 - 0.39)	0.29 (0.22 - 0.38)	0.13 (0.1 - 0.16)	0.36 (0.30 – 0.41)
	2013	0.2 (0.15 - 0.26)	0.36 (0.34 - 0.38)	0.42 (0.35 - 0.48)	0.14 (0.12 - 0.17)	0.38 (0.35 – 0.45)
	2014	0.06 (0.03 - 0.11)	0.36 (0.32 - 0.39)	0.41 (0.32 - 0.50)	0.18 (0.15 - 0.22)	0.5 (0.46 – 0.56)
Flamborough Head and Bempton Cliffs	2010	0.21 (0.15 - 0.28)	0.45 (0.42 - 0.49)	0.45 (0.38 - 0.53)	0.15 (0.12 - 0.17)	0.33 (0.28 – 0.34)
	2011	0.17 (0.11 - 0.25)	0.39 (0.35 - 0.43)	0.26 (0.18 - 0.35)	0.13 (0.1 - 0.16)	0.33 (0.28 – 0.37)
	2012	0.15 (0.1 - 0.22)	0.48 (0.44 - 0.51)	0.45 (0.36 - 0.54)	0.13 (0.11 - 0.16)	0.27 (0.25 – 0.31)

Site	Year	Dawn	Day	Dusk	Night	Nocturnal Activity
	2013	0.22 (0.16 - 0.29)	0.41 (0.38 - 0.43)	0.43 (0.36 - 0.51)	0.25 (0.22 - 0.28)	0.61 (0.57 – 0.65)
	2014	0.21 (0.16 - 0.27)	0.53 (0.51 - 0.55)	0.33 (0.27 - 0.38)	0.16 (0.14 - 0.18)	0.30 (0.27 – 0.32)
	2015	0.22 (0.16 - 0.30)	0.43 (0.39 - 0.47)	0.37 (0.29 - 0.46)	0.13 (0.1 - 0.15)	0.30 (0.25 – 0.32)
Colonsay	2010	0.28 (0.17 - 0.42)	0.42 (0.36 - 0.47)	0.58 (0.44 - 0.7)	0.21 (0.16 - 0.27)	0.5 (0.44 – 0.57)
	2011	0.17 (0.13 - 0.22)	0.35 (0.33 - 0.38)	0.35 (0.29 - 0.4)	0.16 (0.14 - 0.18)	0.45 (0.42 – 0.47)
	2012	0.21 (0.17 - 0.25)	0.38 (0.36 - 0.4)	0.35 (0.3 - 0.39)	0.13 (0.12 - 0.15)	0.34 (0.33 – 0.37)
	2013	0.23 (0.17 - 0.31)	0.37 (0.33 - 0.41)	0.44 (0.35 - 0.52)	0.2 (0.17 - 0.24)	0.54 (0.51 – 0.58)
	2014	0.23 (0.17 - 0.30)	0.41 (0.39 - 0.44)	0.42 (0.34 - 0.49)	0.17 (0.15 - 0.20)	0.41 (0.38 – 0.45)
Orkney	2010	0.37 (0.28 - 0.48)	0.41 (0.35 - 0.48)	0.34 (0.25 - 0.44)	0.26 (0.2 - 0.33)	0.63 (0.57 – 0.68)
	2011	0.2 (0.14 - 0.26)	0.26 (0.22 - 0.3)	0.19 (0.14 - 0.26)	0.15 (0.12 - 0.2)	0.57 (0.54 – 0.66)
	2012	0.11 (0.08 - 0.15)	0.36 (0.33 - 0.39)	0.3 (0.26 - 0.35)	0.13 (0.11 - 0.16)	0.36 (0.33 – 0.41)
	2013	0.25 (0.17 - 0.36)	0.34 (0.32 - 0.37)	0.35 (0.26 - 0.45)	0.15 (0.12 - 0.2)	0.44 (0.37 – 0.54)
	2014	0.13 (0.09 - 0.19)	0.37 (0.35 - 0.38)	0.32 (0.25 - 0.38)	0.19 (0.16 - 0.22)	0.51 (0.45 – 0.57)

Table 6 Activity levels at dawn, during daylight (sunrise – sunset), dusk and at night (sunset-sunrise) in kittiwake at Flamborough Head and Bempton Cliffs in 2017 & 2018 recorded using University of Amsterdam tags. Nocturnal activity is defined as activity at night as a

proportion of activity during daylight (i.e., Night/Day, note calculations may not match due to rounding).

Year	**Month**	**Dawn**	**Day**	**Dusk**	**Night**	**Nocturnal activity**
2017	**All**	0.38 (0.34 – 0.4326)	0.34 (0.32 – 0.35)	0.17 (0.14 – 0.20)	0.07 (0.06 – 0.08)	0.20 (0.19 – 0.21)
	June	0.40 (0.34 – 0.46)	0.33 (0.31 – 0.35)	0.20 (0.16 – 0.24)	0.07 (0.06 – 0.08)	0.22 (0.19 – 0.24)
	July	0.36 (0.30 – 0.42)	0.34 (0.31 – 0.37)	0.10 (0.07 – 0.14)	0.06 (0.48 – 0.07)	0.17 (0.16 – 0.20)
2018	**All**	0.22 (0.17 – 0.28)	0.34 (0.32 – 0.36)	0.31 (0.27 – 0.36)	0.11 (0.10 – 0.13)	0.34 (0.31 – 0.37)
	June	0.11 (0.05 – 0.25)	0.28 (0.25 – 0.30)	0.20 (0.13 – 0.30)	0.10 (0.07 – 0.13)	0.35 (0.30 – 0.44)
	July	0.26 (0.19 – 0.33)	0.36 (0.34 – 0.39)	0.35 (0.30 – 0.41)	0.12 (0.10 - 0.15)	0.34 (0.30 – 0.37)

3.1.3. Gannet

Nocturnal activity in gannets was collected using IGotU GPS tags deployed on birds at the Bass Rock and Alderney, and from UvA tags deployed birds at Flamborough Head and Bempton Cliffs. Levels of nocturnal activity showed substantial variation between colonies and years, from 4 – 31 % of daytime activity (Figure 8, Tables 7 & 8). However, understanding these differences is challenging due to the different tag types used. The longer-term deployment of the UvA tags means it is possible to get a clearer picture of nocturnal activity over the breeding season as whole, in comparison to the IGotU tags which were shorter term deployments, typically focussed on the period around early chick rearing. This may be reflected in the lower levels of activity estimated at night for birds from Flamborough Head and Bempton Cliffs (Figure 9).

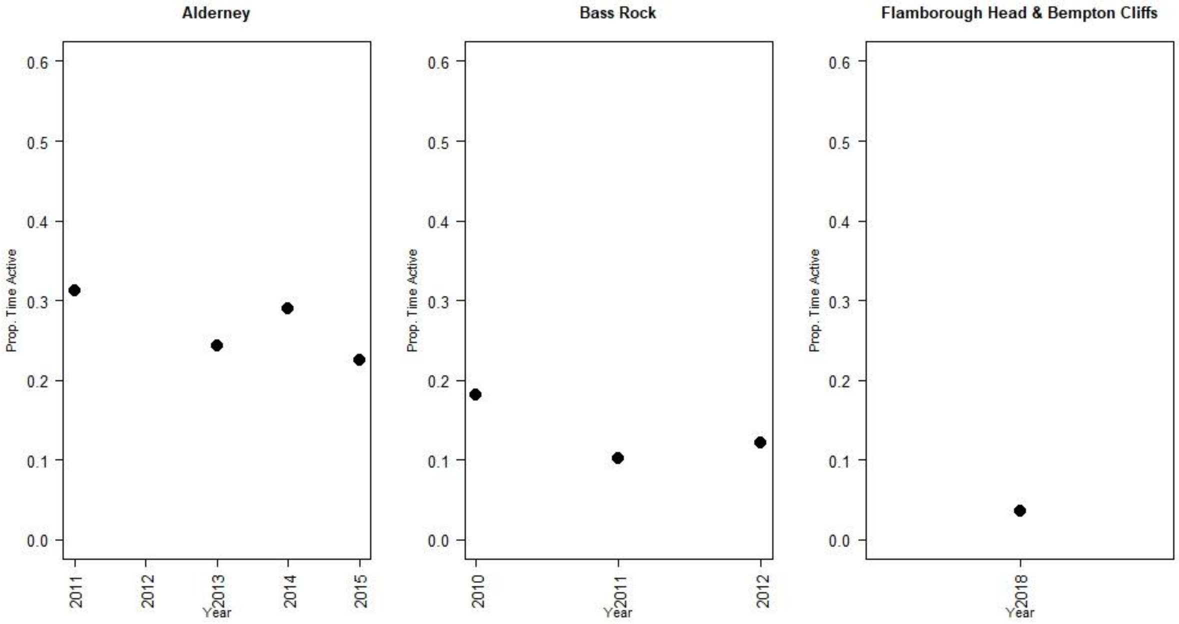


Figure 8 Estimated nocturnal activity levels in gannets at Alderney, Bass Rock and Flamborough Head and Bempton Cliffs

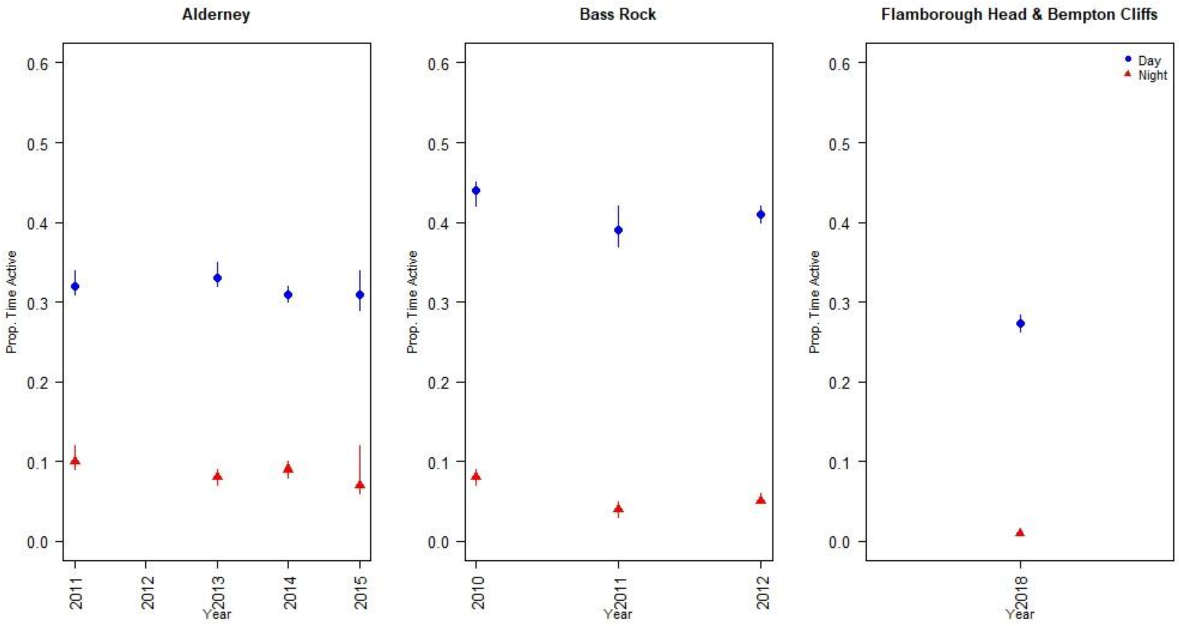


Figure 9 Day and night activity levels for gannet at Alderney, Bass Rock and Flamborough Head and Bempton Cliffs.

Table 7 Activity levels at dawn, during daylight (sunrise – sunset), dusk and at night (sunset-sunrise) in Gannets recorded using IGotU tags. Nocturnal activity is defined as activity at night as a proportion of activity during daylight (i.e., Night/Day, note calculations may not match due to rounding).

Site	**Year**	**Dawn**	**Day**	**Dusk**	**Night**	**Nocturnal Activity**
Alderney	2011	0.08 (0.05 – 0.12)	0.32 (0.31- 0.34)	0.31 (0.26 – 0.37)	0.1 (0.09- 0.12)	0.31 (0.29 – 0.35)
	2013	0.31 (0.27 - 0.36)	0.33 (0.32 - 0.35)	0.23 (0.2 - 0.27)	0.08 (0.07 - 0.09)	0.24 (0.22 – 0.26)
	2014	0.51 (0.46 - 0.56)	0.31 (0.3 - 0.32)	0.4 (0.36 - 0.45)	0.09 (0.08 - 0.1)	0.29 (0.27 – 0.31)
	2015	0.06 (0.04 - 0.12)	0.31 (0.29 - 0.34)	0.29 (0.26 - 0.37)	0.07 (0.06 - 0.12)	0.22 (0.2 – 0.35)
Bass Rock	2010	0.13 (0.1 - 0.16)	0.44 (0.42 - 0.45)	0.45 (0.41 - 0.49)	0.08 (0.07 - 0.09)	0.18 (0.16 – 0.2)
	2011	0.36 (0.32 - 0.4)	0.39 (0.37 - 0.42)	0.26 (0.22 - 0.3)	0.04 (0.03 - 0.05)	0.10 (0.08 – 0.12)
	2012	0.43 (0.39 - 0.46)	0.41 (0.4 - 0.42)	0.21 (0.19 - 0.24)	0.05 (0.05 - 0.06)	0.13 (0.12 – 0.14)
	2015	0.35 (0.31 - 0.15)	0.42 (0.4 - 0.45)	0.22 (0.19 - 0.49)	0.03 (0.03 - 0.09)	0.07 (0.07 – 0.2)

Table 8 Activity levels at dawn, during daylight (sunrise – sunset), dusk and at night (sunset-sunrise) in gannets at Flamborough Head and Bempton Cliffs in 2018 recorded using University of Amsterdam tags. Nocturnal activity is defined as activity at night as a proportion of activity during daylight (i.e., Night/Day, note calculations may not match due to rounding).

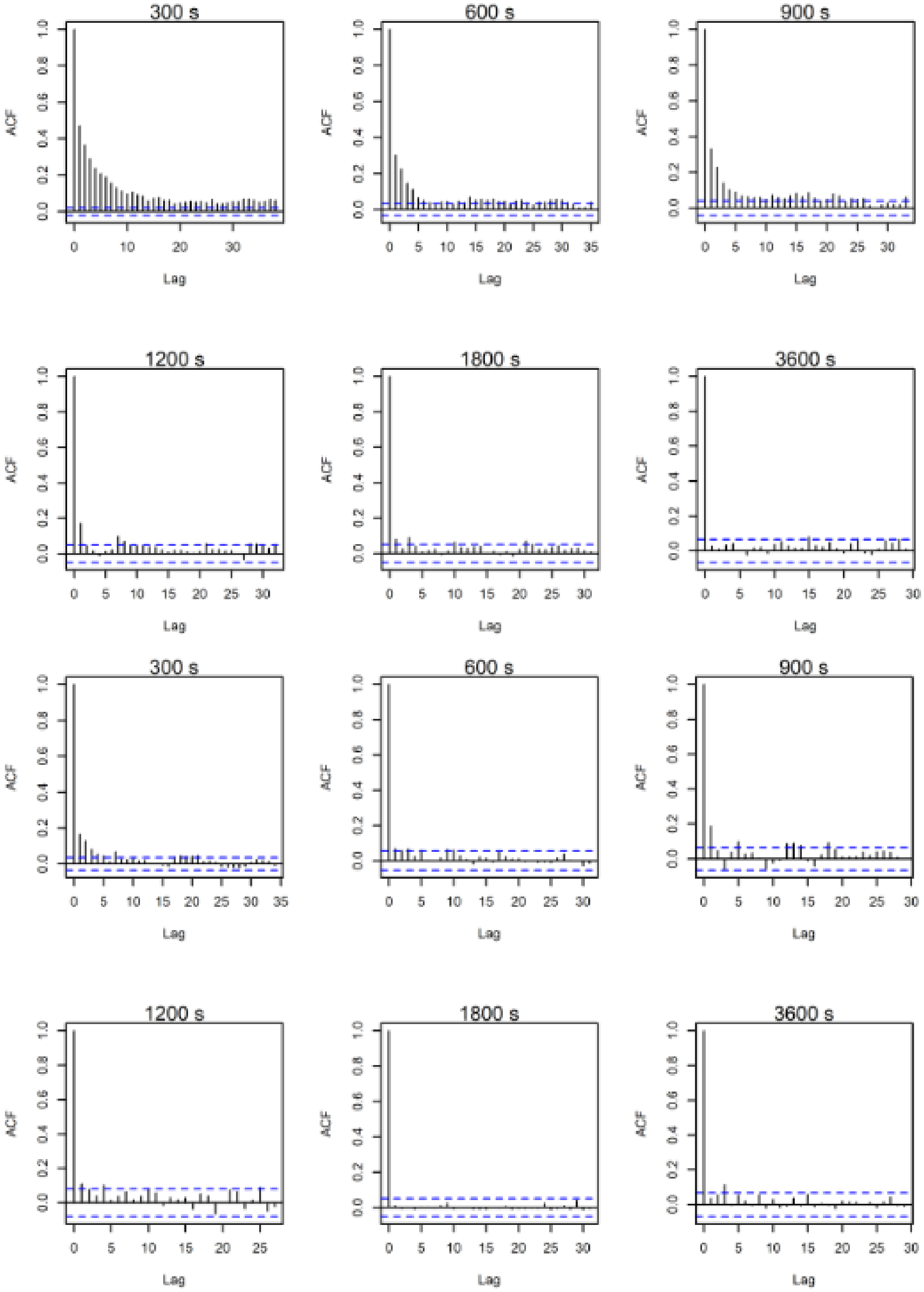
Month	**Dawn**	**Day**	**Dusk**	**Night**	**Nocturnal activity**
All	0.19 (0.17- 0.22)	0.27 (0.26 – 0.28)	0.21 (0.19 – 0.23)	0.01 (0.01 – 0.01)	0.04 (0.03 – 0.05)
July	0.13 (0.10 – 0.17)	0.26 (0.25 – 0.27)	0.19 (0.16 – 0.22)	0.01 (0.01 0.02)	0.05 (0.04 – 0.06)
August	0.27 (0.22 – 0.33)	0.31 (0.28 – 0.33)	0.27 (0.23 – 0.32)	0.01 (0.01 – 0.02)	0.05 (0.048 – 0.05)
September	0.20 (0.15 – 0.28)	0.24 (0.22 – 0.26)	0.12 (0.07 – 0.18)	0.01 (0.00 – 0.01)	0.03 (0.01 – 0.04)

3.2. Flight speed

3.2.1. Autocorrelation assessment

ACF comparisons were carried out for the full dataset including onshore data. Autocorrelation can be assessed visually with reference to an ACF plot (figures 10-12). These plots highlight the significance of any correlation between an estimated flight speed and subsequent estimates of flight speed. The blue lines on these plots indicate significance at p = 0.05 and, ideally, all vertical lines except the first should be between these. Overall, the temporal autocorrelation was very evident in the data at 300s-900s thereafter improving greatly, with best results (i.e., least autocorrelation) at 3,600s (Figs. 10-12). Consequently, the full dataset for all sites was sub-sampled at 3,600s for further comparisons and subsetted for the offshore environment only. An example is shown in figures 10-12 for lesser black-backed gulls from Walney, Skokholm and Orfordness.

(a) Instantaneous speed



(b) Trajectory speed

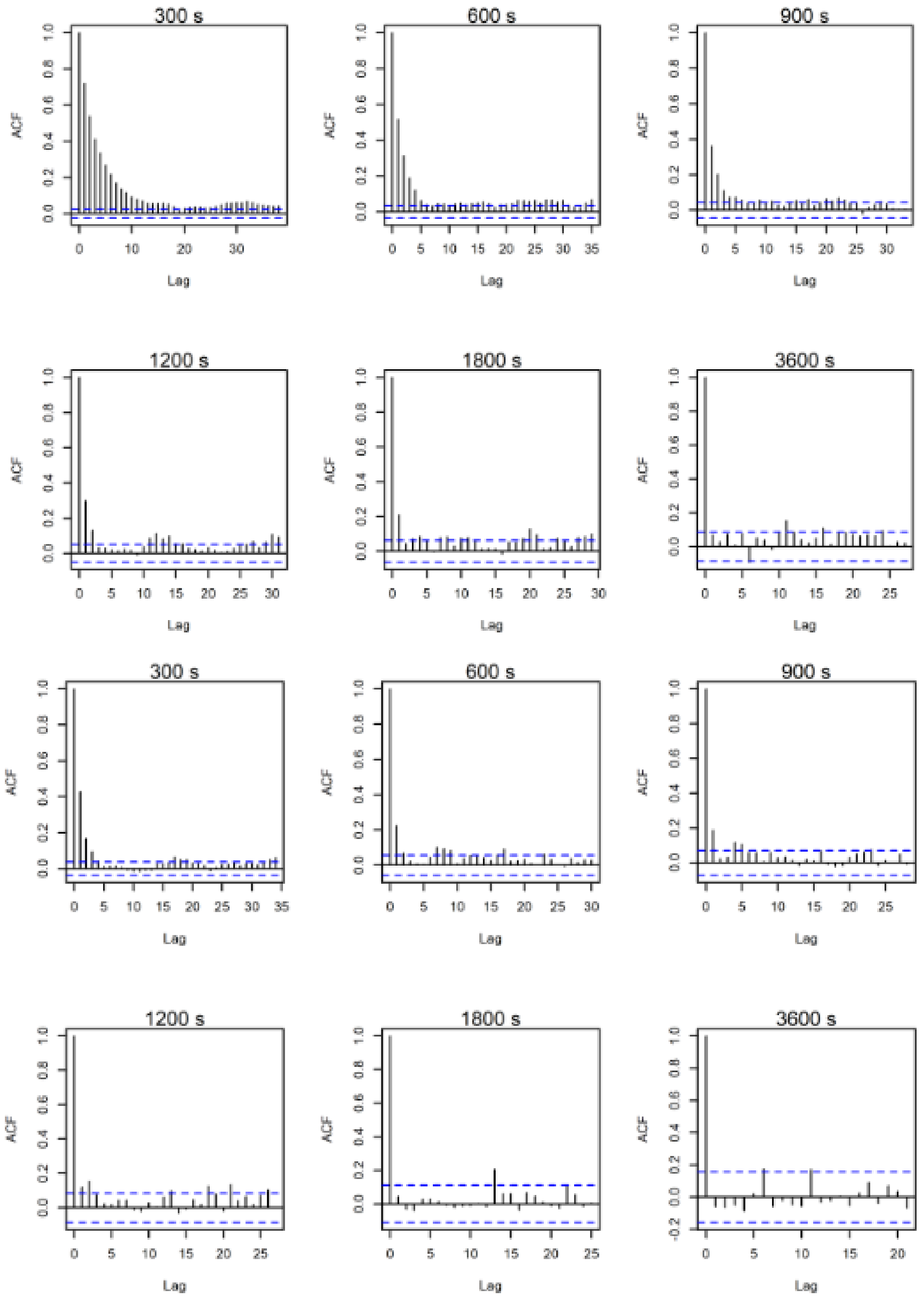
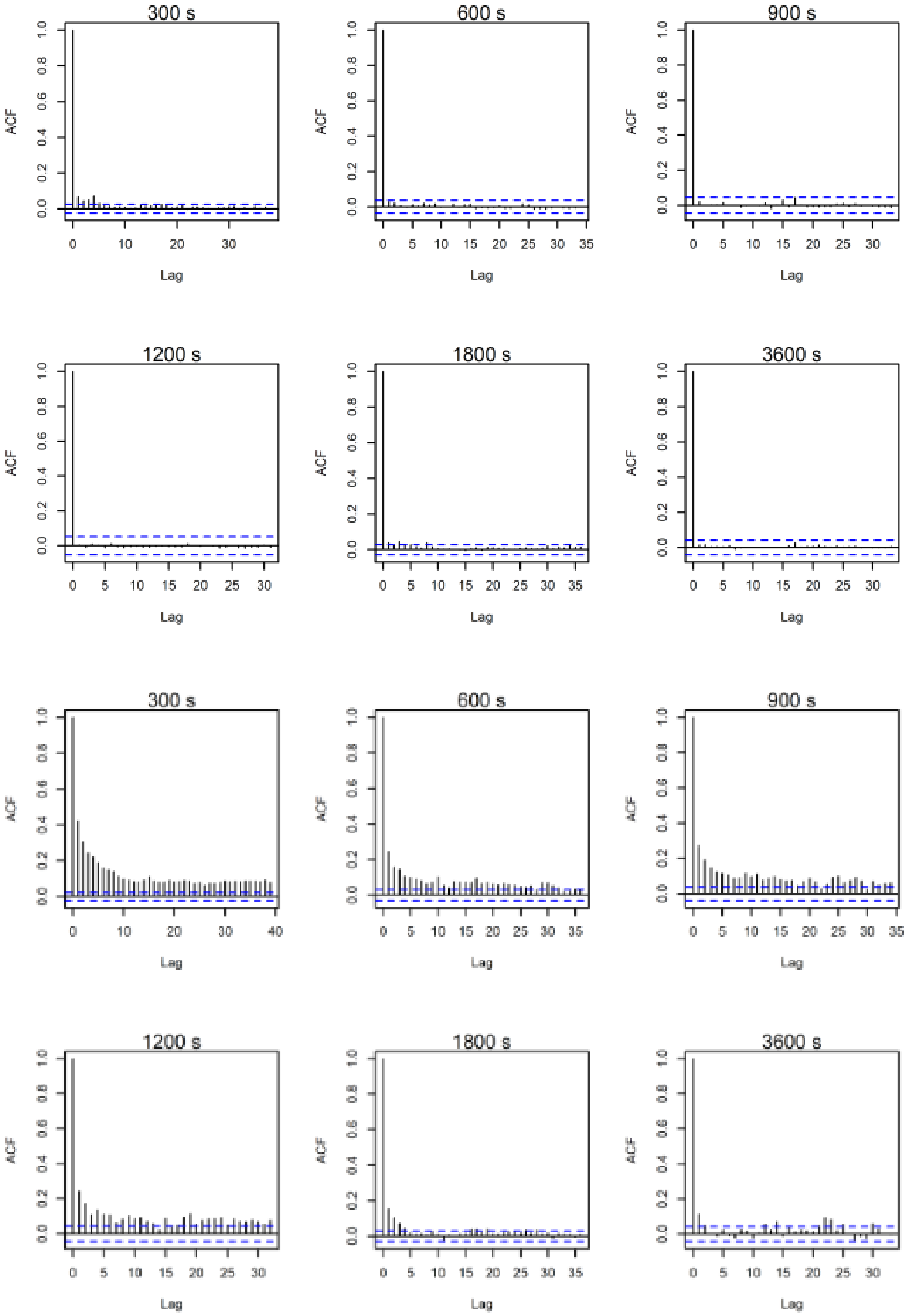


Figure 10 Examples of autocorrelation ACF plots for (a) instantaneous speed and (b) trajectory speed for two individuals in two different years of tracking at Walney

(a) Instantaneous speed



(b) Trajectory speed

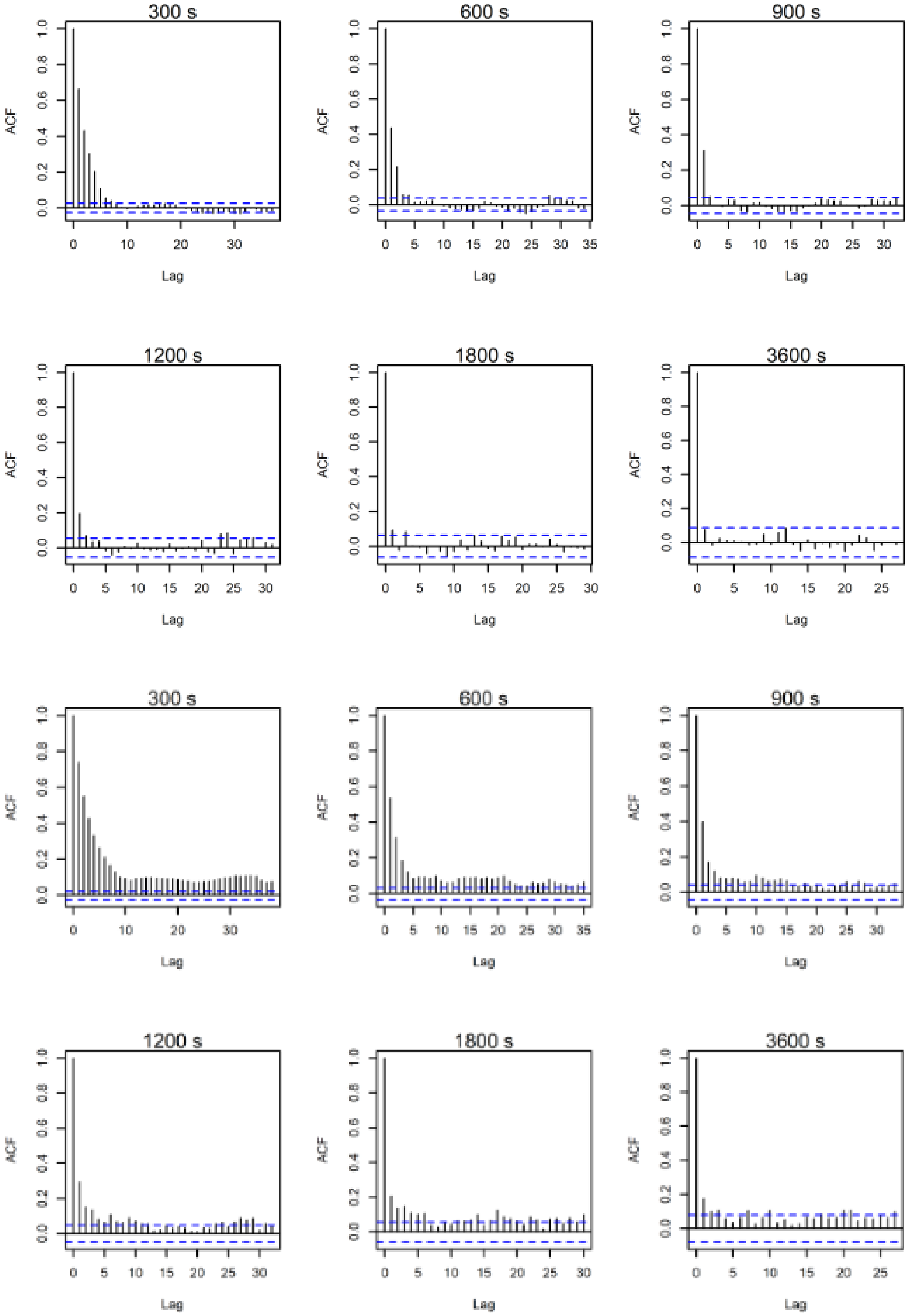
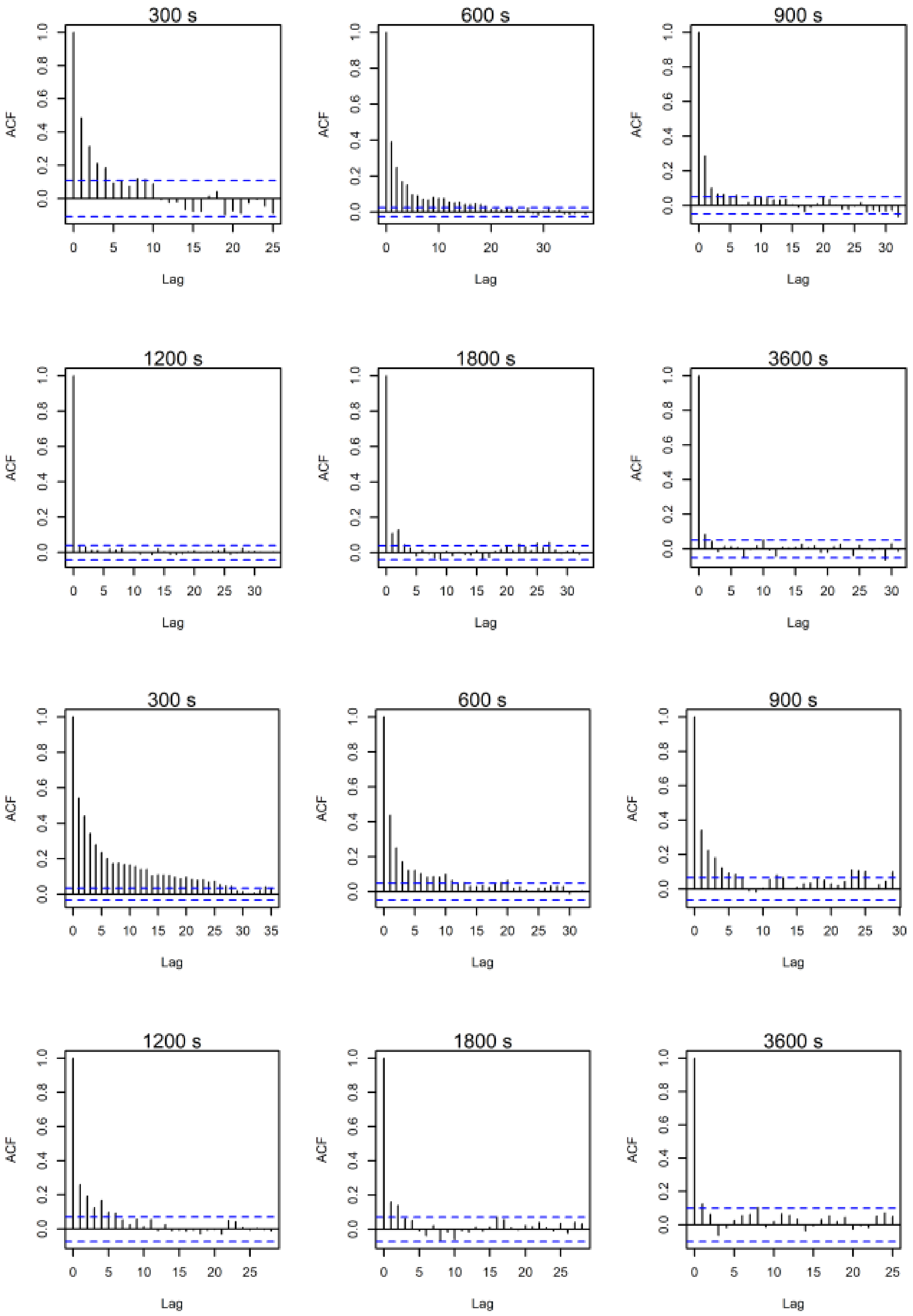


Figure 11 Examples of autocorrelation ACF plots for (a) instantaneous speed and (b) trajectory speed for two individuals in two different years of tracking at Skokholm

(a) Instantaneous speed



(b) Trajectory speed

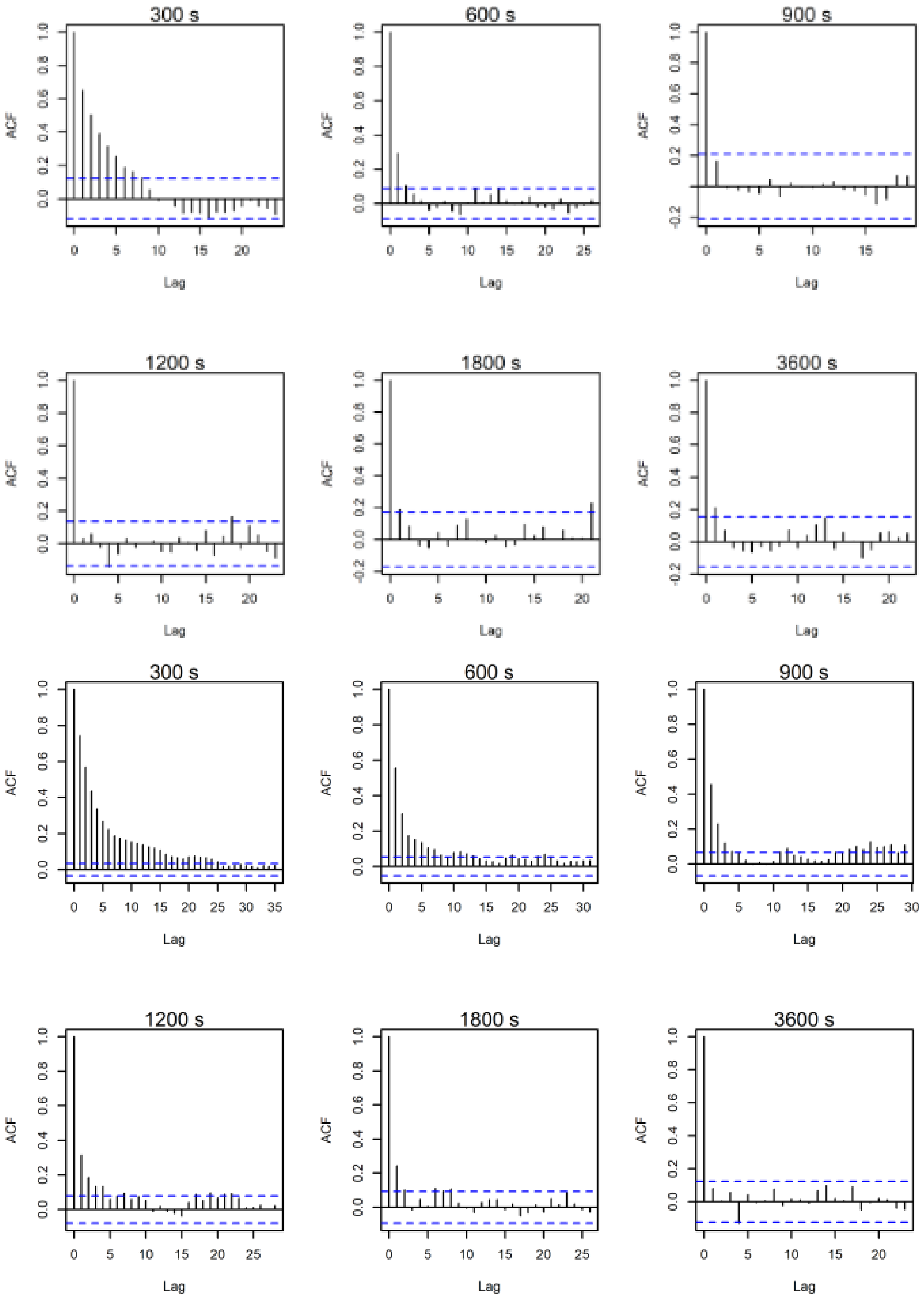


Figure 12 Examples of autocorrelation ACF plots for (a) instantaneous speed and (b) trajectory speed for two individuals in two different years of tracking at Orfordness

3.2.2. Lesser Black-backed Gull Walney

A minimum of five data points were specified for each individual to remove birds with too few data following sub-sampling within the offshore environment at the hourly rate. The resulting offshore dataset was therefore reduced to 1,345 data points for 31 individuals that crossed the offshore environment, from the original offshore dataset at five-minute rates containing 25,432 data points and 37 individuals.

3.2.2.1. Overall statistical comparison between speeds

For South Walney (as was the case at all other colonies), the full GLMM confirmed significantly faster overall speeds offshore than onshore (offshore (1,0) across states: ß = 0.646±0.055, $\chi^2 = 360.61$, df = 1, $P < 0.001$). For Walney offshore movements alone, there was a significant difference between trajectory and instantaneous speeds ($\chi^2 = 312.5$, df = 1, $P < 0.001$) that also varied with state (full two-way interaction: $\chi^2 = 521.52$, df = 3, $P < 0.001$). When assessing the significance of these differences per state through estimated marginal means (Fig 13), there was greatest difference between slower inactive states of stopped and floating on the sea; for commuting (state 3) there was a marginal result with trajectory speed being lower than that of instantaneous, although confidence limits overlapped; for foraging/searching offshore, there was no significant difference between instantaneous and trajectory speeds, although trajectory speeds were again lower than instantaneous. Fastest movements were for commuting for both instantaneous and trajectory speeds.

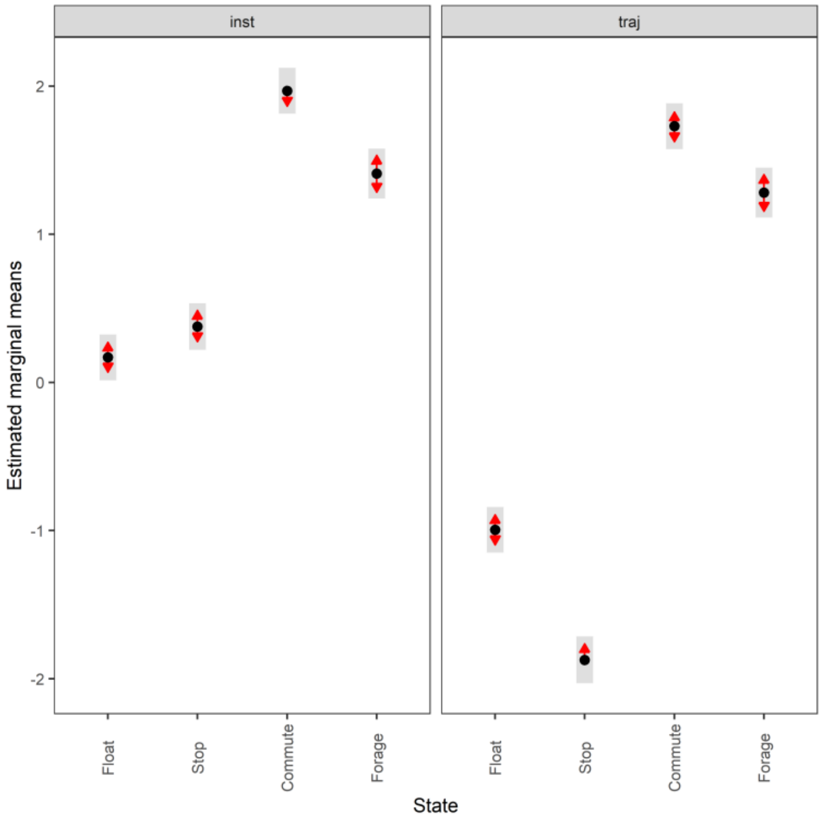


Figure 13. Estimated marginal means of instantaneous and trajectory speeds by EMbC state with significance indicated by red arrows, and confidence limits by grey bars; mean estimates are given as black circles.

3.2.2.2. Summary of distributions

The above analysis by state for each speed type deals with a direct comparison of mean estimates between distributions. However, closer inspection revealed some subtle differences in the distributions that would be overlooked in a direct mean comparison. The distribution of foraging for example, was no different in speed-by-speed type, yet the instantaneous trajectory for Walney showed a double peak in the distribution, one at ca 2 m/s and one at ca 9 m/s, whereas the trajectory speed showed a main peak at about 3 m/s (Fig 14).

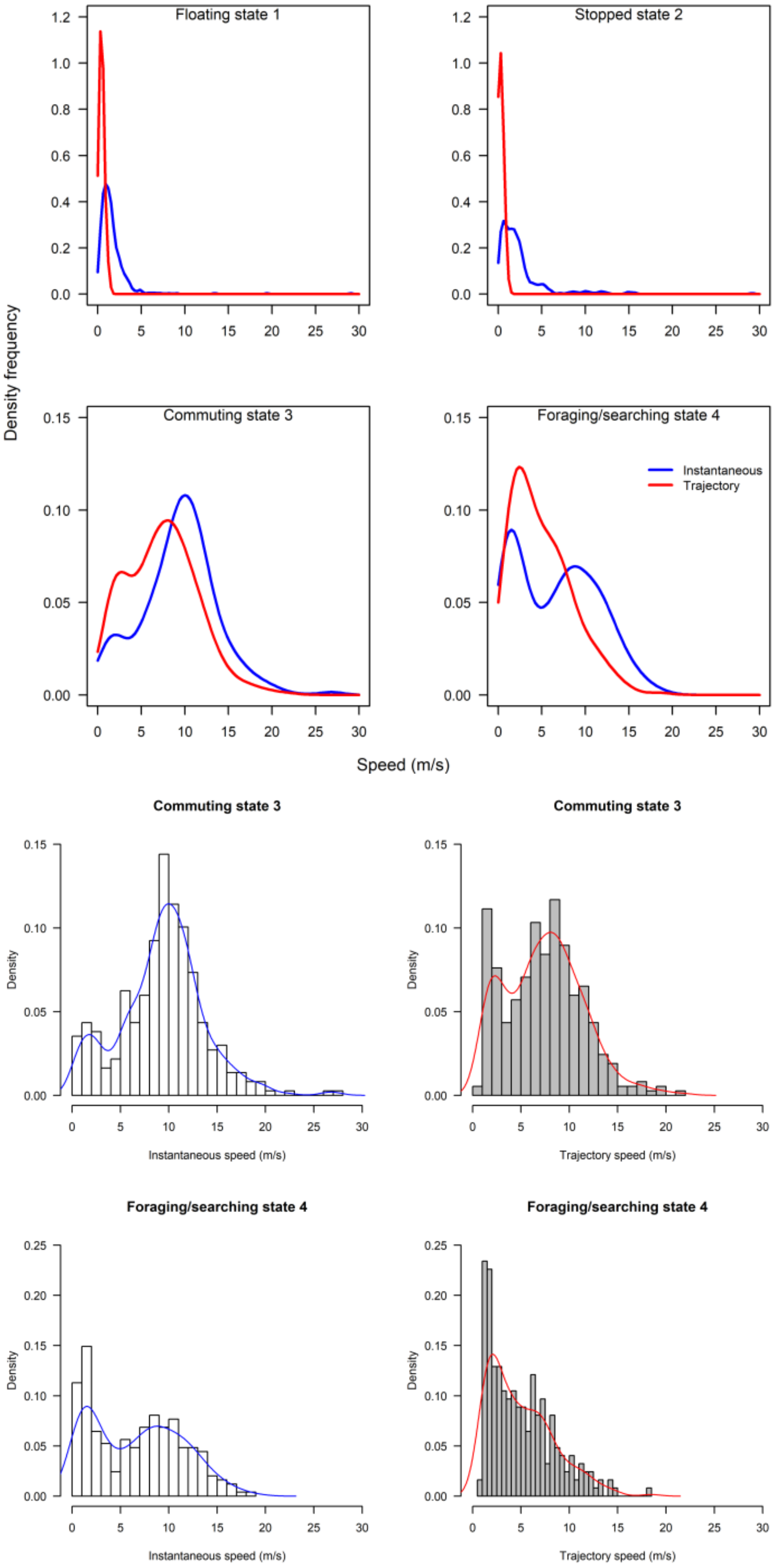
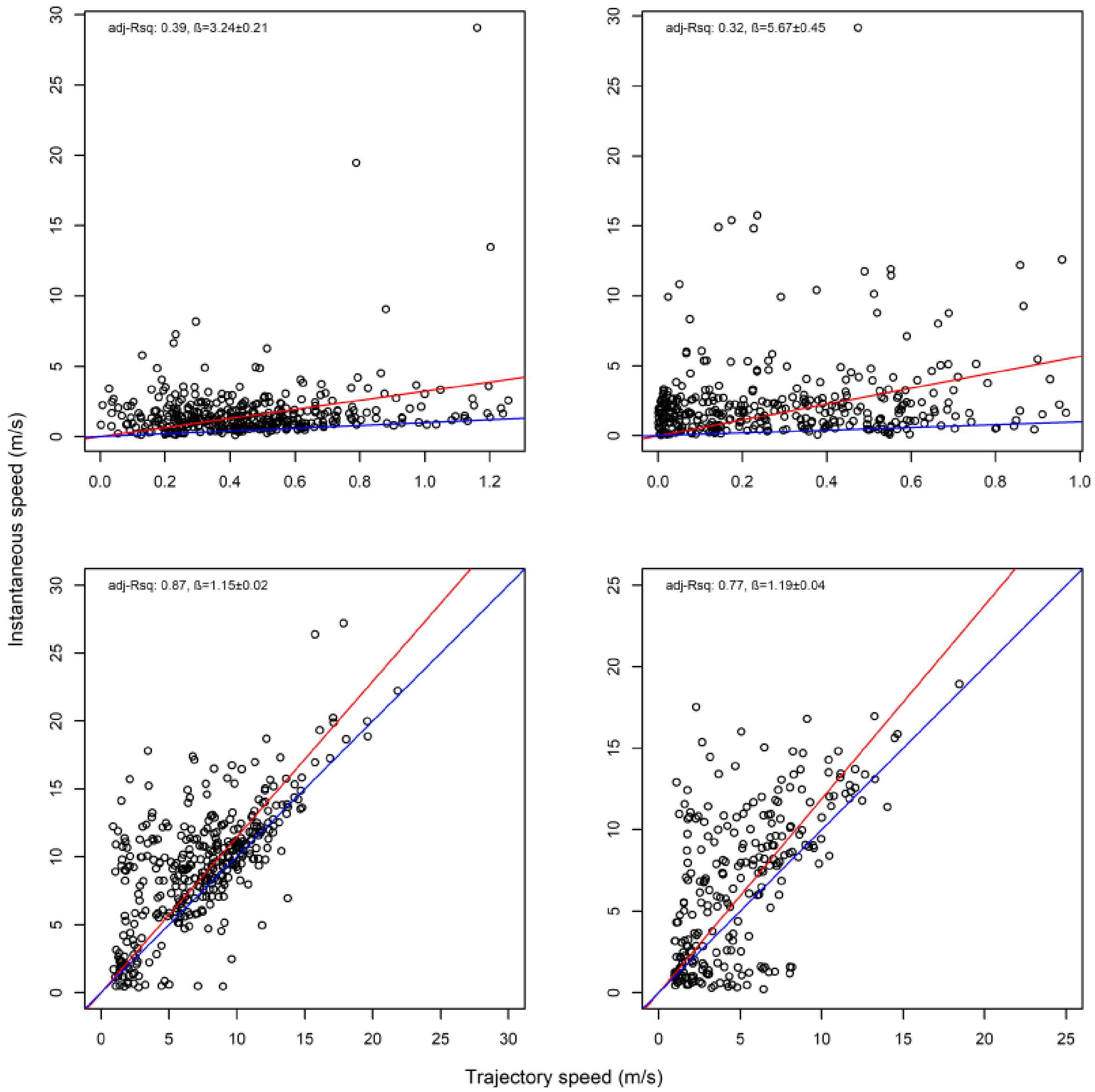


Figure 14 Walney histograms of instantaneous (blue) and trajectory (red) speed; top, all states with density curves; bottom, full histograms, breaks = 25, with overlain density curves

Overall, there was a general bias in underestimating the speed of offshore movement using trajectory speed in comparison to instantaneous velocity (test as above, traj_speed ß = -0.998±0.055 SE, from above full model). These differences were apparent in a direct xy regression (Fig 15), with points biased to the upper left of the 1:1 relationship for all states (as also found by Klaassen et al., 2011 for LBBG during the non-breeding season), and steeper best fit coefficients for commuting and foraging (1.15 and 1.19, respectively). In keeping with the above statistical comparison, the below regressions per state showed much closer relationships for commuting and foraging states than resting ones (Figure 15).

(a) 3600s sub-sample



(b) Original 300s EMbC-classified data

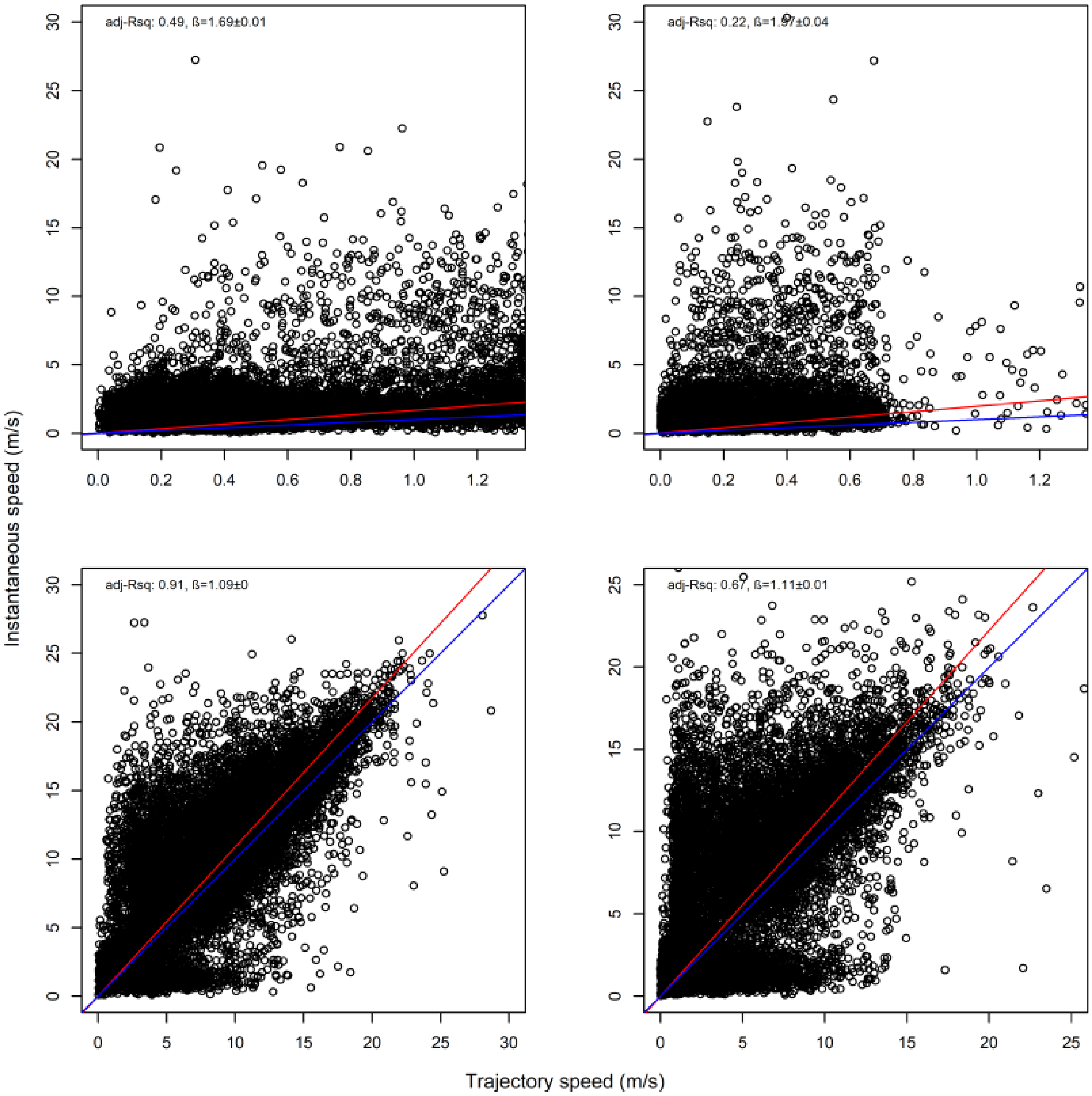
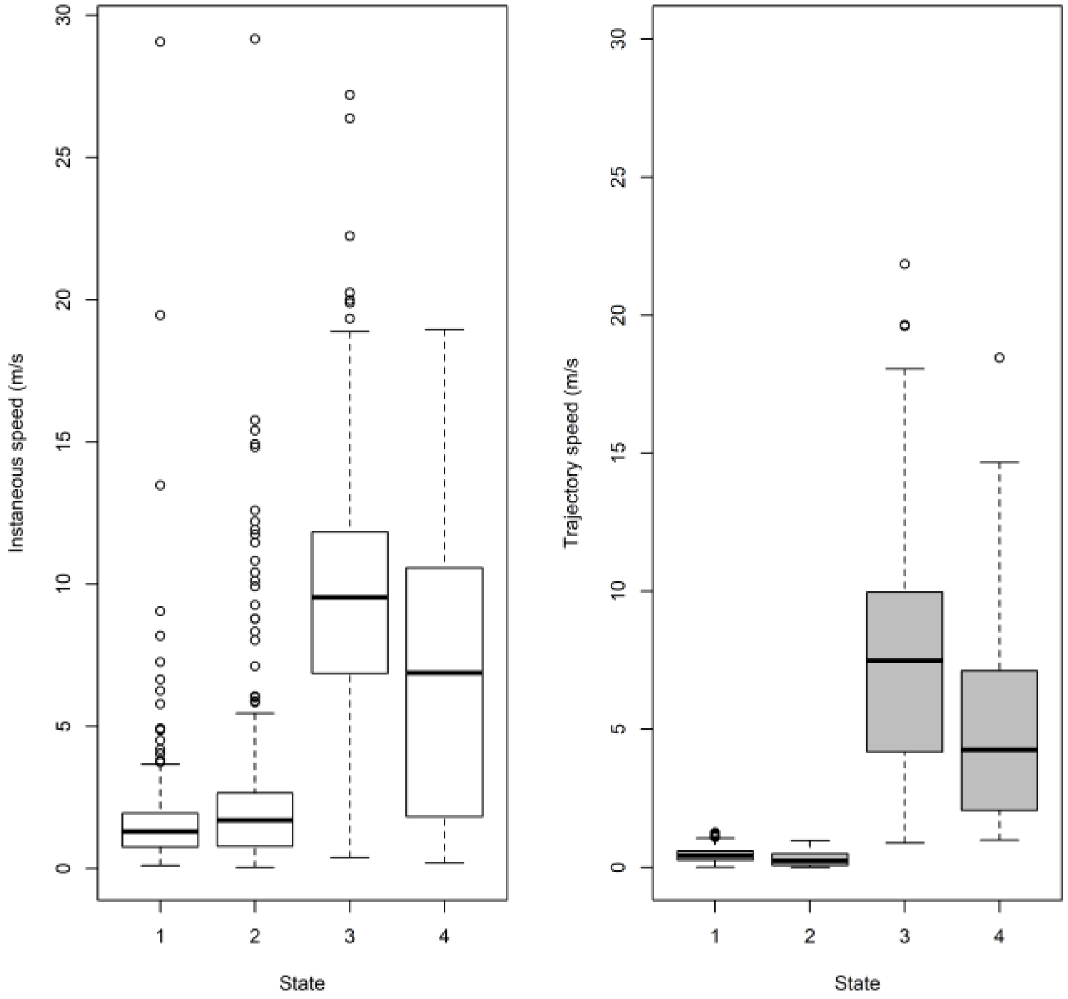


Figure 15 Linear regression of instantaneous speed and trajectory speed, with adjusted R^2 shown per state, the coefficient relationship (red line) and the 1:1 relationship for a perfect fit shown by the blue line (slope 1, intercept zero) for data (a) sub-sampled to a 3,600s rate, and (b) the original 300s dataset.

(a) Sub-sample to 1 hour



(b) Original five minute rate

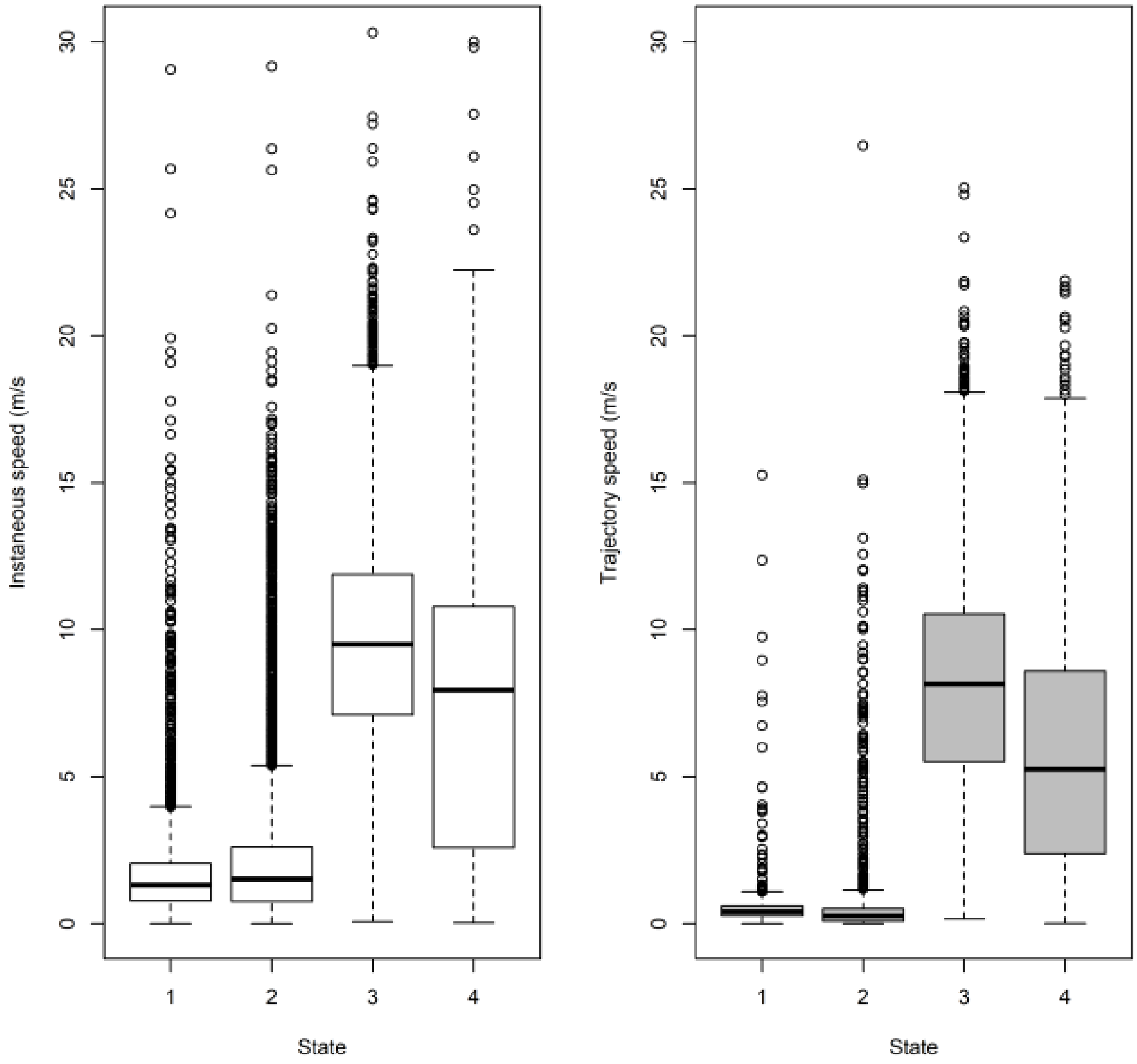


Figure 16 Walney boxplots using the (a) sub-sampled data investigated for formal analysis and (b) the original data at five-minute intervals.

Table 10 Summary of speeds per state (m/s), as obtained through classification of tracking data using a four-state EMbC model, given as median (plus interquartile range in parentheses)

Colony (n birds)	**Data grain**	**Speed type**	**1 (floating)**	**2 (stop)**	**3 (commuting)**	**4 (forage/search)**
Walney (n = 33)	3600s	Instantaneous	1.30 (0.76,1.94)	1.69 (0.77,2.66)	9.53 (6.85,11.82)	6.87 (1.82,10.57)
		Trajectory	0.43 (0.26,0.59)	0.23 (0.08,0.50)	7.49 (4.19,9.97)	4.25 (2.06,7.11)
Walney (n = 37)	300s	Instantaneous	1.32 (0.77,2.05)	1.51 (0.76,2.61)	9.51 (7.12,11.88)	7.94 (2.59,10.79)
		Trajectory	0.42 (0.27,0.60)	0.26 (0.08,0.51)	8.15 (5.51,10.54)	5.25 (2.39,8.59)

Note, the boxplots above (Figure 16) are based on all the data at five minute rates for comparison to Thaxter et al. (2019). By sub-sampling to hourly rates, we lose about 1 m/s from the commuting mean, so fewer points (and some different birds) meant it was not a fair comparison. Full examination is therefore also required using the 300s data. Comparing to the HMM states, the small steps of states 1 and 2 are comparable. However, the difference lies in where the boundary is drawn between commuting and foraging. EMbC draws the line in a slightly different place, with some foraging points classified as commuting by HMM being classified as foraging by EMbC. This results in slightly different speed distributions by method using the original 300s data. For Thaxter et al. (2019), for example, the median commuting and foraging speeds were 9.2 and 3.6 m/s, whereas for EMBC they are 8.2 and 5.3 m/s.

3.2.3. Lesser Black-backed Gull Skokholm

The original dataset for five-minute rates contained 67,761 rows of offshore data for 24 birds that was further subsampled to 5,486 rows for 24 birds at a rate of 3,600s. Given the offshore location of the colony, no birds were dropped from the analysis in the sub-sampling routine.

3.2.3.1. Overall statistical comparison between speeds

For Skokholm offshore movements, as with Walney, speeds offshore were faster than onshore (ß = 1.882±0.039, $P < 0.001$) and there was a significant difference between trajectory and instantaneous speeds ($\chi^2 = 676.37$ df = 1, $P < 0.001$) that also varied with state (full two-way interaction: $\chi^2 = 1744.70$, df = 3, $P < 0.001$).

The results for instantaneous vs trajectory speed were the same as for Walney, with the greatest difference between slower inactive states of stopped and floating on the sea and no significant difference for faster states of commuting and foraging.

3.2.3.2. Summary of distributions

As with Walney, closer inspection revealed subtle differences in the distributions. However, comparison of trajectory and instantaneous speeds showed distributions were similar in overall shape (Fig 17). However, there was a general bias in underestimating the speed of offshore movement using trajectory speed in comparison to instantaneous speed (test as above, traj_speed ß = -0.671±0.025 SE, from above full model). As with Walney, these differences were apparent in a direct xy regression (Fig 18), with points biased to the upper left of the 1:1 relationship for all states, and steeper best fit coefficients for commuting and foraging (1.10 and 1.11, respectively). In keeping with the above statistical comparison, the below regression per state showed much closer relationships for commuting and foraging states than resting ones.

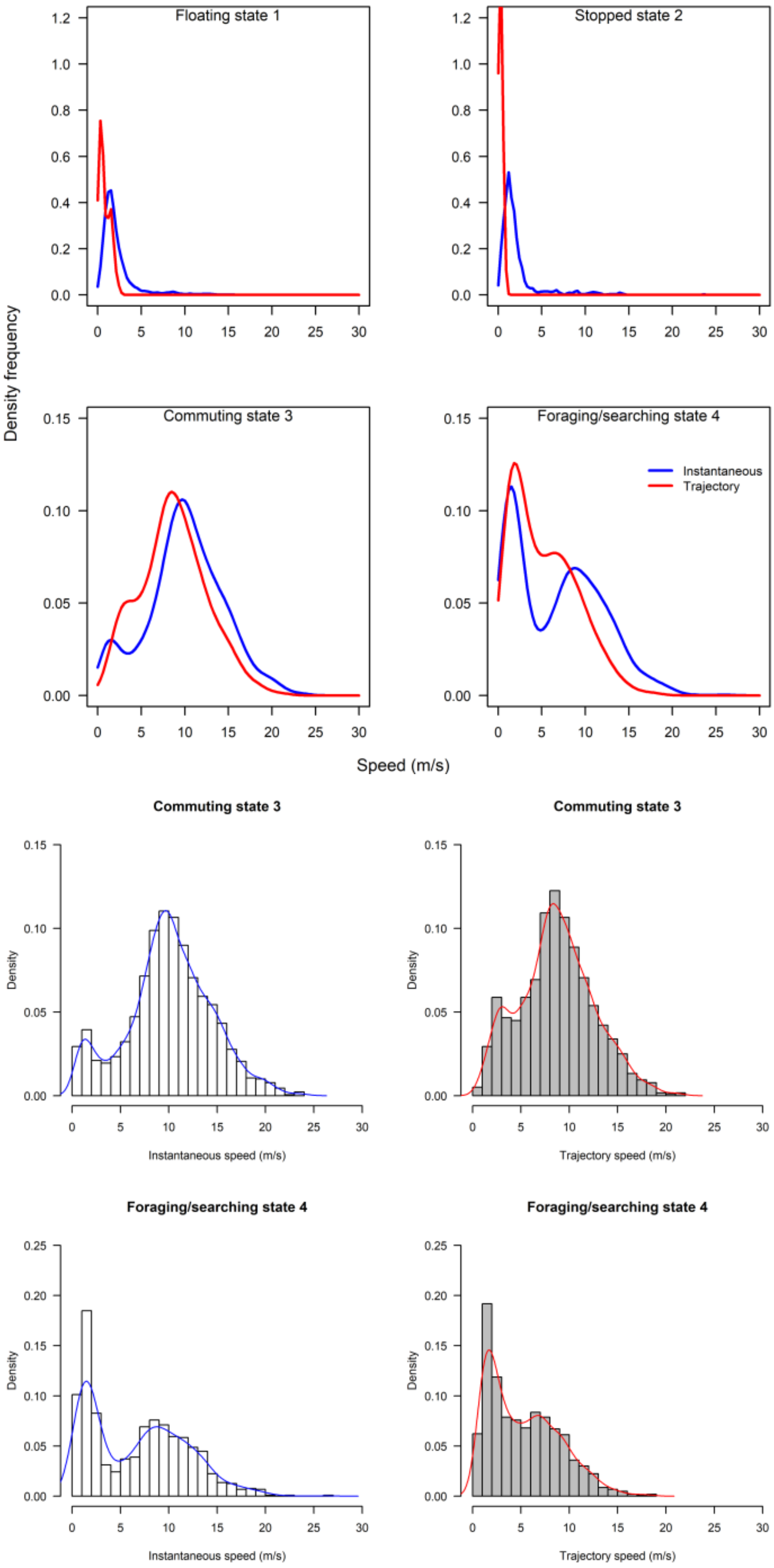
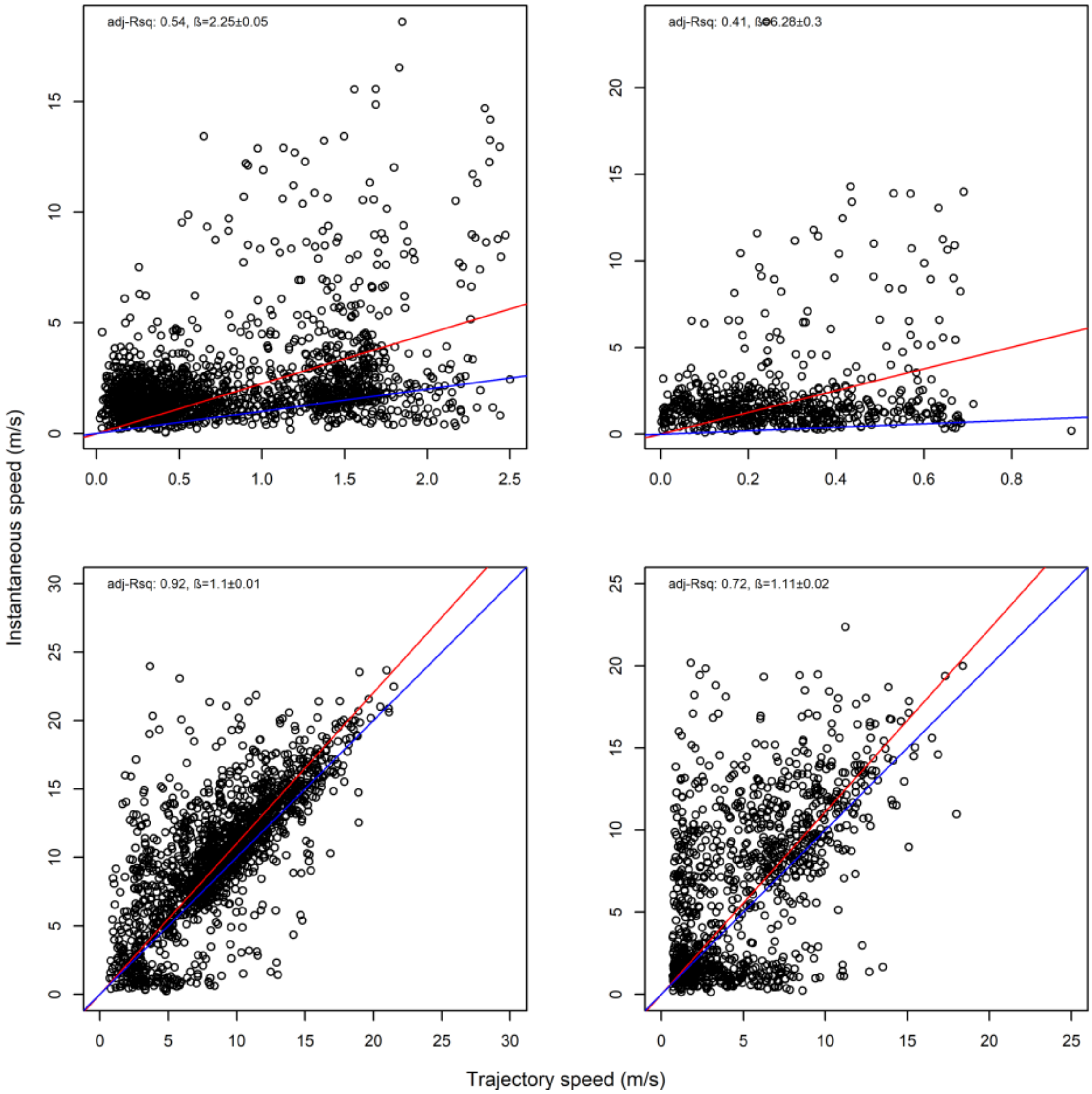


Figure 17 Skokholm histograms of speed; (top) all states with density curves; (bottom) full histograms, breaks = 25, with overlain density curves

(a) 3600s sub-sample



(b) Original 300s EMbC-classified data

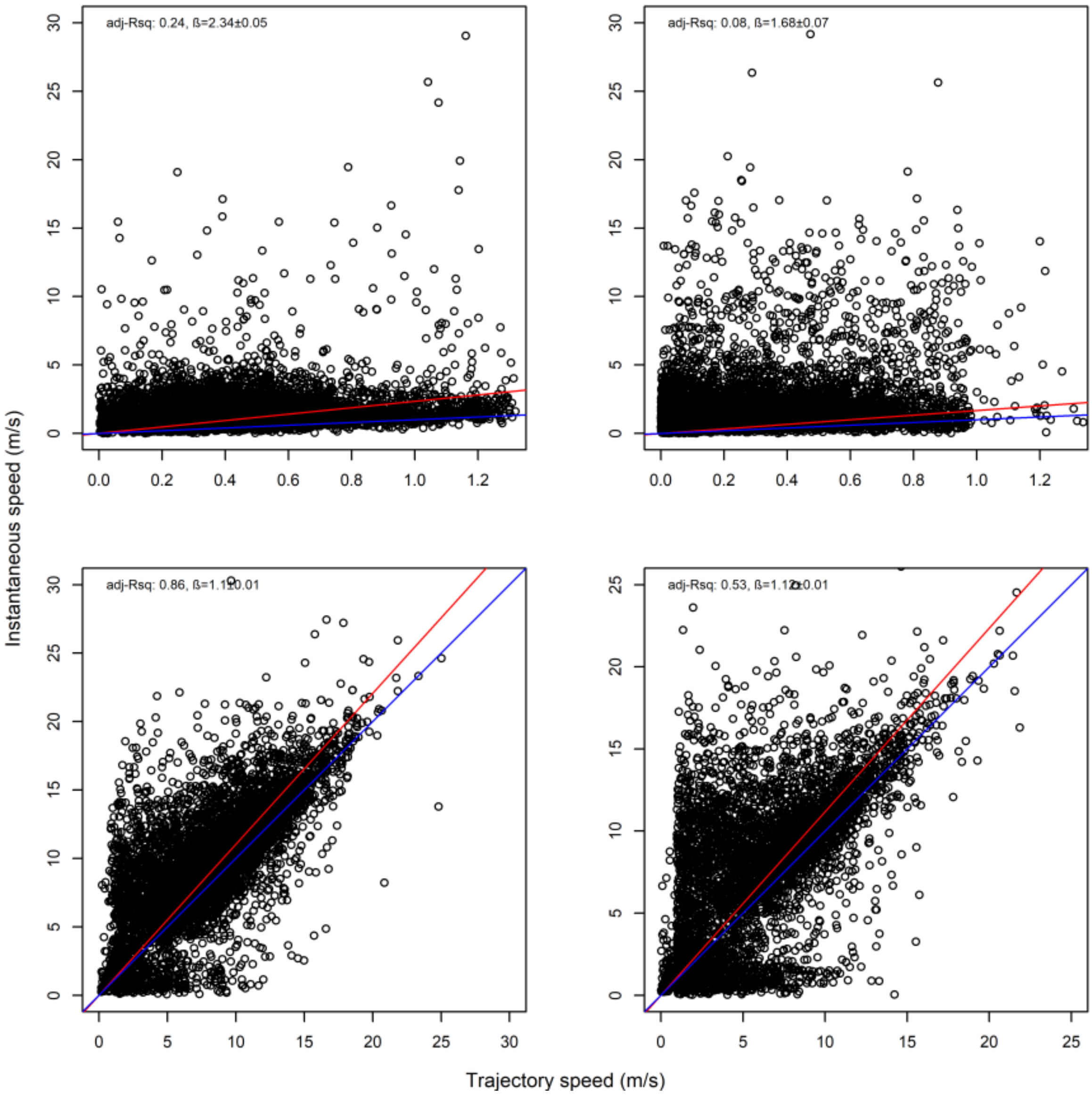
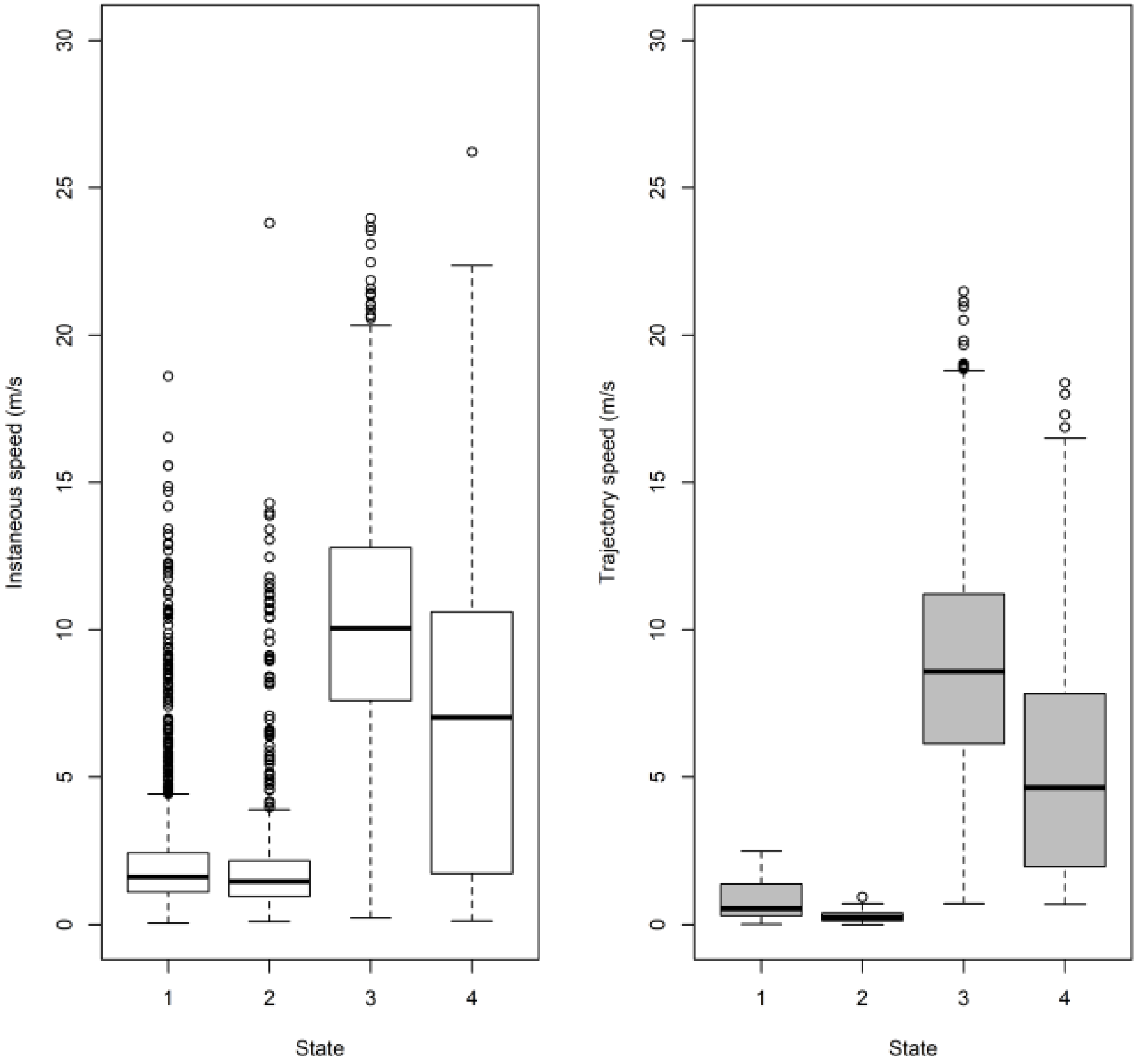


Figure 18 Linear regression of instantaneous speed and trajectory speed for Skokholm, with adjusted R^2 shown per state, the coefficient relationship (red line) and the 1:1 relationship for a perfect fit shown by the blue line (slope 1, intercept zero) for data (a) sub-sampled to a 3600s rate, and (b) the original 300s dataset.

(a) sub-sample to 1 hour



(b) Original five minute rate

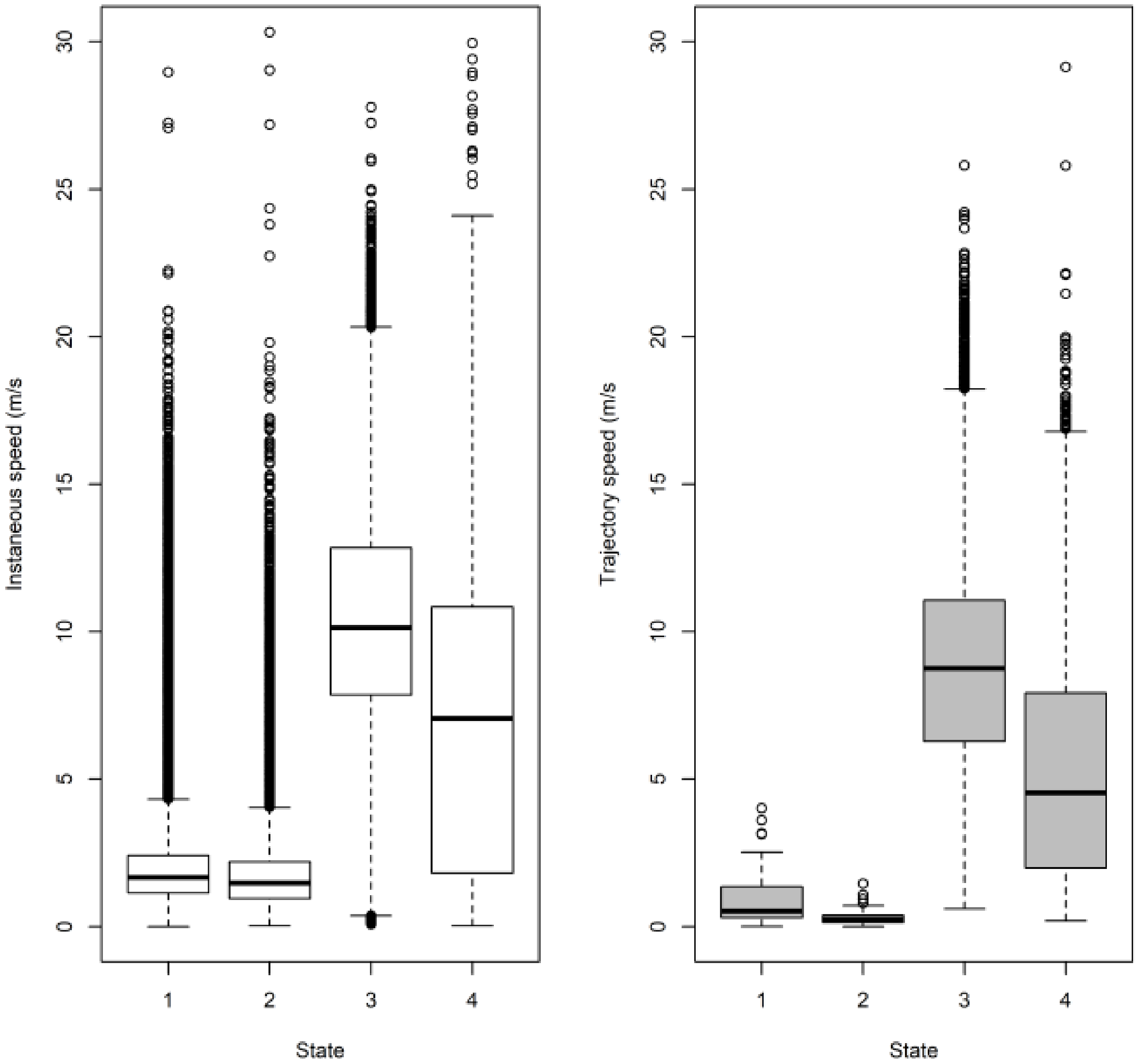


Figure 19 Skokholm boxplots using the (a) sub-sampled data investigated for formal analysis and (b) the original data at five-minute intervals.

Table 11 Summary of speeds per state (m/s) for Skokholm, as obtained through classification of tracking data using a four-state EMbC model, given as median (plus interquartile range in parentheses)

Colony (n birds)	**Data grain**	**Speed type**	**1 (floating)**	**2 (perching)**	**3 (commuting)**	**4 (forage/search)**
Skok (n = 24)	3600s	Instantaneous	1.62 (1.1,2.43)	1.45 (0.96,2.17)	10.05 (7.61,12.79)	7.03 (1.74,10.6)
		Trajectory	0.54 (0.3,1.37)	0.24 (0.13,0.39)	8.58 (6.13,11.21)	4.64 (1.97,7.84)
Skok (n = 24)	300s	Instantaneous	1.66 (1.14,2.41)	1.47 (0.95,2.19)	10.14 (7.85,12.84)	7.06 (1.81,10.83)
		Trajectory	0.52 (0.3,1.35)	0.24 (0.14,0.39)	8.76 (6.28,11.06)	4.53 (1.99,7.92)

As with Walney, when comparing to the HMM states from Thaxter et al., (2019) for Skokholm, the small steps of states 1 and 2 are comparable but again the boundary between commuting and foraging was slightly different, thus reducing the median speed of commuting and increasing foraging. Previous HMM trajectory estimates for Skokholm were 9.43 m/s for commuting and 1.49 for foraging, whereas (using 300s data for equal comparison, Table 11), EMbC estimates were 8.76 and 4.53 m/s. The variation between methods (i.e., HMMs, EMbC) at Skokholm, as shown previously for work at Walney (Thaxter et al. in prep) was therefore greatest for foraging.

3.2.4. Lesser Black-backed Gull Orfordness

The original dataset for five-minute rates contained 21,841 rows of offshore data for 24 birds that was further subsampled to 1,624 rows for 17 birds at a rate of 3,600s. Thus, seven birds were dropped from formal statistical analysis that had fewer than five data points offshore when subsampled to rates of 3,600s.

3.2.4.1. Overall statistical comparison between speeds

For Orfordness offshore movements, as with Walney and Skokholm, speeds offshore were faster than onshore (ß = 1.255±0.087, $P < 0.001$) and there was a significant difference between trajectory and instantaneous speeds ($\chi^2 = 34.87$, df = 1, $P < 0.001$) that also varied with state (full two-way interaction: $\chi^2 = 146.29$, df = 3, $P < 0.001$). The results for instantaneous vs trajectory speed were the same as for the other colonies with the greatest difference between slower inactive states of stopped and floating on the sea and no significant difference for faster states of commuting and foraging.

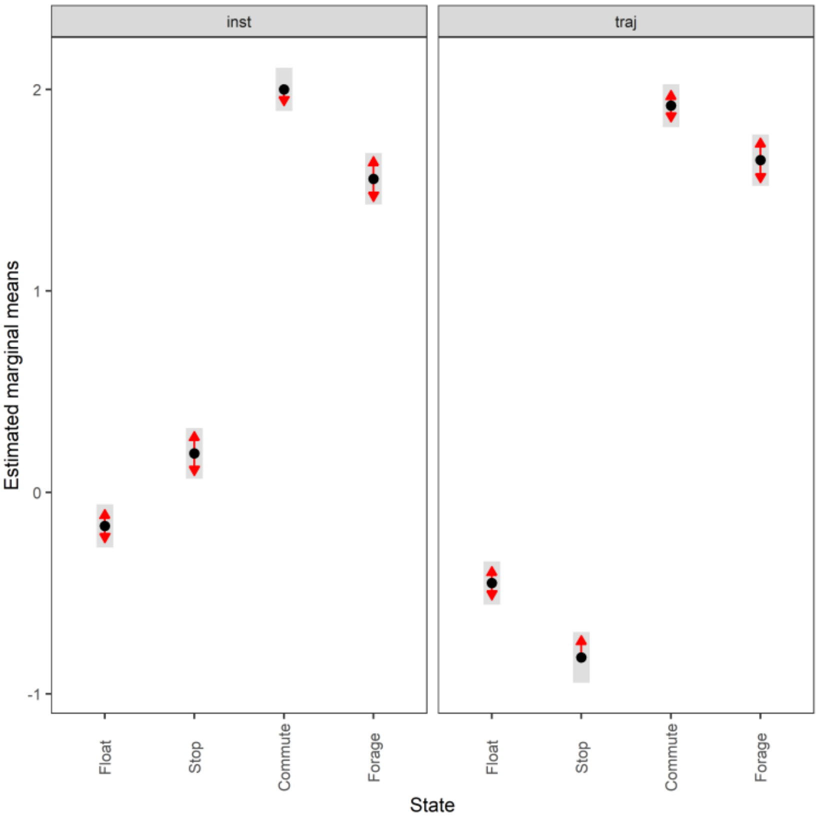


Figure 20. Estimated marginal means of instantaneous and trajectory speeds by EMbC state with significance indicated by red arrows, and confidence limits by grey bars; mean estimates are given as black circles.

3.2.4.2. Summary of distributions

Similar to Walney and Skokholm, some subtle differences were notable in the distributions in comparison of trajectory and instantaneous speeds. Commuting speeds were quite similar in overall shape, and compared to other colonies, there was greater similarity for resting states 1 and 2, but foraging again showed differences in distribution, albeit hidden when comparing overall means statistically above (Fig 21).

For Orfordness there was a general bias in underestimating the speed of offshore movement using trajectory speed in comparison to instantaneous velocity (test as above, traj_speed ß = -0.278±0.047 SE, from above full model), albeit the coefficient being the lowest of all three lesser black-backed gull colonies. As with other lesser black-backed gull colonies, these differences were apparent in a direct xy regression (Fig 22 below), with points biased to the upper left of the 1:1 relationship for all states, and steeper best fit coefficients for commuting and foraging (1.08 for both, respectively). In keeping with the above statistical comparison, the below regression per state showed much closer relationships for commuting and foraging states than resting ones and for Orfordness the coefficient was closest of all colonies to 1.0, but still representing a likely underestimate of speed through trajectory rather than the instantaneous measure.

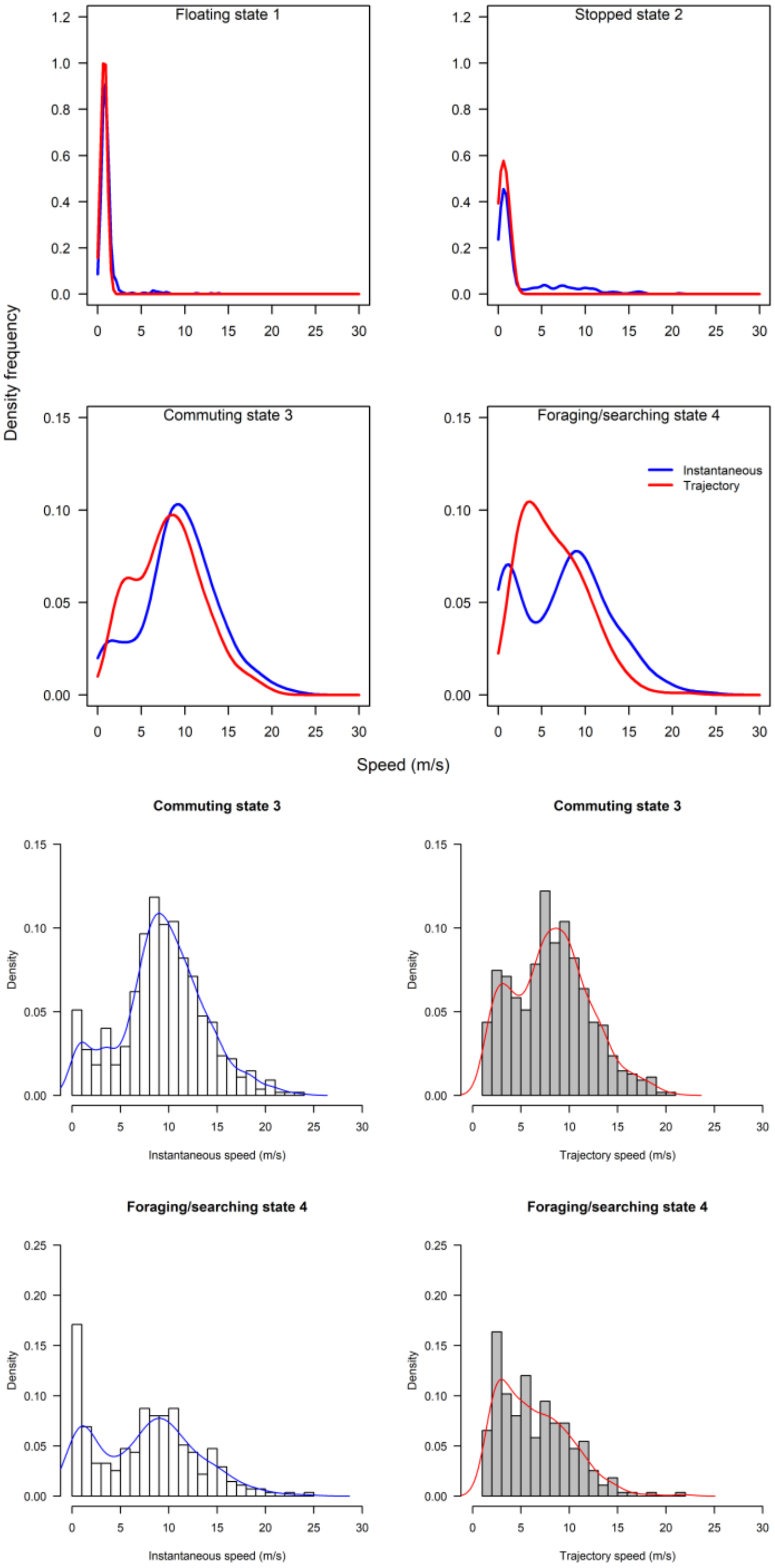
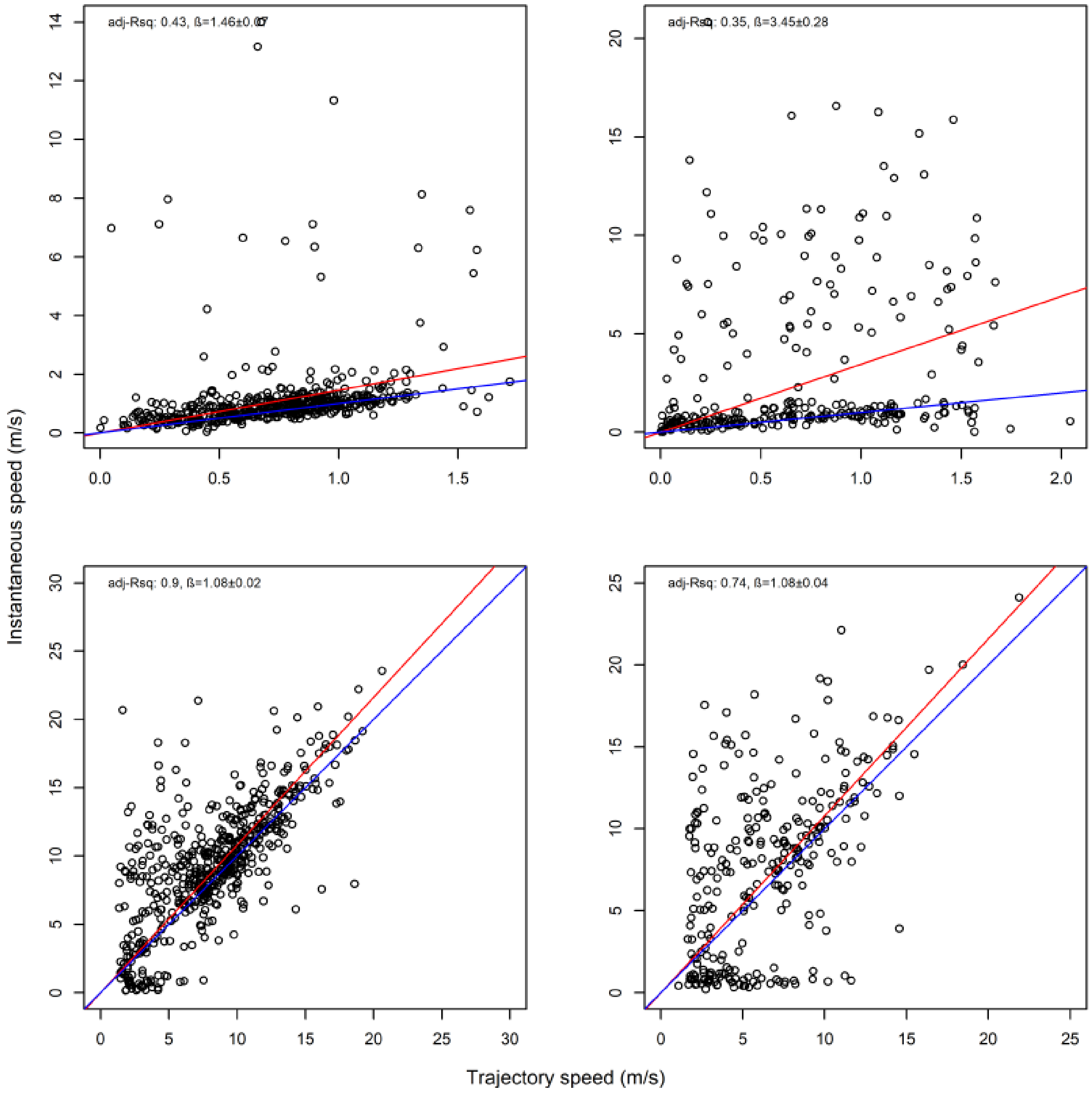


Figure 21 Orfordness histograms of speed; (top) all states with density curves; (bottom) full histograms, breaks = 25, with overlain density curves

(a) 3,600s sub-sample



(b) Original 300s EMbC-classified data

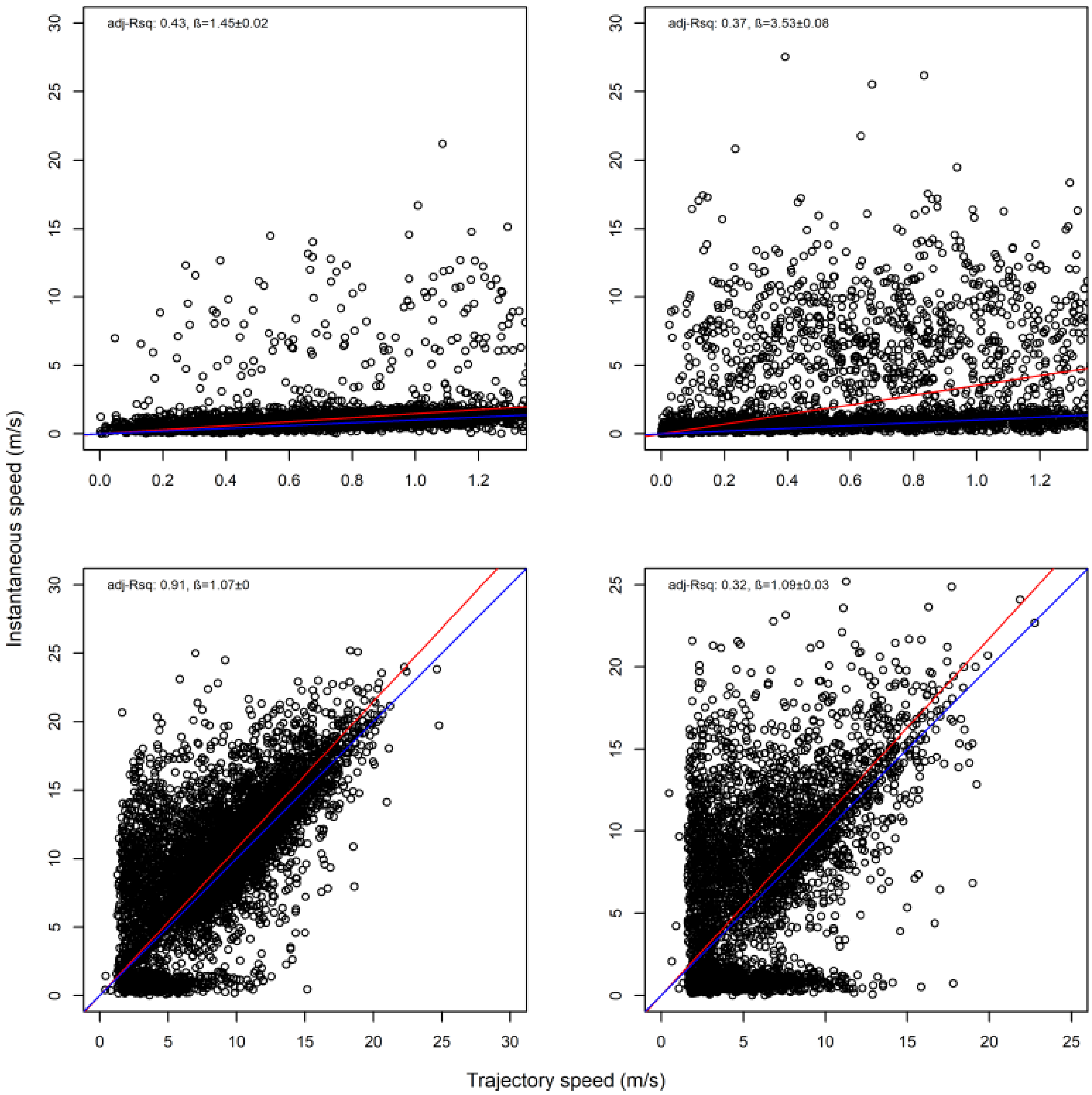
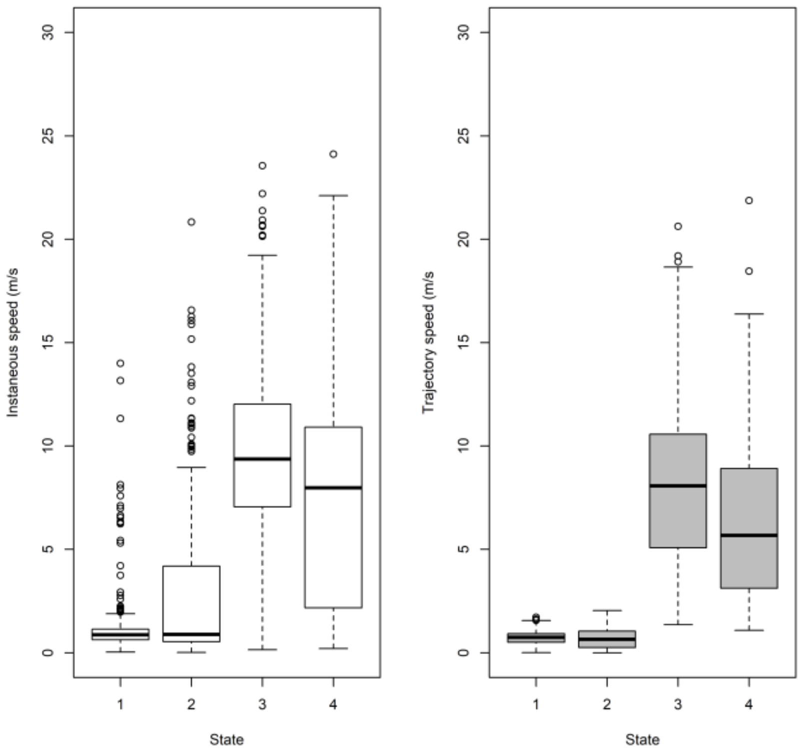


Figure 22 Linear regression of instantaneous speed and trajectory speed for Skokholm, with adjusted R^2 shown per state, the coefficient relationship (red line) and the 1:1 relationship for a perfect fit shown by the blue line (slope 1, intercept zero) for data (a) sub-sampled to a 3,600s rate, and (b) the original 300s dataset.

(a) sub-sample to 1 hour



(b) Original five minute rate

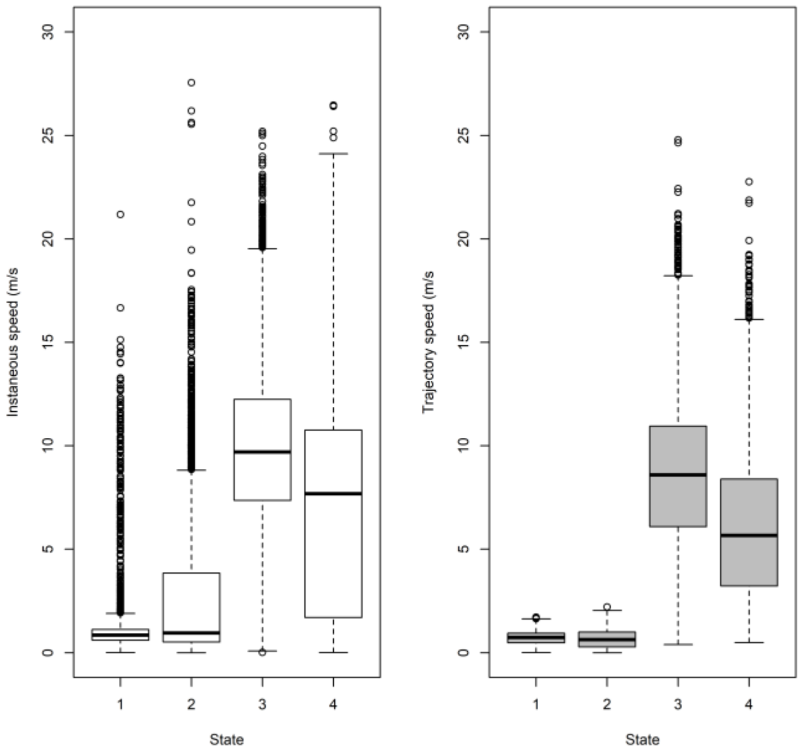


Figure 23 Orfordness boxplots using the (a) sub-sampled data investigated for formal analysis and (b) the original data at five-minute intervals.

Table 12 Summary of speeds per state (m/s) for Skokholm, as obtained through classification of tracking data using a four-state EMbC model, given as median (plus interquartile range in parentheses)

Colony (n birds)	**Data grain**	**Speed type**	**1 (floating)**	**2 (perching)**	**3 (commuting)**	**4 (forage/search)**
Orf (n = 24)	3600s	Instantaneous	0.87 (0.63,1.14)	0.89 (0.54,4.19)	9.37 (7.06,12.03)	7.98 (2.17,10.91)
		Trajectory	0.75 (0.51,0.93)	0.65 (0.25,1.05)	8.07 (5.08,10.57)	5.67 (3.12,8.92)
Orf (n = 17)	300s	Instantaneous	0.85 (0.6,1.13)	0.95 (0.52,3.85)	9.7 (7.36,12.25)	7.69 (1.71,10.75)
		Trajectory	0.74 (0.48,0.95)	0.63 (0.28,1)	8.59 (6.09,10.95)	5.67 (3.23,8.39)

As with other colonies, comparing to the HMM states from Thaxter et al. (2019) for Orfordness, the small steps of states 1 and 2 are comparable but again the boundary between commuting and foraging was slightly different, thus reducing the median speed of commuting and increasing foraging. Previous HMM trajectory speed estimates for Orfordness were 9.65 m/s for commuting and 2.41 for foraging, whereas (using 300s data for equal comparison, Table 12), EMbC estimates were 8.59 and 5.67 m/s. The variation between methods (i.e., HMMs, EMbC) at Orfordness, as shown previously for work at Walney (Thaxter et al. in prep), and Skokholm above, was therefore greatest for foraging activity.

3.2.5. Kittiwake Flamborough Head and Bempton Cliffs SPA

The dataset for kittiwake at Flamborough Head and Bempton Cliffs included 20,287 data points from 36 individuals on 305 foraging trips. Across all behaviours, speeds recorded for offshore movements using GPS ranged from 0.01 m/s to 127 m/s, with a median of 3.08 m/s (95% CIs 1.34 – 8.99) (Figure 24).

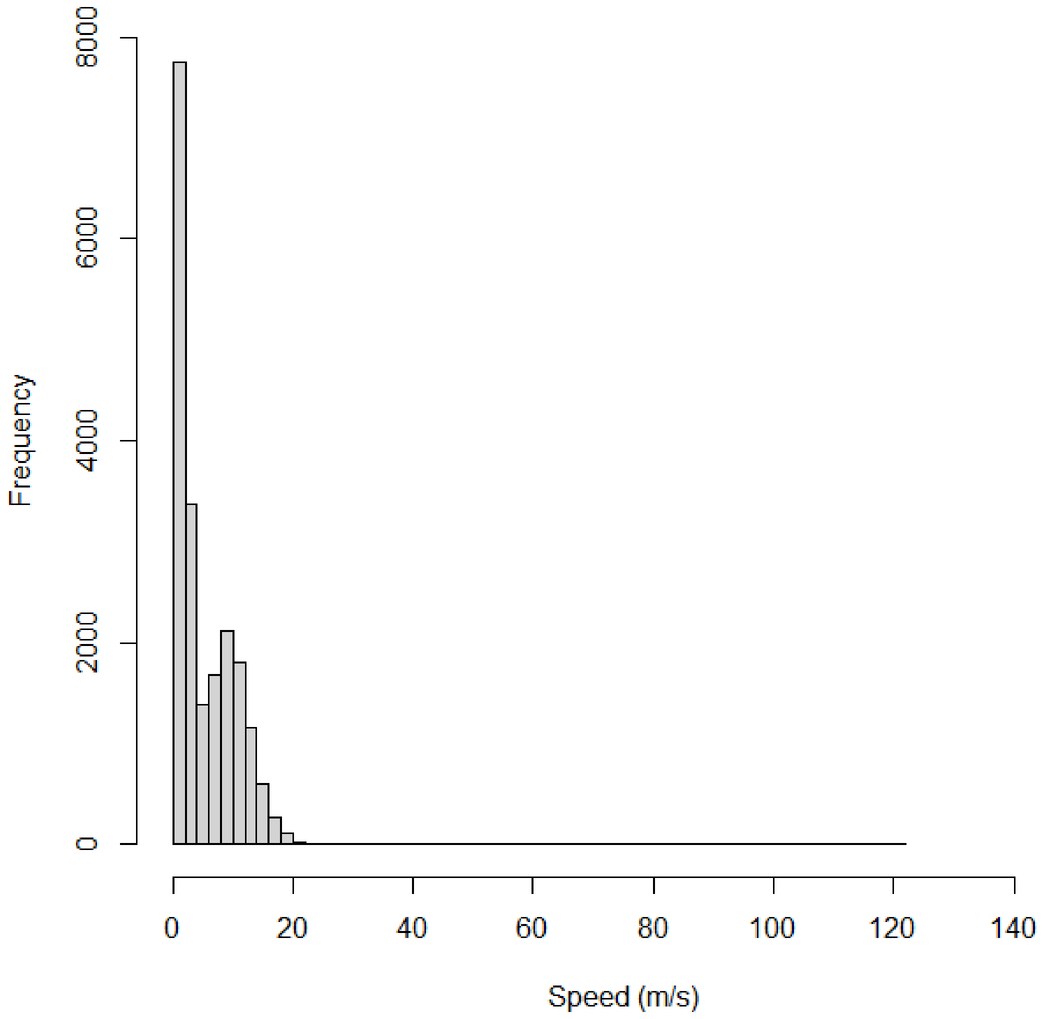


Figure 24 Histogram of flight speeds measured for offshore movements of kittiwakes from Flamborough Head and Bempton Cliffs.

Following behavioural classification with EMbC, there were clear differences in flight speed between behaviours (Figure 24). Commuting flight speeds were faster than foraging flight speeds (Table 13) at 9.73 m/s (95% CIs 6.93 – 12.33) in comparison to 6.07 m/s (95% CIs 1.85 – 9.46). For both foraging and commuting flight, trajectory speeds derived from EMbC with reference to step length were noticeably slower than the instantaneous speeds measured using GPS.

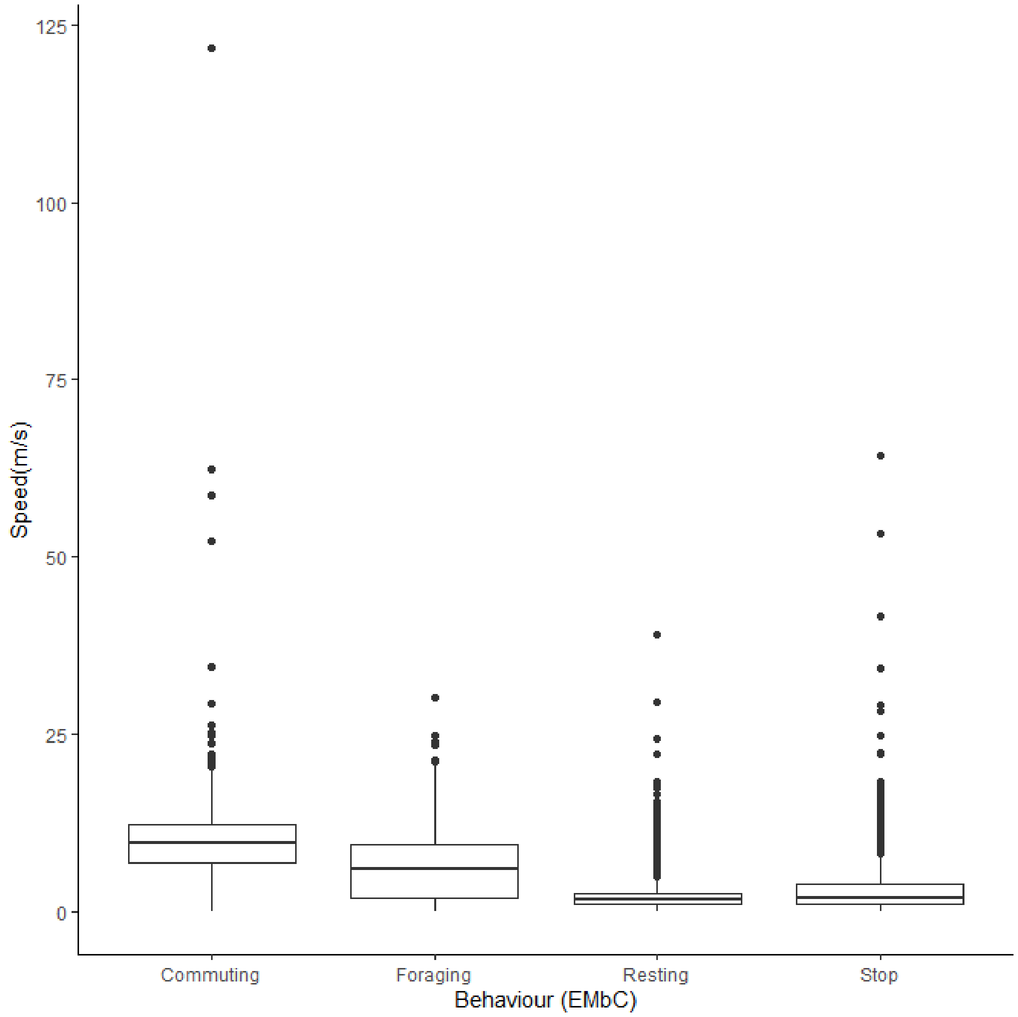


Figure 25 Boxplot of flight speeds for kittiwakes from Flamborough Head and Bempton Cliffs per state obtained from a four state EMbC model.

Table 13 Summary of speeds per state (m/s) for kittiwake from Flamborough Head and Bempton Cliffs, as obtained through classification of tracking data using a four-state EMbC model, given as median (plus interquartile range in parentheses)

Colony (n birds)	**Data grain**	**Speed type**	**1 (floating)**	**2 (Stop)**	**3 (commuting)**	**4 (forage/search)**
Flam (36)	300s	Instantaneous	1.66 (1.01,2.57)	1.84 (0.96,3.82)	9.73 (6.93,12.33)	6.07 (1.85,9.46)
Flam (36)	300s	Trajectory	0.54	0.38	7.58	3.90

3.2.6. Gannet Flamborough Head and Bempton Cliffs

The dataset for gannets at Flamborough Head and Bempton Cliffs included 34,120 data points from 10 individuals on 301 foraging trips. Across all behaviours, speeds recorded for offshore movements using GPS ranged from 0.02 m/s to 42.60 m/s, with a median of 1.36 m/s (95% CIs 0.71 – 12.79) (Figure 26).

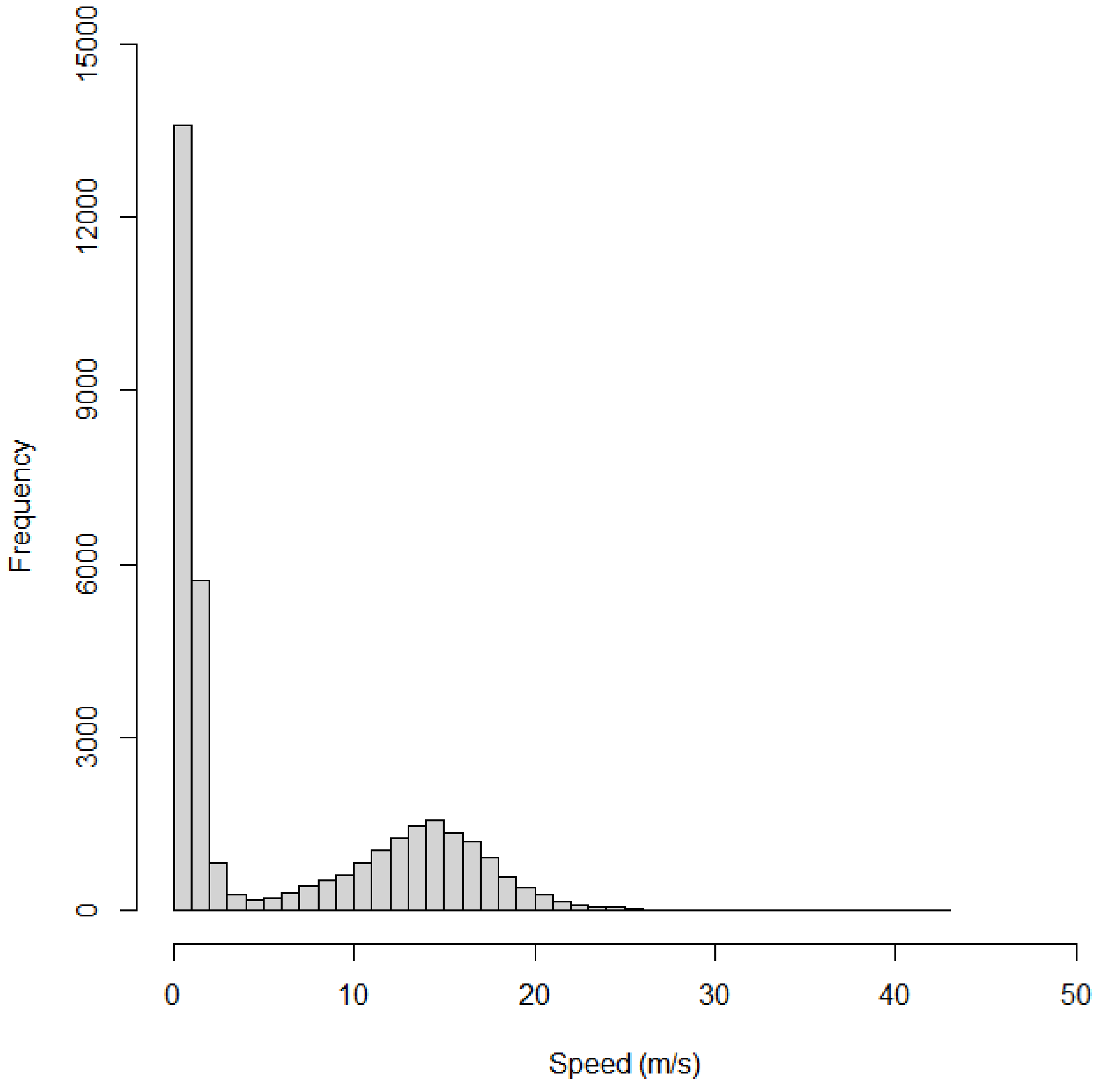


Figure 26 Histogram of flight speeds measured for offshore movements of gannets from Flamborough Head and Bempton Cliffs.

Following behavioural classification with EMbC, there were clear differences in flight speed between behaviours (Figure 27). Commuting flight speeds were faster than foraging flight speeds (Table 14) at 14.01 m/s (95% CIs 11.13 – 16.44) in comparison to 10.79 m/s (95% CIs 1.41 – 14.51).

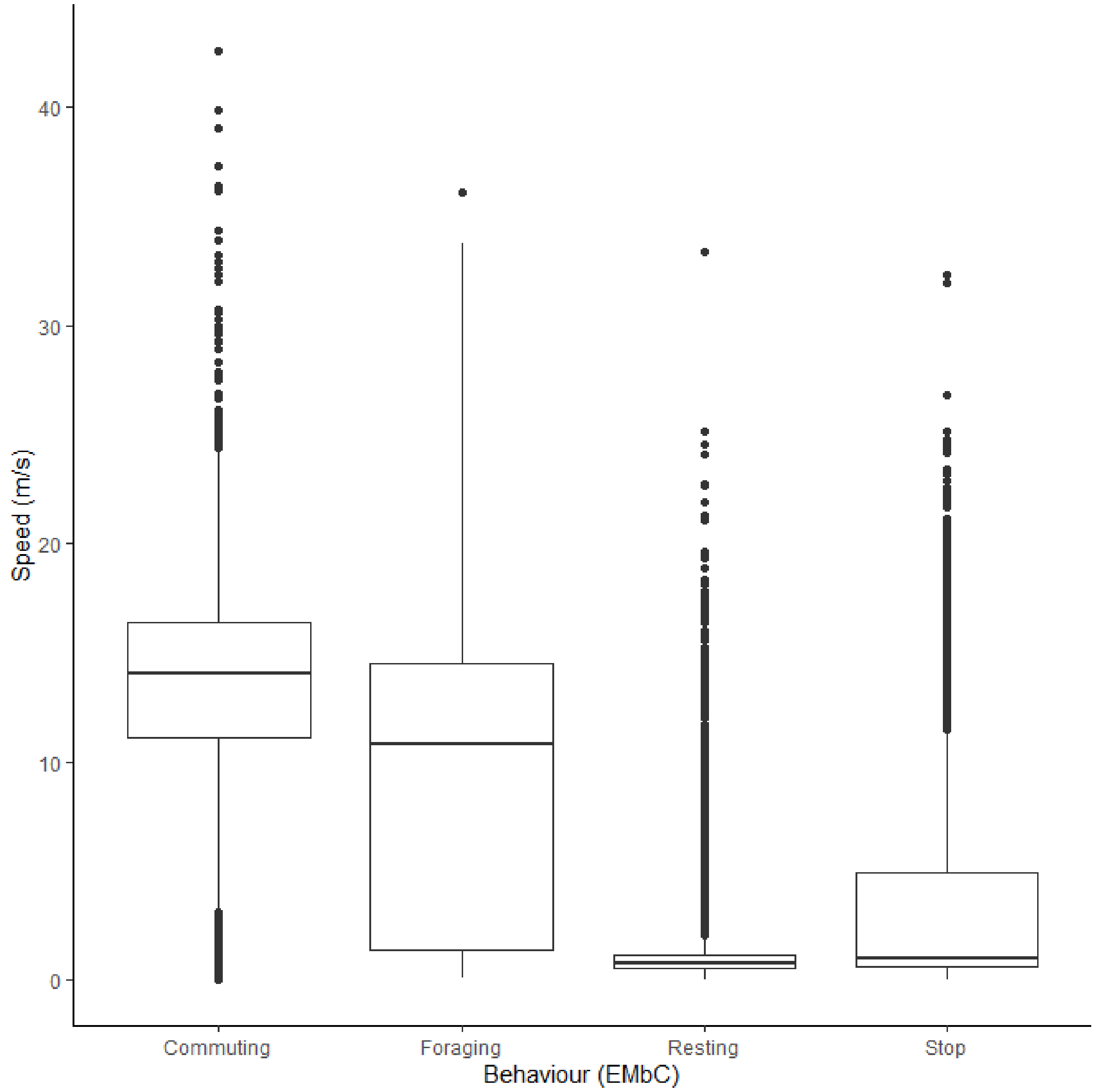


Figure 27 Boxplot of flight speeds for gannets from Flamborough Head and Bempton Cliffs per state obtained from a four state EMbC model.

Table 14 Summary of speeds per state (m/s) for gannets from Flamborough Head and Bempton Cliffs, as obtained through classification of tracking data using a four-state EMbC model, given as median (plus interquartile range in parentheses)

Colony (n birds)	**Data grain**	**Speed type**	**1 (floating)**	**2 (Stop)**	**3 (commuting)**	**4 (forage/search)**
Flam (10)	300s	Instantaneous	0.80 (0.55, 1.15)	1.04 (0.60,4.96)	14.01 (11.13,16.44)	10.79 (1.41,14.51)
Flam (10)	300s	Trajectory	0.46	0.50	10.80	6.29

3.2.7. Flight speed summary

Across all three species, commuting flight speeds were substantially faster than foraging flight speeds (Table 15). At present, recommended generic speeds for the three species considered here are 13.1 m/s for lesser black-backed gull and kittiwake (Alerstam et al., 2007) and 14.9 m/s for gannet (Pennycuick, 1997). Regardless of the approach taken to estimate flight speed from GPS data, these generic flight speeds are substantially faster than those observed in the data presented here, with the exception of the commuting flight speed for gannet.

Comparison of trajectory and instantaneous speeds highlighted that whilst the two are strongly correlated, the trajectory speeds are slower than instantaneous speeds. More detailed analysis of the lesser black-backed gulls revealed that these correlations were strongest for commuting speeds. Whilst a higher sampling rate resulted in trajectory speeds that more closely matched the instantaneous speeds, even at the fastest rate considered here (300s), a noticeable difference remained. This highlights the importance of using instantaneous rather than trajectory speeds.

For lesser black-backed gulls, estimated speeds for each state were broadly consistent across all three sites, regardless of the method used to derive them. As might be expected, commuting flight speeds are noticeably faster than foraging flight speeds with both floating and perching speeds slower still. Generally, differences in sampling rate did not have a significant impact on the speed estimated. However, commuting speeds estimated using HMMs were a closer match to the instantaneous speeds than those estimated using EMBC. For foraging speeds, the reverse was true.

Table 15 Flight speeds (median, plus interquartile range in parentheses) estimated from GPS data for lesser black-backed gull, kittiwake, and gannet.

Species	**Colony**	**State**	**Trajectory**			**Instantaneous**	
			HMM	**EMBC**			
				300	**3600**	**300**	**3600**
Lesser Black-backed Gull	Walney	Floating	0.32 (0.13-0.59)	0.42 (0.27,0.60)	0.43 (0.26,0.59)	1.32 (0.77,2.05)	1.30 (0.76,1.94)
		Perching	0.45 (0.31-0.62)	0.26 (0.08,0.51)	0.23 (0.08,0.50)	1.51 (0.76,2.61)	1.69 (0.77,2.66)
		Commuting	9.17 (7.42-11.26)	8.15 (5.51,10.54)	7.49 (4.19,9.97)	9.51 (7.12,11.88)	9.53 (6.85,11.82)
		Foraging	3.55 (1.99-5.39)	5.25 (2.39,8.59)	4.25 (2.06,7.11)	7.94 (2.59,10.79)	6.87 (1.82,10.57)
	Skokholm	Floating	0.34 (0.22-0.46)	0.52 (0.3,1.35)	0.54 (0.3,1.37)	1.66 (1.14,2.41)	1.62 (1.1,2.43)

Species	Colony	State	Trajectory			Instantaneous	
			HMM	EMBC			
				300	3600	300	3600
		Perching	1.49 (1.23-1.71)	0.24 (0.14,0.39)	0.24 (0.13,0.39)	1.47 (0.95,2.19)	1.45 (0.96,2.17)
		Commuting	9.43 (7.72-11.67)	8.76 (6.28,11.06)	8.58 (6.13,11.21)	10.14 (7.85,12.84)	10.05 (7.61,12.79)
		Foraging	1.49 (0.44-3.70)	4.53 (1.99,7.92)	4.64 (1.97,7.84)	7.06 (1.81,10.83)	7.03 (1.74,10.6)
	Orfordness	Floating	0.26 (0.15-0.37)	0.74 (0.48,0.95)	0.75 (0.51,0.93)	0.85 (0.6,1.13)	0.87 (0.63,1.14)
		Perching	0.81 (0.64-0.99)	0.63 (0.28,1)	0.65 (0.25,1.05)	0.95 (0.52,3.85)	0.89 (0.54,4.19)
		Commuting	9.65 (7.94-11.84)	8.59 (6.09,10.95)	8.07 (5.08,10.57)	9.7 (7.36,12.25)	9.37 (7.06,12.03)
		Foraging	2.41 (1.03-4.48)	5.67 (3.23,8.39)	5.67 (3.12,8.92)	7.69 (1.71,10.75)	7.98 (2.17,10.91)
Kittiwake	Flamborough Head to Bempton Cliffs	Floating		0.54		1.66 (1.01,2.57)	
		Stop		0.38		1.84 (0.96,3.82)	
		Commuting		7.58		9.73 (6.93,12.33)	
		Foraging		3.9		6.07 (1.85,9.46)	
Gannet	Flamborough Head to Bempton Cliffs	Floating		0.46		0.80 (0.55, 1.15)	
		Stop		0.5		1.04 (0.60,4.96)	
		Commuting		10.8		14.01 (11.13,16.44)	
		Foraging		6.29		10.79 (1.41,14.51)	

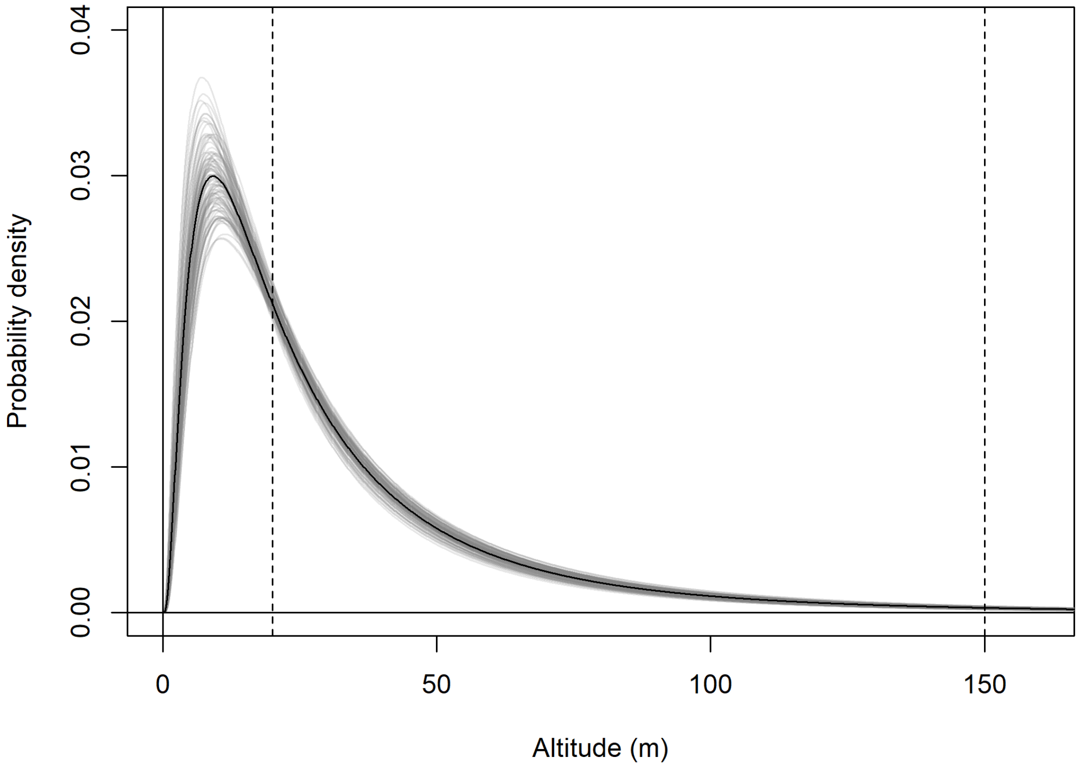
3.3. Flight height

3.3.1. Lesser black-backed gull

For lesser black-backed gull modelled flight height distributions, all parameters had R-hat values of <1.1 and chains had visually converged. There was correlation between the chains for mu and sd for each behavioural state or behavioural state:colony combination. There was a clear difference between modelled commuting and foraging/searching height distributions (Fig. 28). Whilst there was some overlap between these distributions, the bulk of foraging/searching flight was considerably lower than commuting flight.

The fitted flight height distributions were generally similar in shape between behaviours. The distribution for foraging flight was characterized by a low estimated mean, resulting in a peak in probability density close to zero metres. For commuting flight, the peak was at 9.2m.

a)



b)

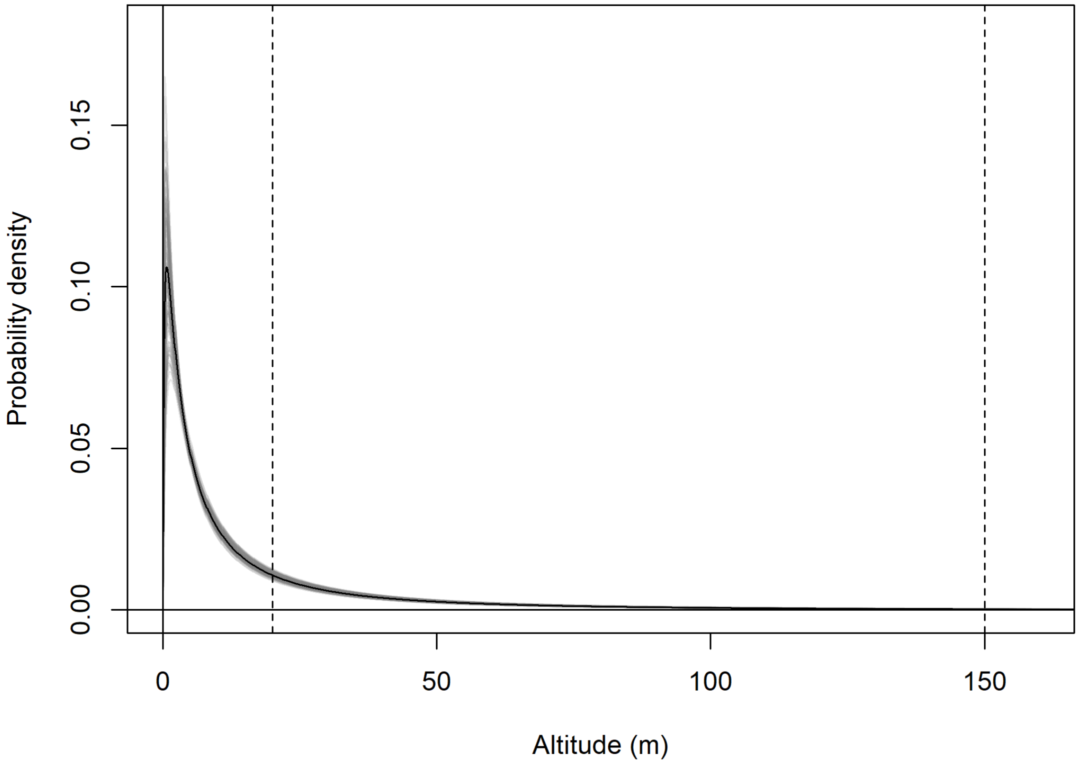


Figure 28 Modelled lesser black-backed gull flight height distributions: a) commuting; b) foraging/searching. Solid black line is lognormal probability density function based on mean estimates for mean and SD; grey lines are lognormal probability density functions based on 100 random paired draws of mean and SD from posterior distribution. Dashed lines delineate the 20-150m collision risk envelope.

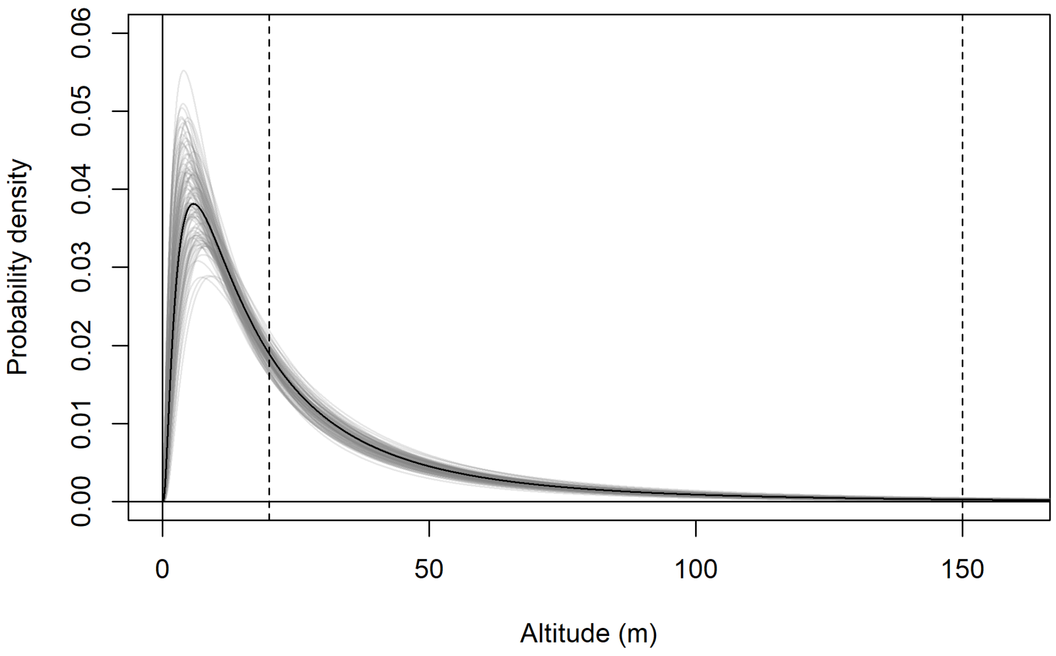
3.3.1.1. Inter-colony similarities

The modelled flight height distributions for lesser black-backed gull commuting height differed little between colonies (Figures 29 and 30; Table 16). Distributions had similar central tendency and overall shape. Individuals tagged at Orfordness typically had the lowest commuting flights, while individuals tagged at Skokholm had the highest.

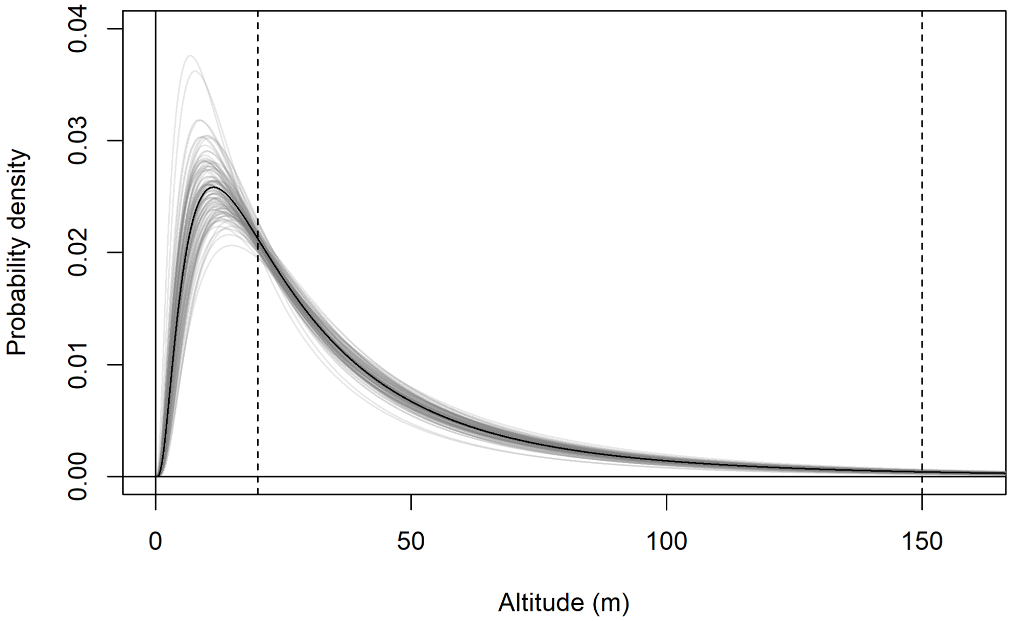
Likewise, the modelled flight height distributions for lesser black-backed gull foraging/searching height differed little in central tendency or shape between colonies (Figure 30; Table 16). However, the relative order of the foraging/searching flight height distributions for different colonies was different to that for commuting height: for foraging/searching flight, individuals tagged at Walney typically had the lowest flights, while individuals tagged at Orfordness typically had the highest. However, the foraging/searching flight height distribution for Orfordness was slightly narrower: the upper limit of the 95% credible interval was 13m and 35m lower than those for Walney and Skokholm, respectively.

The proportion of flight time at risk height followed the same patterns as for the modelled flight height distributions: they were generally similar among colonies (Table 17). For commuting flight, individuals tagged at Orfordness had the lowest proportion of flight time at risk height, while individuals from Skokholm had the highest. For foraging/searching flight, individuals tagged at Walney had the lowest proportion of flight time at risk height, while individuals from Orfordness had the lowest. For individuals tagged at Walney and Skokholm, the proportion of flight time at risk height was much greater for commuting flight than for foraging/searching flight; for individuals tagged at Orfordness the same pattern was evident, but the 95% credible interval for proportion of flight time at risk height overlapped between the behavioural states.

a)



b)



c)

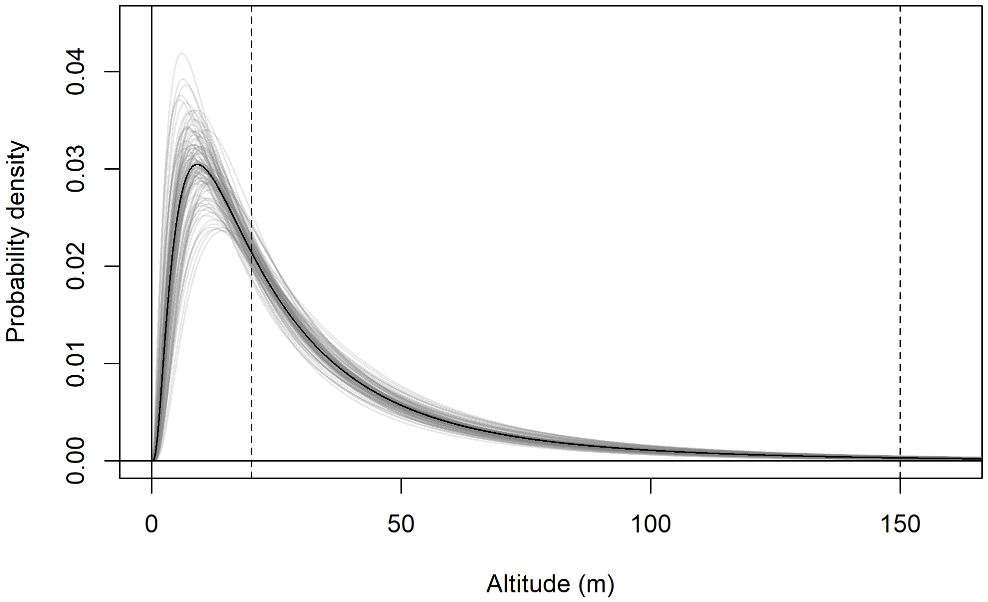
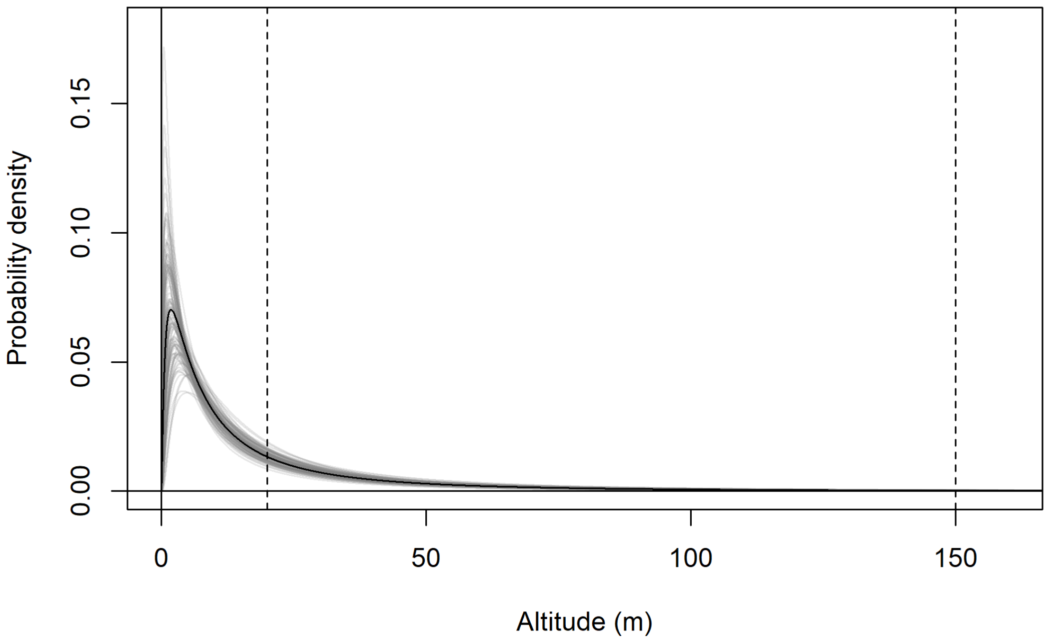
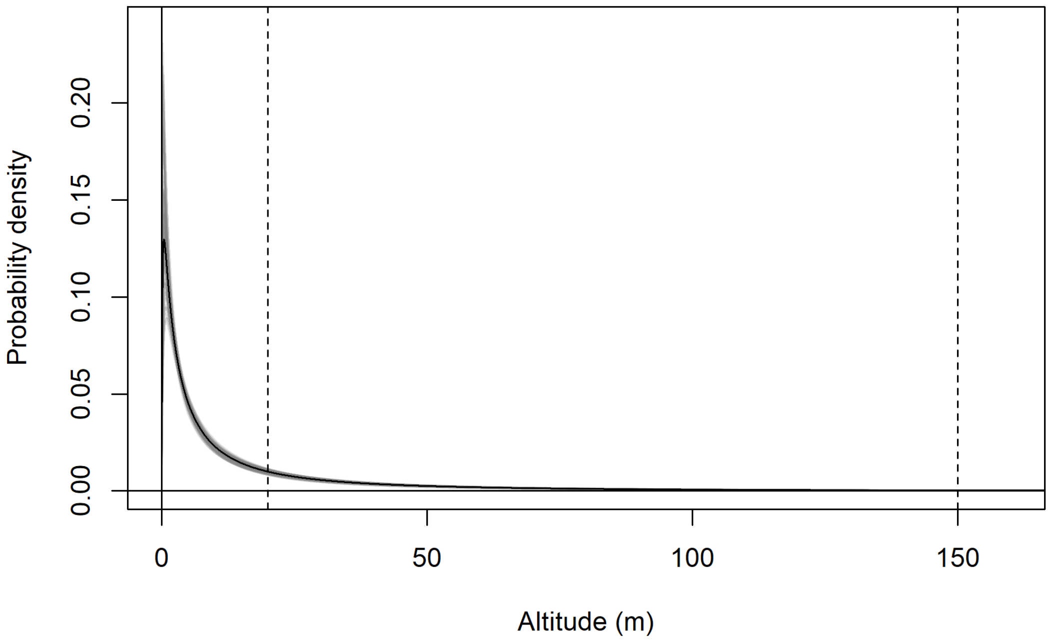


Figure 29 Modelled lesser black-backed gull commuting flight height distributions for: a) Orfordness; b) Skokholm; c) Walney. Black line is lognormal probability density function based on mean estimates for mean and SD; grey lines are lognormal probability density functions based on 100 random paired draws of mean and SD from posterior distribution. Dashed lines delineate the 20-150m risk envelope.

a)


Probability density
0.00
0.05
0.10
0.15
0
50
100
150
Altitude (m)

b)


Probability density
0.00
0.05
0.10
0.15
0.20
0
50
100
150
Altitude (m)

c)

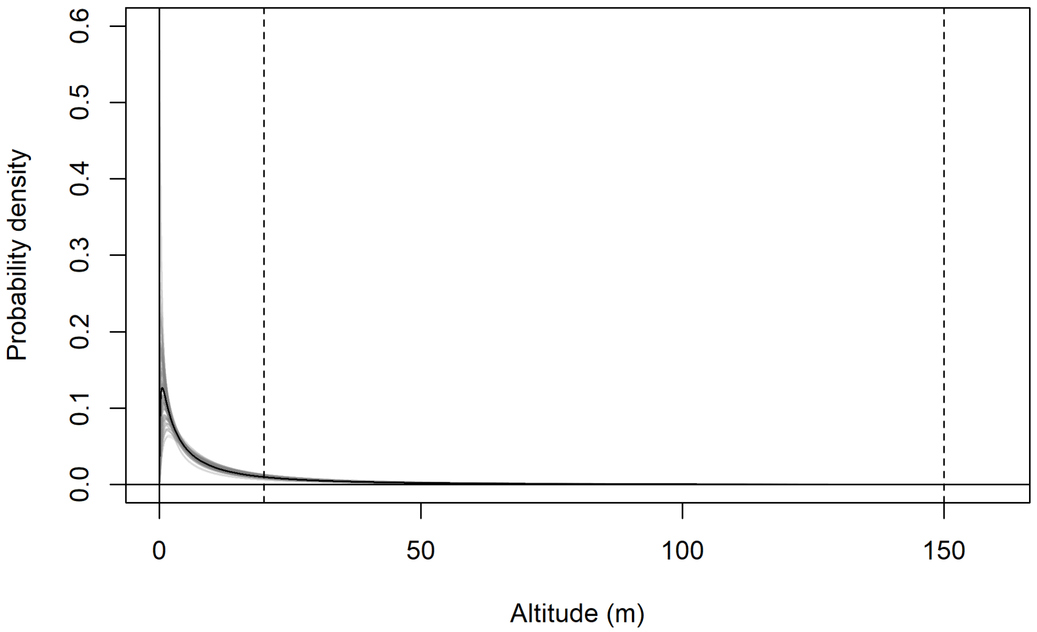


Figure 30 Modelled lesser black-backed gull foraging/searching flight height distributions for: a) Orfordness; b) Skokholm; c) Walney. Black line is lognormal probability density function based on mean estimates for mean and SD; grey lines are lognormal probability density functions based on 100 random paired draws of mean and SD from posterior distribution. Dashed lines delineate the 20-150m risk envelope.

Table 16 Modelled lesser black-backed gull flight height at the study colonies.

Colony	**Median flight height (m) (& 95% CI)**	
	Commuting flight	Foraging/searching
Orfordness	17.5 (0.4-99.0)	10.4 (0.0-89.7)
Skokholm	25.9 (1.1-114.9)	7.8 (0.0-124.7)
Walney	21.7 (1.0-102.5)	7.3 (0.0-102.7)

Table 17 Projected proportion of flight time in 20-150m collision risk envelope for lesser black-backed gull at the study colonies. 95% credible interval is calculated post-hoc, parameterizing the flight height cumulative density function with 100 paired draws of mean and SD from the posterior distribution.

Colony	**Projected % in 20-150m risk envelope (& 95% CI)**	
	Commuting flight	Foraging/searching
Orfordness	42.5 (34.0-50.3)	28.5 (20.1-37.6)
Skokholm	58.4 (49.9-65.8)	24.8 (20.4-28.1)
Walney	51.7 (42.6-61.7)	23.1 (17.8-30.2)

3.3.2. Kittiwake

Estimates of kittiwake flight heights were obtained using altimeters from 16 individuals on 117 foraging trips. In total, 4,790 data points were obtained. Analyses of these data are ongoing (Wischnewski, Sansom, et al., in prep.), consequently a small number of negative altitudes remain in the dataset, and it is important these data are included in any analyses of flight height to ensure all errors are accounted for in final modelled distributions (Péron et al., 2020). The maximum estimated flight height was 412 m above sea level, though most data were much closer to the sea surface with a median height estimate of 4.49 m above sea level (95% CIs 0 – 1.24), and 18% of flight activity within a theoretical 20-150m collision risk window (Wischnewski, Sansom, et al., in prep).

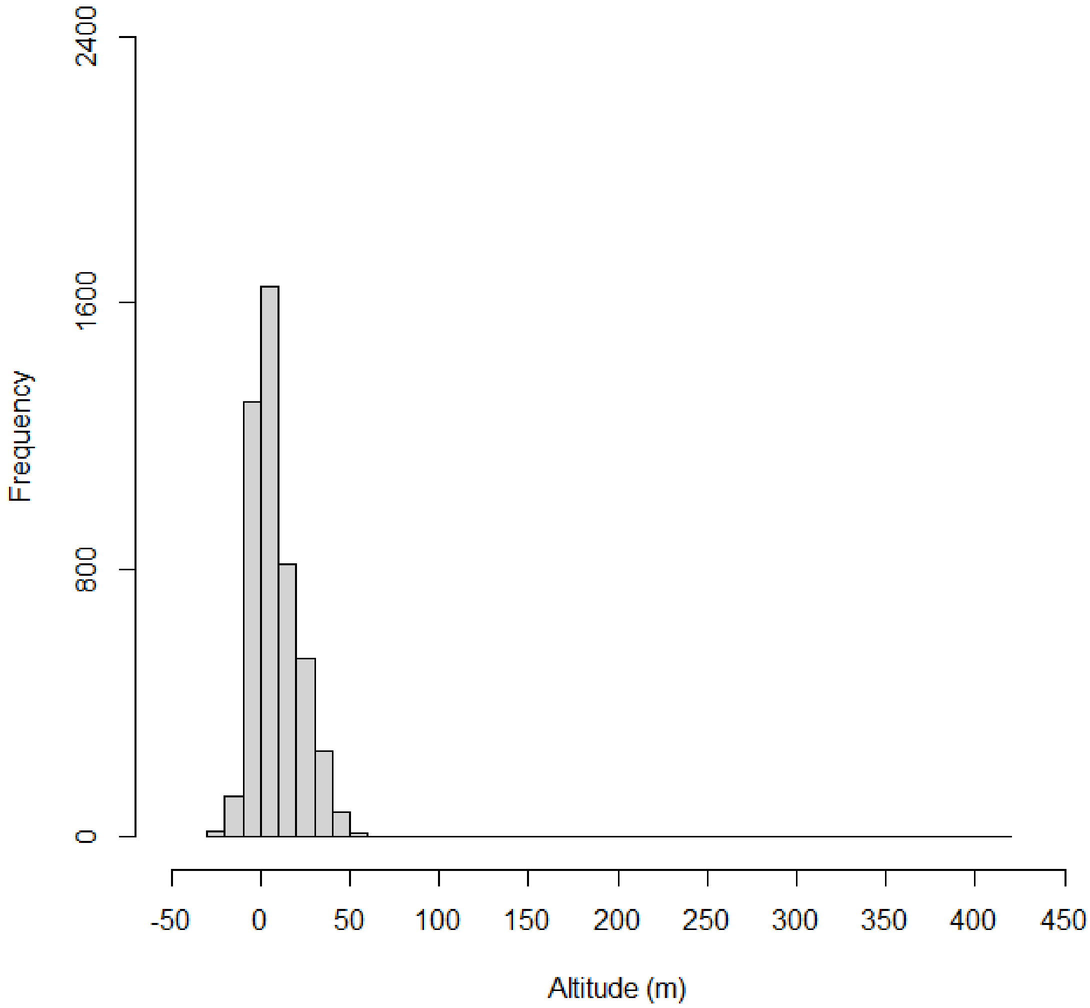


Figure 31 Flight height estimates obtained from altimeters deployed on kittiwakes at Flamborough Head and Bempton Cliffs.

Estimated flight heights during commuting were higher than those estimated during foraging (Figure 32, Table 18). Reflecting this, the proportion of flight activity at collision risk height during commuting flight was more than double that of the proportion at collision risk height during foraging activity (Table 19). Whilst the overall patterns in these data are likely to reflect the true patterns in flight heights (e.g., commuting birds fly higher than foraging birds), the reported values should be treated with caution as the error surrounding these estimates has not been properly quantified and accounted for in the modelling process, resulting in the negative estimates in flight height (Figures 31 & 32).

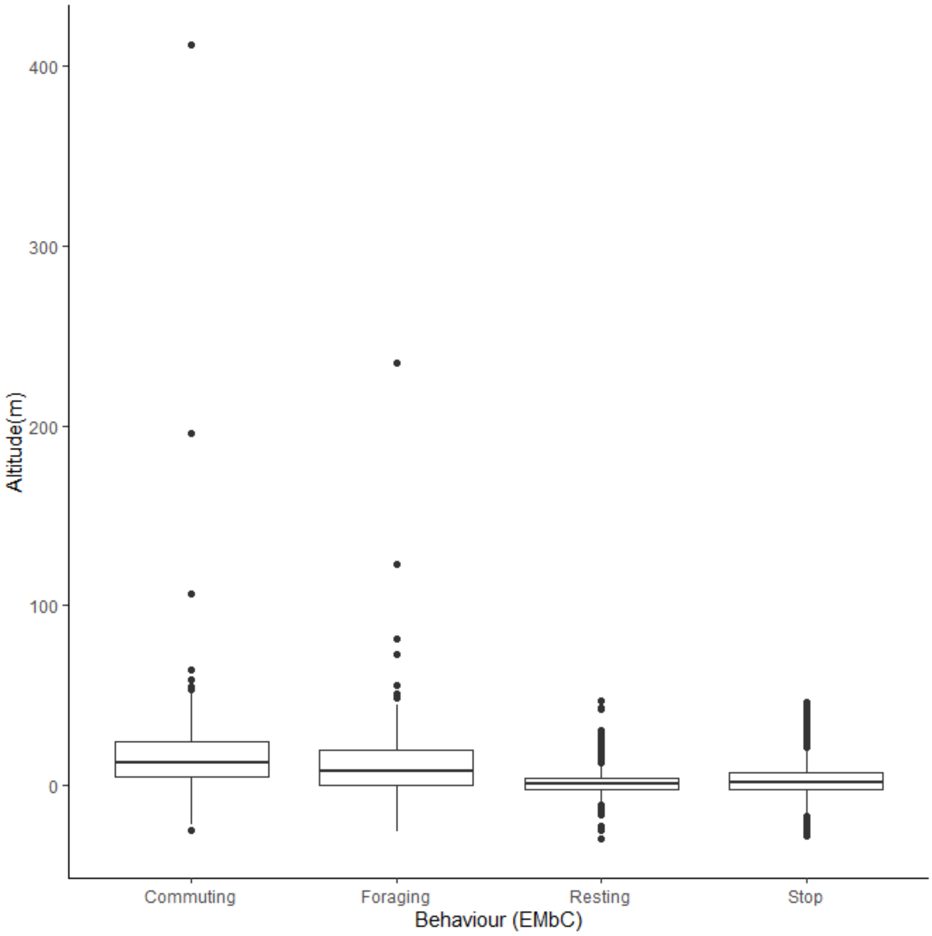


Figure 32 Flight height estimates for kittiwakes at Flamborough Head and Bempton Cliffs

Table 18 Estimated kittiwake flight heights at Flamborough Head and Bempton Cliffs

Colony	**Median flight height (m) (& 95% CI)**	
	Commuting flight	Foraging/searching
Flamborough Head and Bempton Cliffs	12.49 (4.84, 23.90)	7.44 (0.18,19.40)

Table 19 Projected proportion of flight time in 20-150m collision risk envelope for kittiwake at Flamborough Head and Bempton Cliffs.

Colony	**Projected % in 20-150m risk envelope**	
	Commuting flight	Foraging/searching
Flamborough Head and Bempton Cliffs	31	24

3.3.3. Gannet

Estimates of gannet flight heights were obtained using altimeters from 10 individuals on 278 foraging trips. In total, 32,484 data points were obtained. Analyses of these data are ongoing (Wischnewski, Sansom, et al., in prep.), consequently a small number of negative altitudes remain in the dataset, and it is important these data are included in any analyses of flight height to ensure all errors are accounted for in final modelled distributions (Péron et al., 2020). The maximum estimated flight height was 280 m above sea level, though most data were much closer to the sea surface with a median height estimate of 2.76 m above sea level (95% CIs 0 – 12.63), and 15% of flight activity within a theoretical 20-150m collision risk window (Wischnewski, Sansom, et al., in prep). The inclusion of negative flight heights in the data is likely to lead to an under-estimate of the median flight height. However, in this context, the primary interest is in the proportion of birds at collision risk height. As negative flight height records are likely to relate to birds flying below a turbine rotor sweep (Péron et al., 2020), excluding these data may result in an over-estimate of the proportion of birds at collision risk height.

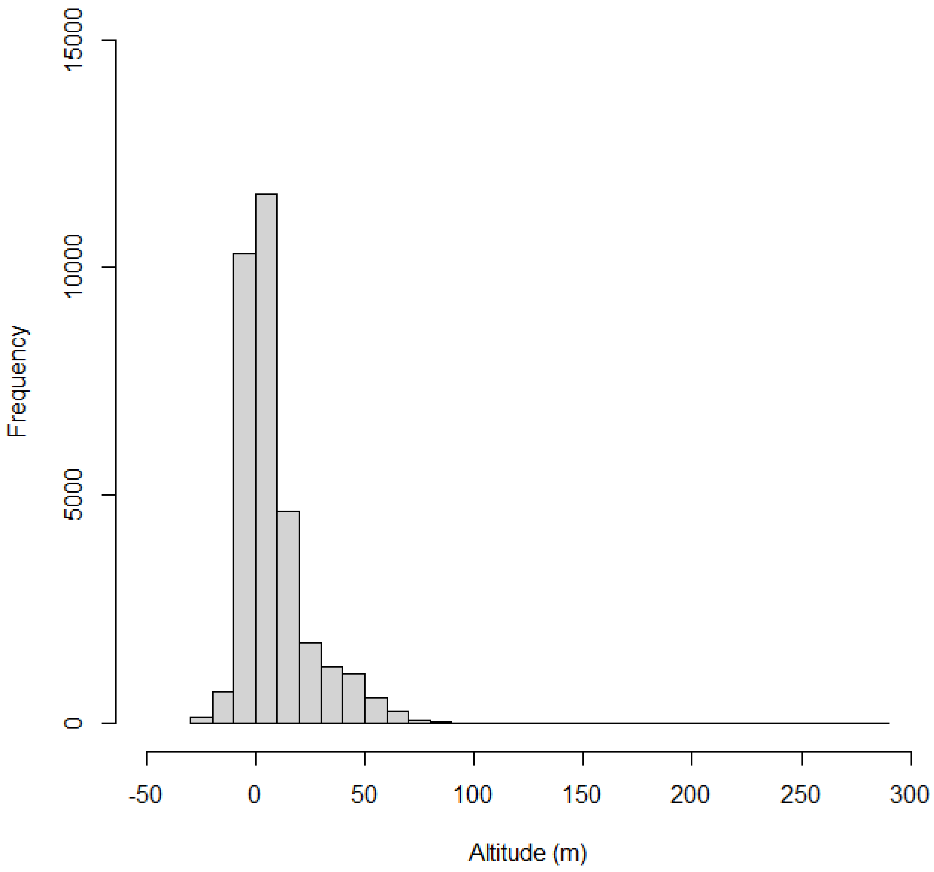


Figure 33 Flight height estimates obtained from altimeters deployed on gannets at Flamborough Head and Bempton Cliffs.

Estimated median flight heights during commuting were slightly higher than those estimated during foraging (Figure 34, Table 20). However, there was greater variability in foraging flight height than was the case for commuting flight, meaning that a slightly higher proportion of foraging flight took place at collision risk height (Table 21). Whilst the overall patterns in these data are likely to reflect the true patterns in flight heights (e.g., commuting birds fly higher than foraging birds), the reported values should be treated with caution as the error surrounding these estimates has not been properly quantified and accounted for in the modelling process, resulting in the negative estimates in flight height (Figures 33 & 34).

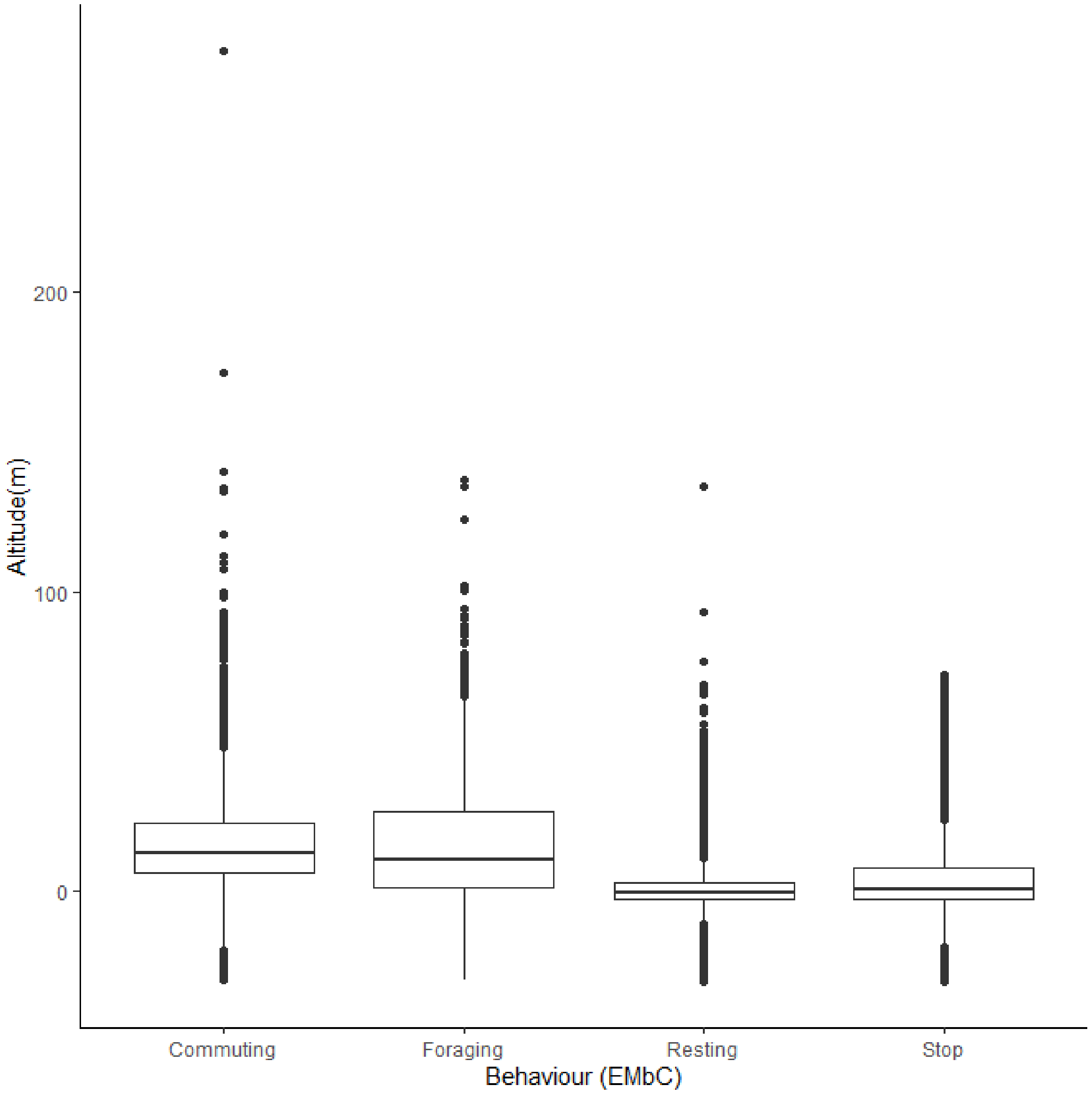


Figure 34 Flight height estimates for gannets at Flamborough Head and Bempton Cliffs

Table 20 Estimated gannet flight heights at Flamborough Head and Bempton Cliffs

Colony	**Median flight height (m) (& 95% CI)**	
	Commuting flight	Foraging/searching
Flamborough Head and Bempton Cliffs	12.8 (5.97,22.77)	10.78 (1.07,26.57)

Table 21 Projected proportion of flight time in 20-150m collision risk envelope for gannets at Flamborough Head and Bempton Cliffs.

Colony	**Projected % in 20-150m risk envelope**	
	Commuting flight	Foraging/searching
Flamborough Head and Bempton Cliffs	29	32

3.3.4. Flight Height Summary

For lesser black-backed gull and kittiwake, there were clear differences in the median flight heights estimated for commuting and foraging flight (Table 22). For gannet, there appeared to be greater overlap in foraging and commuting flight heights. Consistent with previous studies (A. Johnston et al., 2014), lesser black-backed gulls had higher flight heights than either gannet or kittiwake. Reflecting this, lesser black-backed gulls also spent a greater proportion of time within our projected 20-150m collision risk envelope than was the case for the other species (Table 23). Commuting flight heights were similar for gannet and kittiwake (Table 22). However, during foraging flight, gannets tended to fly higher than kittiwakes, spending a greater proportion of time at collision risk height.

Table 22 Modelled flight height for the study species.

Species	**Median flight height (m) (& 95% CI of flight height)**	
	Commuting flight	Foraging/searching
Lesser black-backed gull	22.1 (1.0-107.2)	8.2 (0.0-107.2)
Kittiwake	12.5 (4.8,23.9)	7.44 (0.18,19.40)
Gannet	12.8 (5.9, 22.7)	10.78 (1.07,26.57)

Table 23 Modelled proportion of flight time in 20-150m collision risk envelope for the study species. 95% credible interval is calculated post-hoc, parameterizing the flight height cumulative distribution function with 100 paired draws of posterior mean and SD estimates.

Species	**Projected % in 20-150m risk envelope (& 95% CI)**	
	Commuting flight	Foraging/searching
Lesser black-backed gull	52.1 (45.8-57.6)	25.2 (21.7-29.5)
Kittiwake	31	24
Gannet	29	32

4. Discussion

At present, there are significant uncertainties surrounding input parameters for collision risk models (Masden et al., 2021), meaning that precautionary values must be used in assessments. The uncertainty, and resultant precaution, can be reduced through the collection of better data to parameterize these models. GPS data offer the potential to do this. Our analyses demonstrate how GPS data can be used to generate estimates of nocturnal activity, flight height and flight speed. However, these parameters vary among behavioural states, and can vary among colonies and through time.

4.1. Nocturnal Activity

At present, the recommended values for nocturnal activity are based on the rankings presented in Garthe & Hüppop (2004) with scores of 1-5 reflecting activity levels of 0, 25, 50, 75 and 100% of day time activity (Band, 2012). Based on the rankings from Garthe & Hüppop(2004), nocturnal activity levels for lesser black-backed gull and kittiwake were 50% of daytime activity levels, and for gannet, it was 25% (Table 24).

Table 24 Comparison of nocturnal activity levels estimated in the present study with those currently recommended for use in the Band (2012) model.

	Current recommendation	Estimate from GPS data
Lesser black-backed gull	50%	7-41%
Gannet	25%	4-31%
Kittiwake	50%	17-63%

Previous analysis of data from gannets suggests that actual levels of nocturnal activity may be lower than that recommended in current guidance (Furness et al., 2018). Of the datasets considered in Furness et al. (2018), the 2013 data from Alderney were also considered in our analysis. Our estimate of nocturnal activity from that dataset (24%) was higher than the value presented in Furness et al. (2018) from the same dataset (15.6%). This difference is likely to have arisen due to the fact that the classification in Furness et al. (2018) was based on flight speed only, whilst in our study classifications were based on behaviour inferred from EMbC and likely to be more reflective of activity estimates than those based on point estimates of speed.

Nocturnal activity levels for all three species were found to vary among years and sites (Table 24; Figures 4,6 and 8). Understanding the reasons for these differences in gannets and kittiwakes is complicated by the fact that data were collected using both IGotU and UvA tags. The data from IGotU tags were collected over 2-3 days, typically around the start of chick-rearing, and consequently may not be representative of the breeding season as a whole. The UvA data are collected over a longer time period, so may be more representative of nocturnal activity over the breeding season as a whole. However, kittiwake data were collected from Flamborough Head and Bempton Cliffs using IGotU tags from 2010 – 2015 and using UvA tags in 2017 and 2018. Estimates of nocturnal activity from the IGotU tags were not inconsistent with those obtained using UvA tags (Figure 6). This suggests that the data collected using the IGotU tags may be representative of the wider chick-rearing period. However, such a comparison is only possible for kittiwakes at Flamborough Head and Bempton Cliffs as this was the only species-site combination for which data from both tag types was available.

For all three species, the proportion of time spent active at night was broadly consistent between sites and years, but there was more variation in the proportion of time spent active during the day (Figures 5, 7 and 9). This may reflect differences in foraging areas between years and colonies. For example, kittiwakes at Rathlin Island showed substantial differences in foraging ranges between 2009 and 2010 (Chivers et al., 2012). If foraging activity is concentrated in daylight hours, then in years when birds have to travel further in order to access sufficient resources to successfully fledge young, the proportion of time birds spend active at night relative to the proportion of time spent active during the day is likely to be reduced. This highlights the importance of considering wider environmental conditions when assessing the proportion of time birds spend active at night. Such an understanding is crucial to determining the potential transferability of estimates of nocturnal activity between sites.

4.2. Flight Speed

Flight speed is used twice in the Band (2012) Collision Risk Model, firstly to estimate the flux rate, and secondly to estimate the probability of collision. Consequently, the model is sensitive to estimates used for flight speed, especially in relation to the flux rate (Masden et al., 2021). At present, recommended estimates for flight speed are based on generic values (e.g. Alerstam et al., 2007; Pennycuick, 1997) collected during a limited range of conditions, and often based on limited sample sizes. Our analysis suggests that typical flight speeds may be lower than those reported in these previous studies, which are often collected in areas which may not be representative of conditions experienced offshore (Alerstam et al., 2007; Pennycuick, 1997). Accounting for these differences can result in a substantial reduction in the predicted collision rate (Masden et al., 2021).

For all three species, commuting speeds were faster than foraging speeds. In the context of the Band (2012) Collision Risk Model, this means that the estimated probability of collision will be higher for foraging birds, but the flux rate will be higher for commuting birds. However, whilst the impacts of flight speed on the probability of collision and flux rate act in opposite directions, these do not cancel one another out (Masden et al., 2021). Consequently, collision rates based on commuting speeds will be greater than those based on foraging speeds. At present, average speeds combining both commuting and foraging flight are used in collision modelling, but it may be possible to account for these differences through modifications to the model.

In previous analyses, estimates of foraging and commuting speeds were derived from the step lengths estimated from Hidden Markov Models (Thaxter et al., 2019). Further analysis of data from lesser black-backed gulls demonstrates that there is strong correlation between the trajectory speeds estimated using EMbC and the instantaneous speeds estimated from GPS for both foraging and commuting flight (Figures 15, 18, 22). As might be expected, correlations were strongest for the fastest sampling rates. However, despite these strong correlations, there was a systematic bias, with the estimated trajectory speeds slower than the instantaneous speeds.

4.3. Flight Height

4.3.1. Overall conclusions

For lesser black-backed gull and kittiwake, we found that commuting flight tended to be higher than foraging flight (Table 22). This is consistent with previous findings for lesser black-backed gull (Corman & Garthe, 2014). For gannet, flight heights were similar for both foraging and commuting flights (Table 20). However, the “stop” behaviour may also reflect finer scale foraging as it is characterized by tracks with high tortuosity and low speed. Flight heights for the “stopped” behaviour were at, or close to the sea surface (Figure 34). The nuances of these different foraging behaviours, and their implications for collision risk, would benefit from further investigation.

For lesser black-backed gulls, we found that estimated flight heights were broadly similar among colonies for foraging flight, but that there were greater differences among colonies in relation to commuting flight height (Tables 16 & 17). Birds from Orfordness had lower median flight heights and spent a lower proportion of their time at collision risk height during commuting flights than was the case for birds from Walney or Skokholm. Similarly, gannets considered in our analyses from Flamborough and Bempton Cliffs had lower estimated heights for both foraging and commuting flight than was the case for birds from the Bass Rock (Cleasby et al., 2015). These data highlight the potential for differences in flight heights among sites, especially in relation to commuting flight.

Flight heights have previously been reported for these species measured using approaches including GPS (Corman & Garthe, 2014; Ross-Smith et al., 2016), altimeter (Cleasby et al., 2015), laser rangefinder (Borkenhagen et al., 2018; Harwood et al., 2018) and LiDAR (Cook et al., 2018). Analyses of these data have highlighted the potential for spatial and temporal variation in species flight heights. Our analyses highlight how some of this variation may be linked to behaviour in any given place at any given time. Where flight heights are estimated from survey data, it may be possible to use the outputs from our analyses to identify areas where birds are likely to be foraging or commuting. However, this must be done with caution. There are differences between flight heights estimated using different methodologies, although, it is unclear the extent to which these reflect genuine differences in flight heights as a result of spatial or temporal patterns, or differences in the bias, error, and precision with which these measurements are made, and further research is needed to properly understand this.

4.3.2. Limitations

We identified negative bias in GPS altitudes for lesser black-backed gulls tagged at North Sea colonies and addressed this by adjusting the data. However, it is not known whether the adjustments made fully resolved the bias. Most importantly, any uncertainty in the mean bias was not carried forward into the remainder of the analysis, and future studies should aim to explicitly model any potential GPS data biases within the observation error model. The modelled commuting heights for lesser black-backed gulls tagged at Orfordness were lower than those for individuals from colonies in the Irish Sea. By exploring precisely how

GPS altitudes were calculated, future work could determine whether there is any remaining altitude bias in the data, and whether any remaining apparent altitude bias has an ecological cause.

4.4. Implications for assessment of collision risk

Of the parameters considered here, flight speed appears to be reasonably consistent among colonies, at least in the case of lesser black-backed gulls (Table 15). However, there appears to be more variation in both nocturnal activity and flight height among colonies. Consequently, if GPS data are to be used to assess parameters used in collision risk modelling, this may need to be done on a site-specific basis, particularly in relation to the estimation of commuting flight heights.

Estimates of collision risk based on GPS data are likely to be greater in areas used for commuting than those used for foraging. In part, this reflects the behaviour of the birds, with a higher proportion of commuting birds at collision risk height than is the case for foraging birds. However, it also reflects the model assumptions and is driven by the influence of flight speed in the estimation of the flux rate (Masden et al., 2021). This highlights a key challenge in the use of GPS data in the Band (2012) Collision Risk Model. Avoidance rates are estimated by comparing observed collision rates to those predicted in the absence of any avoidance behaviour. Consequently, these account for both the behaviour of the birds and any errors in how collision rates are estimated. Flight speed strongly influences the estimation of the flux rate, and therefore predicted collision rate. At present, the predicted collision rate in the absence of avoidance behaviour is derived using generic estimates of flight speed (e.g. Alerstam et al., 2007), which are often substantially faster than those estimated using GPS for both foraging and commuting flight, regardless of whether these have been derived from instantaneous or trajectory speeds. This means that flux rates, and therefore collision rates, estimated using generic flight speed estimates will be higher than those estimated using GPS flight speed estimates for both foraging and commuting flights, and that the over-estimation will be greatest in areas used for foraging. As a result, avoidance rates (based on comparisons of predicted and observed collision rates) derived from generic flight speeds would be higher than those based on the GPS speeds. Given the difference between foraging and commuting flight speeds, and the difference in flight heights between the two behaviours, this is also likely to mean that incorporating behaviour into collision risk models may also require the estimation of different avoidance rates.

5. Acknowledgements

This project was funded by the Scottish Government and Crown Estate Scotland. We wish to thank Marine Scotland and the project steering group for support and guidance throughout this project.

The project would not have been possible without the collaboration of others who supplied data. We thank the RSPB for supplying data collected as part of the FAME and STAR projects. The Gannet and Kittiwake tracking data from Bempton Cliffs collected by RSPB on behalf of Ørsted and supplied by Lucy Wright. Francis Daunt (CEH) supplied data for Kittiwakes from the Isle of May. Keith Hamer (University of Leeds) supplied data for Gannets from the Bass Rock and Jon Green (University of Liverpool) supplied Gannet data collected from Alderney in collaboration with the Alderney Wildlife Trust and its' Track A Gannet programme and additional data from Puffin Island. Lesser Black-backed Gull data were collected by BTO as part of projects funded by the Department for Business, Energy and Industrial Strategy (BEIS) Offshore Energy Strategic Environmental Assessment research programme and Ørsted.

6. References

Alerstam, T., Rosén, M., Bäckman, J., Ericson, P. G. P., & Hellgren, O. (2007). Flight Speeds among Bird Species: Allometric and Phylogenetic Effects. *PLoS Biology*, *5*(8), e197. https://doi.org/10.1371/journal.pbio.0050197

Babcock, M., Aitken, D., Lloyd, I., Wischnewski, S., & Barratt. (2018). *Flamborough and Filey Coast SPA Seabird Monitoring Programme 2018 Report*.

Band, B. (2012). Using a collision risk model to assess bird collision risks for offshore wind farms. Retrieved August 23, 2017, from https://www.bto.org/sites/default/files/u28/downloads/Projects/Final_Report_SOSS02_Band1ModelGuidance.pdf

Band, W. (2012). Using a collision risk model to assess bird collision risks for offshore windfarms. SOSS, The Crown Estate, London, UK.

Band, W., Madders, M., & Whitfield, D. P. (2007). Developing field and analytical methods to assess avian collision risk at Wind Farms. In M. de Lucas, G. F. E. Janss, & M. Ferrer (Eds.), *Birds and wind farms: risk assessment and mitigation*. Madrid: Quercus.

Bivand, R., & Lewin-Koh, N. (2021). maptools: Handling Spatial Objects. R package version 1.1-2. Retrieved from https://cran.r-project.org/package=maptools

Bodey, T. W., Cleasby, I. R., Bell, F., Parr, N., Schultz, A., Votier, S. C., & Bearhop, S. (2018). A phylogenetically controlled meta-analysis of biologging device effects on birds: Deleterious effects and a call for more standardized reporting of study data. *Methods in Ecology and Evolution*, *9*(4), 946–955. https://doi.org/10.1111/2041-210X.12934

Borkenhagen, K., Corman, A.-M., & Garthe, S. (2018). Estimating flight heights of seabirds using optical rangefinders and GPS data loggers: a methodological comparison. *Marine Biology*, *165*(1), 17. https://doi.org/10.1007/s00227-017-3273-z

Brooks, M. E., Kristensen, K., van Bentham, K. J., Magnusson, A., Berg, C. W., Nielsen, A., … Bolker, B. M. (2017). glmmTMB Balances speed and flexibility among packages for zero-inflated Generalized Linear Mixed Modelling. *The R Journal*, *9*, 378–400.

Chamberlain, D. E., Rehfisch, M. R., Fox, A. D., Desholm, M., & Anthony, S. J. (2006). The effect of avoidance rates on bird mortality predictions made by wind turbine collision risk models. *Ibis*, *148*, 198–202.

Chivers, L. S., Lundy, M. G., Colhoun, K., Newton, S. F., Houghton, J. D. R., & Reid, N. (2012). Foraging trip time-activity budgets and reproductive success in the black-legged kittiwake. *Marine Ecology Progress Series*, *456*, 269–277. https://doi.org/10.3354/MEPS09691

Cleasby, I. R., Morrissey, B. J., Bolton, M., Owen, E., Wilson, L., Wischnewski, S., & Nakagawa, S. (2021). What is our power to detect device effects in animal tracking studies? *Methods in Ecology and Evolution*, *12*(7), 1174–1185. https://doi.org/10.1111/2041-210X.13598

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 wind farms. *Journal of Applied Ecology*, *52*(6), 1474–1482. https://doi.org/10.1111/1365-2664.12529

Clewley, G. D., Clark, N. A., Thaxter, C. B., Green, R. M., Scragg, E. S., & Burton, N. H. K. (2021). Development of a weak-link wing harness for use on large gulls (Laridae): methodology, evaluation and recommendations. *Seabird*, *33*, 18–34.

Cook, A.S.C.P., Ward, R. M., Hansen, W. S., & Larsen, L. (2018). Estimating Seabird Flight Height Using LiDAR. *Scottish Marine and Freshwater Science*, *9*(14). Retrieved from https://data.marine.gov.scot/dataset/estimating-seabird-flight-height-using-lidar

Cook, A S C P, Humphreys, E. M., Masden, E. A., & Burton, N. H. K. (2014). *The Avoidance Rates of Collision Between Birds and Offshore Turbines*. Edinburgh. Retrieved from http://www.gov.scot/Resource/0046/00464979.pdf

Cook, Aonghais S.C.P., Humphreys, E. M., Bennet, F., Masden, E. A., & Burton, N. H. K. (2018). Quantifying avian avoidance of offshore wind turbines: Current evidence and key knowledge gaps. *Marine Environmental Research*, *140*, 278–288. https://doi.org/10.1016/J.MARENVRES.2018.06.017

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. https://doi.org/10.1007/s10336-014-1094-0

Evans, T. J., Young, R. C., Watson, H., Olsson, O., & Åkesson, S. (2020). Effects of back-mounted biologgers on condition, diving and flight performance in a breeding seabird. *Journal of Avian Biology*, *51*(11). https://doi.org/10.1111/JAV.02509

Fijn, R. C., & Gyimesi, A. (2018). Behaviour related flight speeds of Sandwich Terns and their implications for wind farm collision rate modelling and impact assessment. *Environmental Impact Assessment Review*, *71*, 12–16. https://doi.org/10.1016/J.EIAR.2018.03.007

Forsythe, W. C., Rykiel, E. J., Stahl, R. S., Wu, H., & Schoolfield, R. M. (1995). A model comparison for daylength as a function of latitude and day of year. *Ecological Modelling*, *80*(1), 89–75.

Furness, R. W., Garthe, S., Trinder, M., Matthiopoulos, J., Wanless, S., & Jeglinski, J. (2018). Nocturnal flight activity of northern gannets Morus bassanus and implications for modelling collision risk at offshore wind farms. *Environmental Impact Assessment Review*, *73*, 1–6. https://doi.org/10.1016/J.EIAR.2018.06.006

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. https://doi.org/10.1016/j.jenvman.2013.01.025

Garriga, J., Palmer, J. R. B., Oltra, A., & Bartumeus, F. (2016). Expectation-Maximization Binary Clustering for Behavioural Annotation. *PLOS ONE*, *11*(3), e0151984. https://doi.org/10.1371/JOURNAL.PONE.0151984

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*(4), 724–734.

Garthe, Stefan, & Huppop, O. (2004). Scaling possible adverse effects of marine wind farms on seabirds: Developing and applying a vulnerability index. *Journal of Applied Ecology*, *41*(4), 724–734. https://doi.org/10.1111/j.0021-8901.2004.00918.x

Hartig, F. (2022). DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models. R Package version 0.4.5. Retrieved from https://cran.r-project.org/package=DHARMa

Harwood, A. J. P., Perrow, M. R., & Berridge, R. J. (2018). Use of an optical rangefinder to assess the reliability of seabird flight heights from boat-based surveyors: implications for collision risk at offshore wind farms. *Journal of Field Ornithology*. https://doi.org/10.1111/jofo.12269

Johnson, D. S., London, J. M., Lea, M. A., & Durban, J. W. (2008). CONTINUOUS-TIME CORRELATED RANDOM WALK MODEL FOR ANIMAL TELEMETRY DATA. *Ecology*, *89*(5), 1208–1215. https://doi.org/10.1890/07-1032.1

Johnston, A., & Cook, A. S. C. P. (2016). *How high do birds fly? Development of methods and analysis of digital aerial data of seabird flight heights. BTO Research Report No. 676*. Thetford. Retrieved from https://www.bto.org/research-data-services/publications/research-reports/2016/how-high-do-birds-fly-development-methods

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*(1), 31–41. https://doi.org/10.1111/1365-2664.12191

Johnston, D., Thaxter, C., Boersch-Supan, P., Humphreys, E., Bouten, W., Clewley, G., … Cook, A. (2021). Investigating avoidance and attraction responses in lesser black-backed gulls Larus fuscus to offshore wind farms. *Marine Ecology Progress Series*. https://doi.org/10.3354/MEPS13964

Klaassen, R. H. G., Hake, M., Strandberg, R., & Alerstam, T. (2011). Geographical and temporal flexibility in the response to crosswinds by migrating raptors. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1710), 1339–1346. https://doi.org/10.1098/RSPB.2010.2106

Largey, N., Cook, A. S. C. P., Thaxter, C. B., McCluskie, A., Stokke, Bå. G., Wilson, B., & Masden, E. A. (2021). Methods to quantify avian airspace use in relation to wind energy development. *Ibis*. Blackwell Publishing Ltd. https://doi.org/10.1111/ibi.12913

Lenth, R. V. (2022). emmeans: Estimated Marginal Means, aka Least-squares means. R package version 1.7.2.

Mallory, M. L., & Gilbert, C. D. (2008). Leg-loop harness design for attaching external transmitters to seabirds. *Marine Ornithology*, *36*, 183–188. Retrieved from http://www.marineornithology.org/content/get.cgi?rn=788

Masden, E. A. (2015). *Developing an avian collision risk model to incorporate variability and uncertainty*. Edinburgh: Scottish Government.

Masden, E. A., & Cook, A. S. C. P. (2016). Avian collision risk models for wind energy impact assessments. *Environmental Impact Assessment Review*, *56*, 43–49. https://doi.org/10.1016/j.eiar.2015.09.001

Masden, E. A., Cook, A. S. C. P., McCluskie, A., Bouten, W., Burton, N. H. K., & Thaxter, C. B. (2021). When speed matters: The importance of flight speed in an avian collision risk model. *Environmental Impact Assessment Review*, *90*, 106622. https://doi.org/10.1016/j.eiar.2021.106622

Masden, E. A., McCluskie, A., Owen, E., & Langston, R. H. W. (2015). Renewable energy developments in an uncertain world: The case of offshore wind and birds in the UK. *Marine Policy*, *51*, 169–172. https://doi.org/10.1016/j.marpol.2014.08.006

McClintock, B. T., & Michelot, T. (2018). momentuHMM: R package for generalized hidden Markov models of animal movement. *Methods in Ecology and Evolution*, *9*(6), 1518–1530. https://doi.org/10.1111/2041-210X.12995

McGregor, R., King, S., Donovan, C. R., Caneco, B., Webb, A., Webb, A., & Wilson Marine Scotland Science JaredWilson, J. (2018). *A Stochastic Collision Risk Model for Seabirds in Flight Authorisations Responsibility Name Signature Date Distribution List Name Organisation Email Address*. Retrieved from https://www.gov.scot/Resource/0053/00536606.pdf

Pennycuick, C. (1997). Actual and "optimum" flight speeds: field data reassessed. *Journal of Experimental Biology*, *200*(17).

Péron, G., Calabrese, J. M., Duriez, O., Fleming, C. H., García-Jiménez, R., Johnston, A., … Shepard, E. L. C. (2020). The challenges of estimating the distribution of flight heights from telemetry or altimetry data. *Animal Biotelemetry*, *8*(1), 1–13. https://doi.org/10.1186/s40317-020-00194-z

Ross-Smith, V. H., Thaxter, C. B., Masden, E. A., Shamoun-Baranes, J., Burton, N. H. K., Wright, L. J., … Johnston, A. (2016). Modelling flight heights of lesser black-backed gulls and great skuas from GPS: a Bayesian approach. *Journal of Applied Ecology*, *53*(6), 1676–1685. https://doi.org/10.1111/1365-2664.12760

Schaub, T., Klaassen, R. H. G., Bouten, W., Schlaich, A. E., & Koks, B. J. (2019). Collision risk of Montagu's Harriers *Circus pygargus* with wind turbines derived from high-resolution <scp>GPS</scp> tracking. *Ibis*, ibi.12788. https://doi.org/10.1111/ibi.12788

Searle, K., Butler, A., Mobbs, D., Trinder, M., McGregor, R., Cook, A., … Daunt, F. (n.d.). *Study to examine how seabird collision risk, displacement and barrier effects could be integrated for assessment of offshore wind developments*.

Seward, A., Taylor, R. C., Perrow, M. R., Berridge, R. J., Bowgen, K. M., Dodd, S., … Bolton, M. (2021). Effect of GPS tagging on behaviour and marine distribution of breeding Arctic Terns Sterna paradisaea. *Ibis*, *163*(1), 197–212. https://doi.org/10.1111/IBI.12849

Skov, H., Heinänen, S., Norman, T., Ward, R. M., & Méndez-Roldán, S. Ellis, I. (2018). *ORJIP Bird Collision and Avoidance Study. Final report*. United Kingdom.

Thaxter, C. B., Johnston, D. T., Clewley, G. D., Humphreys, E. M., & Cook, A. S. C. . (2019). *Improving our understanding of seabird behaviour at sea*.

Thaxter, Chris 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: A case study of lesser black-backed gull Larus fuscus in the UK. *Biological Conservation*, *186*, 347–358. https://doi.org/10.1016/j.biocon.2015.03.027

Thaxter, Chris B., Ross-Smith, V. H., Clark, J. A., Clark, N. A., Conway, G. J., Marsh, M., … Burton, N. H. K. (2014). A trial of three harness attachment methods and their suitability for long-term use on Lesser Black-backed Gulls and Great Skuas. *Ringing and Migration*, *29*(2), 65–76. https://doi.org/10.1080/03078698.2014.995546

Thaxter, Chris B., Ross-Smith, V. H., Clark, J. A., Clark, N. A., Conway, G. J., Masden, E. A., … 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*(2), 279–290. https://doi.org/10.1111/ibi.12340

Tjomlov, R. S., Skov, H., Armitage, M., Barker, M., Cuttat, F., & Thomas, K. (2021). *Resolving key uncertainties of seabird flight and avoidance behaviours at offshore wind farms. Annual Report for April 2020 to October 2020. Report to AOWFL.*

Toke, D. (2011). The UK offshore wind power programme: A sea-change in UK energy policy? *Energy Policy*, *39*(2), 526–534. https://doi.org/10.1016/j.enpol.2010.08.043

Wakefield, E. D., Owen, E., Baer, J., Carroll, M. J., Daunt, F., Dodd, S. G., … Bolton, M. (2017). Breeding density, fine-scale tracking, and large-scale modeling reveal the regional distribution of four seabird species. *Ecological Applications*, *27*(7), 2074–2091. https://doi.org/10.1002/eap.1591

Wischnewski, S., McCluskie, A., Bouten, W., Adlard, S., Babcock, M., & Wright, L. J. (n.d.). Plasticity in offshore space-use and behaviour across time governs the susceptibility of seabirds to offshore wind farms.

Wischnewski, S., Sansom, A., McCluskie, A., Bouten, W., Adlard, S., Aitken, D., … Wright, L. J. (n.d.). Temporal and spatial patterns in the offshore behaviour and distribution of kittiwakes: Lessons for Marine Spatial Planning.

7. Appendix 1: Workshop Summaries

Part 1: Data Collection

Attendees: Aonghais Cook (BTO), Daniel Johnston (BTO), Gary Clewley (BTO), Liz Humphreys (BTO), Chris Thaxter (BTO), Jacob Davies (BTO), Philipp Boersch Supan (BTO), Aly McCluskie (RSPB), Lucy Wright (RSPB), Ian Cleasby (RSPB), Saskia Wischnewski (RSPB), Francis Daunt (UKCEH), Alex Robbins (NatureScot), Martin Perrow (ECON), Sean Sweeney (APEM), Tim Kasoar (APEM), Matt Hazleton (NIRAS), Ross MacGregor (MacArthur Green), Mark Trinder (MacArthur Green), Drew Milne (Marine Scotland), Tom Evans (Marine Scotland)

Device attachment

Before deploying a bird-mounted device such as a GPS tag, permission must be obtained from the Special Methods Technical Panel (SMTP) of the BTO Ringing Committee. To enable SMTP to properly evaluate proposals, and respond to any feedback, it is recommended that all applications are submitted at least three months prior to the deployment of any devices. A number of approaches to attach GPS tags, or other devices, to birds exist including, leg or ring mounting, tape mounting to a birds' tail or back, glue mounting to a birds' back and using a leg-loop or backpack harness (e.g. Clewley et al., 2021; Evans et al., 2020; Mallory & Gilbert, 2008; Seward et al., 2021). Attachment times for these methods vary from c. 5 minutes for more simple methods to c. 10-20 minutes for more complex approaches (Figure 1).

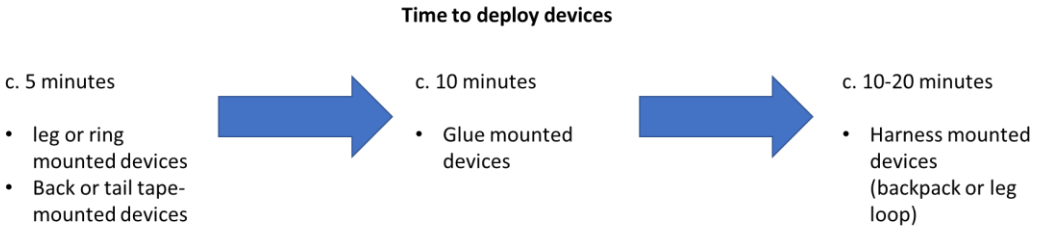


Figure 1 Typical time required to deploy a bird-mounted device using different attachment methodologies.

The most appropriate attachment methodology will depend on the species and objectives of any study. Attachment methodologies vary in their longevity (Figure 2). Generally, tape-mounted devices will remain attached for the shortest duration (days-weeks), glue mounted devices will remain attached for a few weeks, while harness or ring-mounted devices can last for longer time periods (1 year +). However, it is important to note that weak-link harnesses, which are designed to fail after a given time period, have been developed in order to reduce impacts on birds (Clewley et al., 2021). Consequently, glue or tape mounted deployments may be most suitable for short-term collection of data on habitat use or behaviour during the breeding season, while harness or ring-mounted devices are required for the collection of year-round data, and data outside the breeding season.

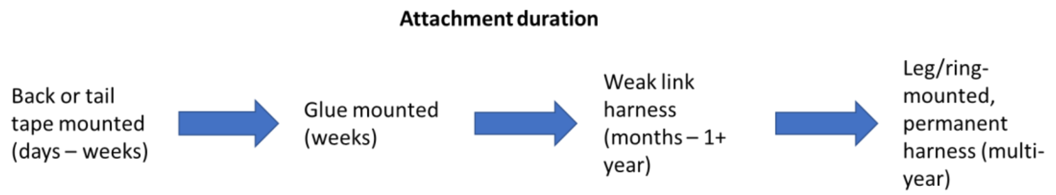


Figure 2 Typical duration of attachment for bird-mounted devices fitted using different attachment methodologies.

Generally, leg-mounted approaches are likely to be suitable for each of the key species of concern to the offshore wind industry at present (Table 1). However, these are limited to smaller devices such as geolocators or time-depth-recorders. Tape mounted devices have also been used successfully with the species considered here. However, these may be subject to relatively short deployments as they are vulnerable to removal by some species, particularly large gulls. In recent years, there have also been issues when using tape to mount devices on bird's backs. These are thought to be linked to feather quality and structure (S. Wischnewski *Pers. Comm.*). Whilst glue mounted devices may be deployed over longer time periods than those deployed using tape, careful consideration must be made of species moult status. Birds in active moult are more prone to losing devices as they shed feathers. Careful consideration must also be given to the glue used to attach devices, particularly those that produce an exothermic reaction when exposed to an activator. Whilst, harnesses have previously been successfully used on large gulls but there may be adverse impacts on other species (Thaxter et al., 2014, 2016). In a recent trial on kittiwakes, backpack harnesses were found to be associated with an unacceptable level of abrasion and removed (Clewley et al. *in prep.*). Abrasion was also noted on birds fitted with leg-loop harnesses, whilst these devices were also removed, it was felt that a revised leg-loop design may prevent this, and a further trial using this approach is planned for the 2022 breeding season. It is considered unlikely that harness methodologies would be licensed for diving species (e.g., guillemot, razorbill and gannet) as a result of the potential for increased drag underwater from devices positioned in this way. Regardless of the attachment methodology selected, specialist training will be required by anyone deploying devices, particularly in relation to harnesses, which are associated with a greater risk to bird welfare.

Table 1 Suitability of device attachment methodologies for UK seabirds. ✔ Suitable, ✓ may be suitable with further consideration, ✘ not suitable, * not tested but unlikely to be suitable for diving species.

	Leg-mounted	Tape mounted	Glue Mounted	Leg-loop harness	Backpack harness
Guillemot	✔	✔		*	*
Razorbill	✔	✔		*	*
Gannet	✔	✔		*	*
Kittiwake	✔	✔	✓	✓	✘
Lesser black-backed Gull	✔	✓	✓	✓	✔
Herring Gull	✔	✓	✓	✓	✔
Great Black-backed Gull	✔	✓			✓

Device effects

As part of any deployment, it is important to collect data on potential device effects. There are two reasons for this:

1) To ensure that devices are not adversely effecting the birds.
2) To understand the extent to which data from tagged individual may or may not be representative of the wider population.

In any process in which a bird is captured, handled and fitted with a device, there will always be an effect. The key questions to consider are whether the process has an unacceptable impact on the individual concerned, and whether, as a result of this process, the recorded behaviour of the individual is no longer likely to reflect that of the population more widely.

A range of data may be collected in order to assess potential device effects (Bodey et al., 2018). This includes demographic data such as productivity and return rates the following breeding season, as well as behavioural data such as nest attendance rates and parental change-over rates. The data collected often varies on a study-by-study basis, and may reflect the visibility of the colony concerned, the accessibility of that colony and the potential for any disturbance effects if it is necessary to enter the colony. Where multiple devices have been deployed at a single colony, it is also possible to investigate how device weight, position and attachment methodology influences bird’s distribution at sea. However, it is noted that unpicking these factors may be challenging given the sample sizes involved.

Data have typically been collected by comparing tagged birds to a control group of marked birds. However, there is growing interest in comparing data from a third group of birds that have not been handled (e.g. Seward et al., 2021). This would help us to understand whether any effects are the result of the device and attachment methodology or, the result of handling. Where a colony is easily observable, data on productivity can be collected by observing a subset of nests where neither parent has been captured. Where there is an existing cohort of marked individuals (e.g., with colour-rings) these nests can also be monitored to provide data on nest attendance and return rates for birds that have not been captured as part of the tagging study. If appropriate, data collected as part of monitoring (e.g., productivity rates) for tag effects should be added to the Seabird Monitoring Programme (SMP) database.

For a well-designed tracking study, device effects should be small. Given the relatively small sample sizes involved in tracking studies, many will lack the statistical power to detect any device effects (Cleasby et al., 2021). Power to detect impacts may be increased by pooling results across multiple studies (e.g. Bodey et al., 2018). To facilitate this, there is a need for researchers working on the same species across multiple colonies to co-ordinate data collection and move towards more standardised assessments of tag effects. These standardised assessments are likely to vary on a species-by-species basis, with key considerations relating to the relative accessibility of different colonies and the potential for disturbance. However, these considerations should not be seen as a barrier to collecting additional data where circumstances allow.

Sampling rates

Faster sampling rates allow for the collection of higher resolution tracks, and more accurate GPS estimates of altitude. However, there is a trade-off between sampling rate and battery life. As battery life is proportional to weight, this means that the size of the species being tracked can impose a limit on the sampling rate that can be maintained over the course of a study. Where batteries get drained too quickly, this can result in an incomplete record of a bird's foraging movements and may not accurately reflects its true foraging distribution. This may pose challenges for analyses of species space use (e.g. Wakefield et al., 2017).

Some tags offer the utility to apply geo-fences to data, whereby higher resolution data can be collected within a given area (e.g., a wind farm), with lower sampling rates to preserve battery life elsewhere. Ultimately, the choice of sampling rate will be influenced by the question being asked. If the aim of a study is to investigate the distribution and habitat usage of birds at sea (Thaxter et al., 2015), a lower sampling rate, with coarser resolution spatial information may be appropriate in order to minimize any potential data gaps and incomplete foraging trips. However, if the aim is to collect GPS flight height estimates (Ross-Smith et al., 2016), or investigate fine-scale movements of birds in relation to wind farms (D. Johnston et al., 2021), higher resolution data will be required. However, this may come at a cost of a less complete understanding of species at sea distribution. This choice should be discussed and agreed with funders, and other stakeholders, at the outset of any study.

GPS/Altimeter measurements of flight height

Flight height estimates may be obtained directly from GPS data or, through recording pressure data using an altimeter.

For GPS estimates of flight height are made relative to modelled estimates of mean sea-level. There are often significant errors associated with flight heights estimated from GPS, these are related to the number of satellites used to record a bird's position, cloud cover and sampling rate. It is important to account for these errors in the modelling process (e.g. Péron et al., 2020; Ross-Smith et al., 2016). There may also be error associated with the estimation of mean sea level. However, using behavioural classification, this error can be accounted for by calibrating flight height estimates derived from times at which birds were classified as floating on the sea surface.

Altimeters are generally power-efficient, without the need for the high-resolution data required for GPS flight height estimates. This is valuable in relation to battery life, meaning distributional data can be collected alongside the flight height estimates. However, processing the data collected by altimeters to convert pressure measurements into altitude estimates is more computationally intensive than processing GPS flight height estimates. Altimeters measure pressure in bursts of 10 Hz, these are then converted to estimates of altitude as follows:

$$h = \frac{KT}{mg} \ln\left(\frac{P}{P_0}\right) \text{ Eq. 1}$$

where h is the altitude in meters, K is the universal gas constant for air, T is the temperature in Kelvins, m is the molar mass of air, g is acceleration due to gravity, P_0 is the pressure at sea level and P is the pressure recorded by the altimeter. There are a number of potential sources of data for estimating P_0 including local measurements from offshore buoys, modelled estimates from sources like ECMWF ERA 5 and measurements obtained from the altimeters when birds are known to be floating on the sea surface. Given that pressure is known to vary both spatially and temporally, there may be a need to combine data in order to obtain a calibrated estimate of pressure at sea level (Figure 3). These calibrated estimates of P_0 can then be used in Eq. 1 to estimate the flight altitude of a bird at any given point. However, when using approaches such as this, it is important to note that broad-scale patterns in pressure can change quickly, and that there may be some drift in the calibration of tags. Consequently, there may be greater uncertainty in species which engage in less floating behaviour. In these circumstances, it would be valuable to consider other potential sources of local pressure data, for example that measured from LiDAR buoys, or met masts within windfarms.

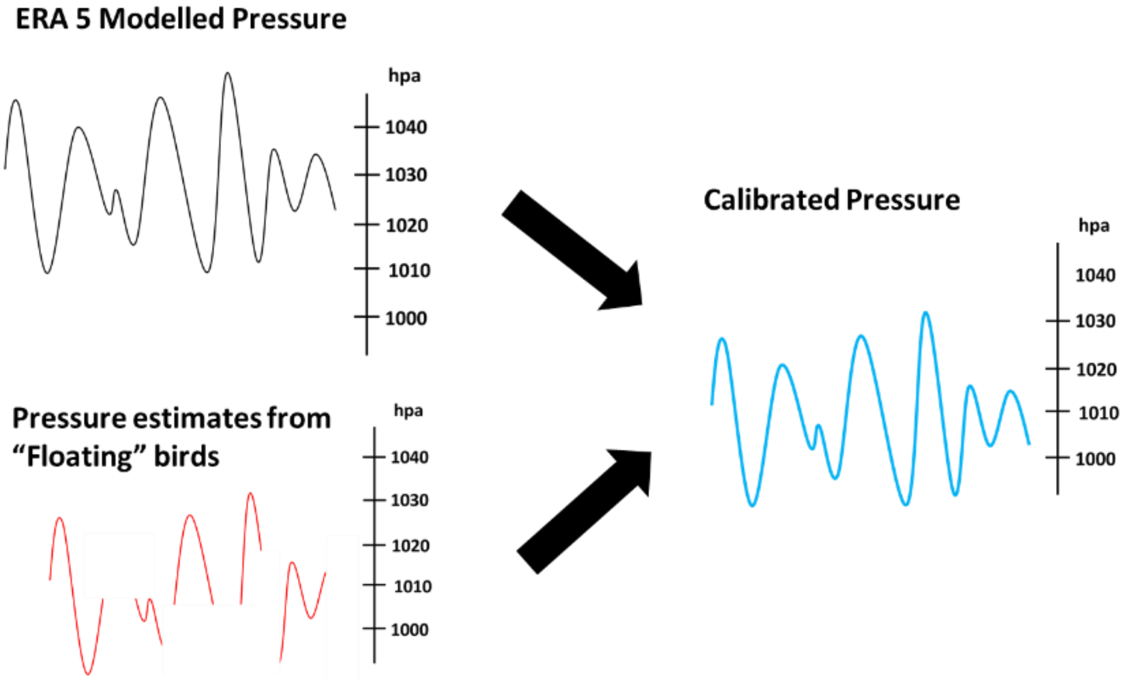


Figure 3 Combining modelled pressure estimates from ERA 5 dataset with estimates of pressure from floating birds, presumed to be at sea level, to obtain a calibrated estimate of pressure at sea level.

Where the two methodologies have been combined, altimeter estimates of flight height are highly correlated with the GPS estimates. However, the estimates of flight height obtained using altimeters are generally higher, and have greater precision, than those obtained using GPS. Regardless of whether flight heights are estimated using GPS or altimeters, calibrating these estimates with reference to points at which birds have been identified as floating on the sea surface is a valuable step towards reducing uncertainty associated with the data.

Part 2: Use of data in Collision Risk Modelling

Attendees: Aonghais Cook (BTO), Gary Clewley (BTO), Liz Humphreys (BTO), Chris Thaxter (BTO), Jacob Davies (BTO), Philipp Boersch Supan (BTO), Aly McCluskie (RSPB), Lucy Wright (RSPB), Saskia Wischnewski (RSPB), Francis Daunt (UKCEH), Alex Robbins (NatureScot), Sean Sweeney (APEM), Matt Boa (APEM), Matt Hazleton (NIRAS), Ross MacGregor (MacArthur Green), Mark Trinder (MacArthur Green), Tom Evans (Marine Scotland)

Behavioural classification

There may be pronounced differences in species flight heights and speeds in relation to different behavioural classifications (e.g. foraging or commuting flight) which have important implications for the assessment of collision risk (Cleasby et al., 2015; Masden et al., 2021; Thaxter et al., 2019). Classifications are typically based on the tortuosity of tracks and distance travelled between GPS points (Figure 4). In addition to potentially offering a means to deriving behaviour specific estimates of parameters for collision risk models, these approaches potentially also offer a means to better understand the consequences of displacement and barrier effects.

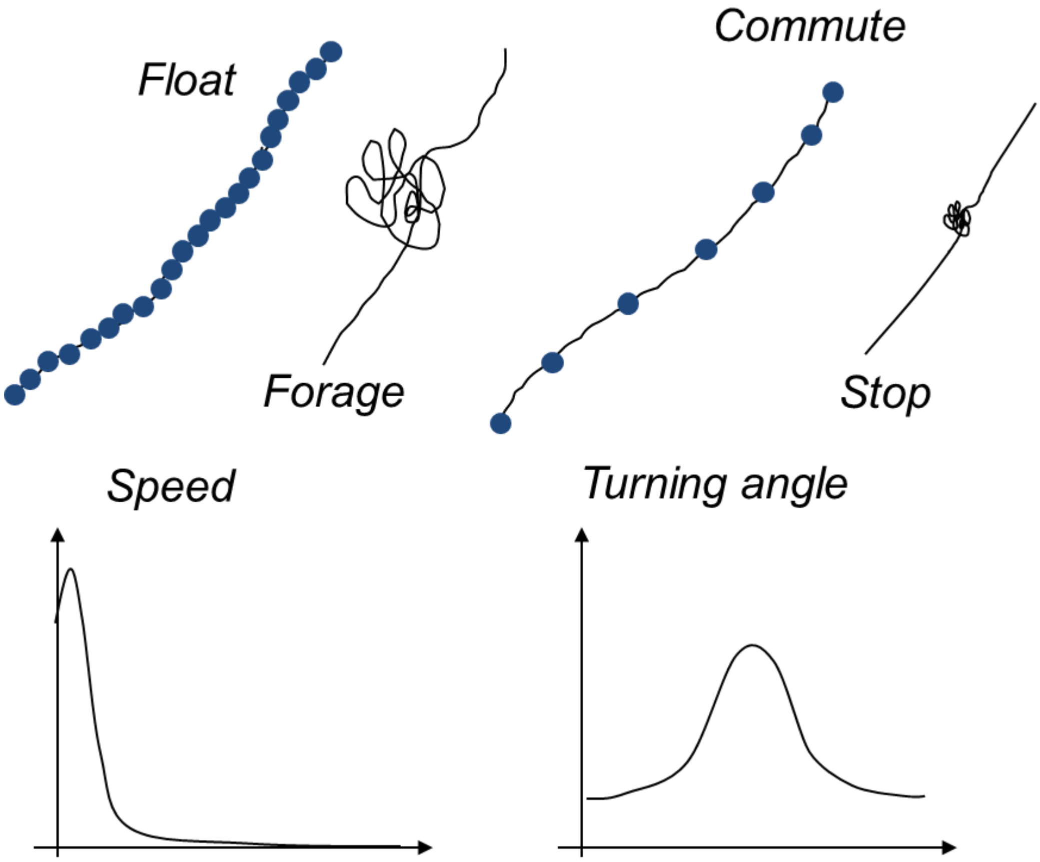


Figure 4 Behavioural classifications are based on the step length between GPS points, akin to flight speed, and the tortuosity or tracks (measured by turning angle).

A variety of different approaches are available from simple rules-based methods (e.g., based on flight speed) to more complex approaches based on machine-learning and neural networks. At present, the most widely used methods are Hidden Markov Models (HMMs) (McClintock & Michelot, 2018) and Expectation-Maximisation Binary Clustering (EMbC) (Garriga et al., 2016). The choice of approach will depend both on the data available, and the objectives of the study. Generally, analysis is based on step lengths and turning angles estimated from GPS data (Figure 4). However, it is possible to incorporate other data, for example from accelerometers or time-depth-recorders, to refine these classifications further (Thaxter et al., 2019). Where the aim is to simply partition behaviour into foraging and commuting flight (e.g., to obtain behaviour-specific estimates of flight height and speed), approaches like EMbC offer a fast and robust means to do this. However, if the aim is to better understand drivers of behaviour (e.g., to investigate how collision risk may change in different conditions), alternative approaches which can incorporate covariates, such as HMMs are required. However, this can bring challenges as HMMs are more sensitive to gaps in data. If this is the aim of a study, it will have implications for sampling rates and battery life that will need to be considered at the outset of that study. Regardless of the approach taken for behavioural classification, careful ecological interpretation of the behavioural states identified is required, and the number of states identified may vary between species (Thaxter et al., 2019).

It is important to consider the representativeness of any behavioural classifications. At present, data relate to the breeding season only, and only to breeding birds. There is a need to consider how representative data are of non-breeding birds, and birds outside the breeding season.

Flight Speed

Flight speed is used by the Band (2012) collision risk model twice. Firstly, to estimate the flux rate, and secondly to estimate the probability of collision. Consequently, flight speed is among the parameters that the model is most sensitive to (Masden et al., 2021). At present, estimates of flight speed are based on values presented in studies such as Alerstam et al. (2007), which are often derived from limited sample sizes and durations of observations. The rapid expansion of GPS tracking studies for seabirds offers a valuable source of data for flight speed estimates (Largey et al., 2021).

Flight speed can be estimated from GPS tags in two ways: 1) by estimating the distance travelled between two GPS fixes with known time intervals (trajectory speed), and 2) using the Doppler effect referencing the time taken for the signal to travel between the tag and satellite(s) (e.g. Fijn & Gyimesi, 2018) to give an instantaneous measurement of speed. Whilst the two speeds are strongly correlated, the trajectory speed systematically under-estimates flight speed, as measured instantaneously (Figure 5), though this effect decreases as sampling rate increases. At present, whilst the instantaneous speed is not routinely reported as part of the output from all tags, there should not be a technical barrier to enabling this, and it is recommended that this request is made to tag manufacturers when ordering tags.

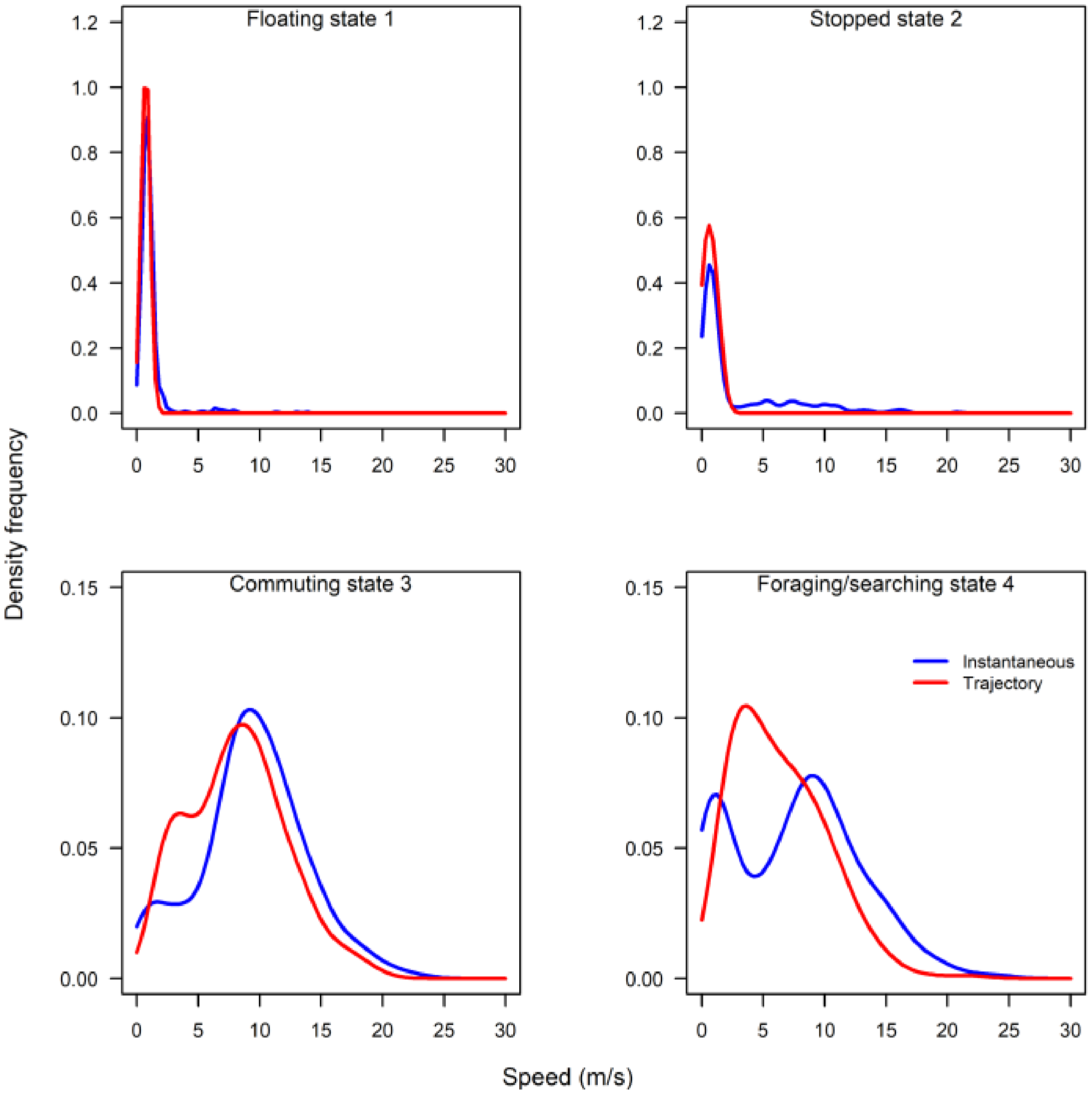


Figure 5 Estimates of lesser black-backed gull flight instantaneous (derived using Doppler effect) and trajectory (derived by estimating distance travelled between fixes) speeds derived for different behavioural states.

For both foraging and commuting flight, recorded speeds were lower than those reported by Alerstam et al. (2007). Foraging speeds were substantially slower than commuting speeds (Table 2). As data are restricted to birds at breeding colonies, there are concerns in relation to how representative these speeds may be for non-breeding birds, or birds outside the breeding season. However, it is also noted that similar criticisms could be applied to the speeds recommended in current guidance which were derived from more limited sample sizes in a more restricted set of conditions. To overcome some of the challenges related to understanding how representative data are, flight speed estimates could be obtained from birds with long-term GPS data collected outside the breeding season (e.g., Lesser black-backed gulls). Recorded flight speeds could also be compared to those collected using other methodologies including radar (Tjomlov et al., 2021) and laser rangefinders (Skov et al., 2018), with a view to integrating measurements across methodologies.

Table 2 Flight speeds from Alerstam et al. (2007) and for foraging and commuting flight estimated using instantaneous speed from GPS.

Species	Colony	Alerstam et al. (2007)	Foraging	Commuting
Lesser black-backed gull	Walney	13.1	7.94	9.51
Lesser black-backed gull	Skokholm		7.06	10.14
Lesser black-backed gull	Orfordness		7.69	9.70
Kittiwake	Flamborough Head and Bempton Cliffs	13.1	6.06	9.70
Gannet	Flamborough Head and Bempton Cliffs	14.9	10.79	14.08

Using the lower flight speeds estimated from GPS in the Band (2012) model will result in lower predicted collision rates as a result of a reduction in the predicted flux rate (Masden et al., 2021). Following behavioural classification, these flight speeds can be refined further into estimates for foraging and commuting flight (Table 5). During the breeding season, where there is clear separation between areas used for foraging and those used for commuting, it may be straightforward to recommend the use of behaviour specific flight speeds for collision risk modelling, though noting concerns about the representativeness of these data for non-breeding individuals. However, where this delineation is less clear, if estimates of behaviour-specific flight speed are to be used, it may be necessary to combine these using a weighted average based on the proportion of time spent in foraging or commuting flight.

Flight height

Estimates of the proportion of birds at collision risk height are a key parameter for assessing collision risk in relation to offshore wind farms (Band, 2012; Johnston et al., 2014). Species flight heights may be estimated using a range of different technologies including radar, LiDAR, GPS, altimeters and laser rangefinders (Largey et al., 2021). However, estimates of species flight heights from different technologies may be subject to systematic bias, error and individual variation (Péron et al., 2020). Consequently, it is better to characterise the variation in species flight heights using a distribution, rather than relying on individual point estimates.

GPS estimates of species flight heights are known to be subject to error (Ross-Smith et al., 2016). Whilst this is mostly obviously manifested by a substantial proportion of birds flying below the sea surface, flight height estimates of birds flying above the sea surface will also be subject to this error. However, we know that this error is correlated with the number of satellites associated with each estimate, meaning that we can model this by partitioning out the observation error and the true variation in species flight heights using a state-space model following Ross-Smith et al. (2016). Using this approach, we can see that the raw altitude data obscure a peak in the flight height distribution, and over-estimate the proportion of birds at higher altitudes (Figure 6).

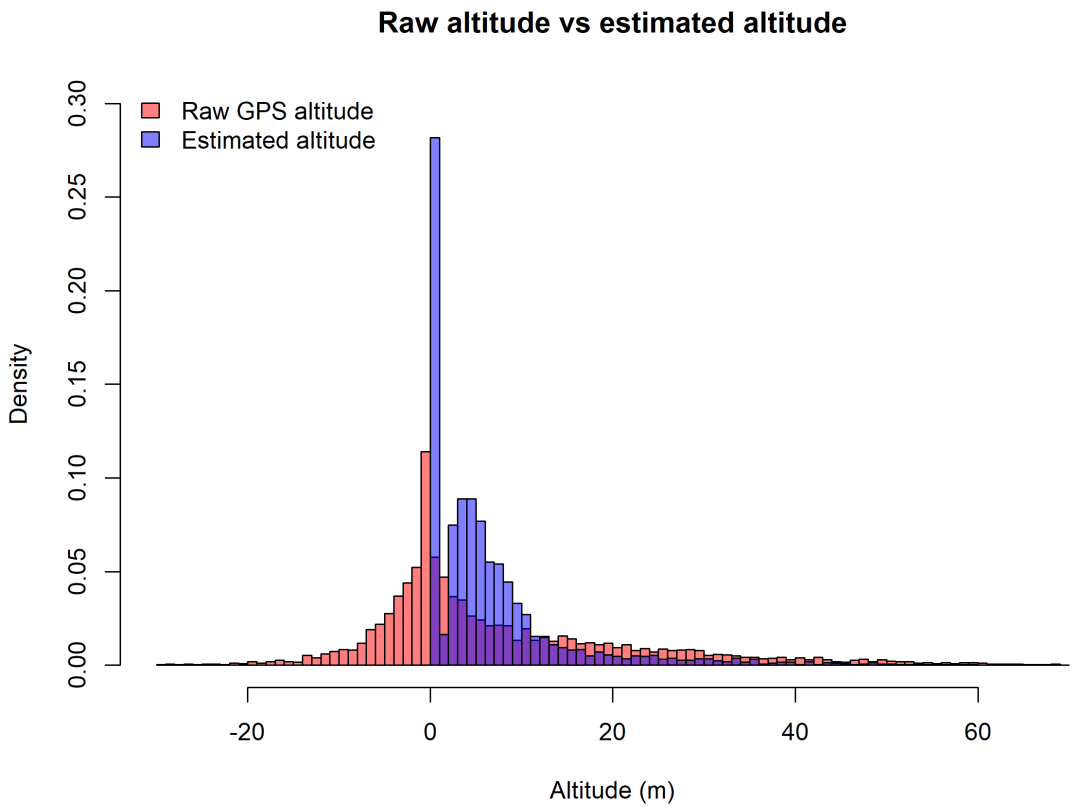


Figure 6 Raw GPS estimates of altitude for kittiwakes within the Buchan Ness to Collieston Coast SPA compared to altitudes estimated once the error in these measurements had been modelled.

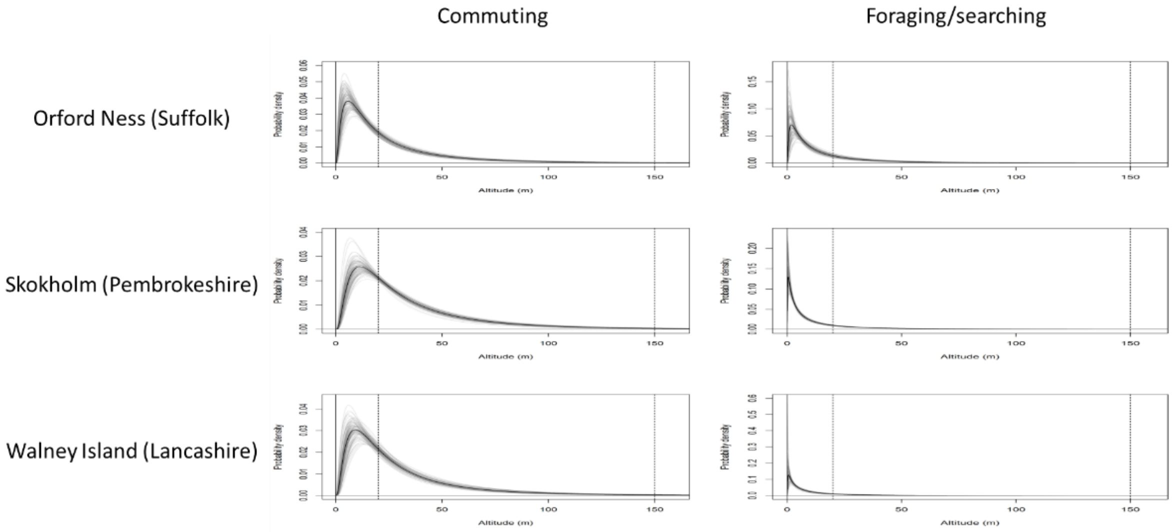


Figure 7 Flight height distributions for foraging and commuting lesser black-backed gulls at Orford Ness, Skokholm and Walney Island.

As with flight speed, we can partition GPS data into foraging and commuting behaviour and estimate flight height distributions for each (Figure 7). For lesser black-backed gulls, commuting flights were generally higher than foraging flights, with more time spent at collision risk height, indicating increased collision risk for commuting behaviour. As with flight speed, this offers the potential for behaviour-specific estimates of flight height to be used for collision risk modelling.

Avoidance Rates

Outputs from collision risk models are highly sensitive to the values assumed for avoidance (Chamberlain et al., 2006; Masden et al., 2021). At present, the avoidance rates used in collision risk models account for model error in addition to any behavioural avoidance (Masden et al., 2021). Avoidance rates are calculated by comparing observed collision rates to those predicted in the absence of avoidance (Cook et al., 2014; Cook et al., 2018). Consequently, whilst it is possible to estimate avoidance behaviour using GPS tracking data (Johnston et al., 2021), these values cannot be used as avoidance rates for the purposes of collision risk modelling.

Integrating GPS data into assessments of collision risk

There are two potential roles for GPS data in the assessment of collision risk. Firstly, data can be used to refine estimates of the values of parameters, such as flight height, flight speed and nocturnal activity, that are used in collision risk models (e.g. Cleasby et al., 2015; Fijn & Gyimesi, 2018; Furness et al., 2018; Masden et al., 2021; Ross-Smith et al., 2016). Secondly, GPS data could be used to refine existing models, or develop new models, to better account for the bird behaviour in the assessment of collision risk (e.g. Schaub et al., 2019; Searle et al., n.d.).

At present, there is considerable uncertainty underpinning assessments of the impacts of offshore wind farms (Masden et al., 2015). In keeping with the precautionary principle, these means that conservative estimates must be used for the parameters used in collision risk models. This leads to concerns that precaution gets magnified through the assessment process, leading to assessments that are overly precautionary. As a result, this uncertainty contributes to a situation whereby several of the projects put forward as part of the ScotWind leasing round cannot proceed unless evidence can be put forward to release them from high levels of ornithological constraint.

Recent analyses highlighted that basing collision estimates on flight speeds measured using GPS, rather than the current recommended values, could reduce predicted collision rates in lesser black-backed gulls at a wind farm cluster in North West England by 12% (Masden et al., 2021). Further refinements in model parameters, such as accounting for when birds are foraging or commuting, may also contribute to reductions in predicted collision rates. Refinements such as these enable us to reduce the precaution in assessments of collision risk by reducing uncertainty surrounding input parameters.

It is important to consider the implications of refinements to model parameters for estimates of avoidance rates. At present, estimates of avoidance incorporate model error, which will, at least partially, include misspecification of input parameters. As highlighted by Masden et al. (2021), this is particularly true in relation to the impact of flight speed on the estimated flux rate. A reduced flight speed, as is the case for the GPS flight speed estimates considered here relative to current recommended values, will reduce the estimated flux rate, and consequently the number of collisions predicted in the absence of avoidance. As avoidance rates are estimated by comparing predicted and observed collision rates, this may mean that where lower flight speeds are used, revised, lower avoidance rates should be used as well. This highlights a key challenge in integrating GPS data into assessments of collision risk. Whilst the potential to reduce precaution through better estimation of input parameters is a positive, it is still unclear the extent to which this may improve (or otherwise) estimates of collision risk. The key to better understanding this will be to ensure that studies such as Skov et al. (2018), or that currently underway in Aberdeen Bay (Tjomlov et al., 2021), are carried out in such a way that they enable the validation of collision risk models.

Recommendations

Tags

The type of tag used for a study will have implications for the attachment methodology that is used, the data that are collected and the analyses that are possible. Consequently, the choice of tag should be discussed with project funders and other relevant stakeholders at the outset of a project. There will be a trade-off between battery life and sampling rate, which will have implications for the collection of distribution data, fine-scale movement data and flight height information (if using GPS). Where distribution data are key, lower sampling rates should be used in order to preserve battery life and limit data gaps and incomplete trips. If possible, altimeters should be prioritised for the collection of flight height data as these have a minimal impact on battery life. Where higher resolution data are required, it may be possible to preserve battery life through the use of geo-fences to limit the locations in which these data are collected (e.g., within a wind farm).

Key considerations in relation to tag features:

- Potential to include geo-fences for fast and slow sampling rates.
- Altimeters for flight height measurements
- Output instantaneous flight speeds as estimated using Doppler effect.

Tag effects

It should be acknowledged that in any tracking study, there will be tag effects. However, the key considerations should be whether these effects have an unacceptable impact, either on the birds, or on the quality of the data that is being collected. In many cases, these effects may be small and, given the sample sizes of tagged birds in any individual study, we may lack the statistical power to detect them. Differences in site accessibility and visibility mean that the data to assess tag effects will vary between colony. The exact set of parameters (e.g., productivity, return rates, attendance rates) that can be collected will vary between species and sites. In determining which parameters to collect, it is important to ensure any unnecessary disturbance to the breeding colony is avoided. Where a single species is tracked at multiple sites, it is important to ensure these studies are co-ordinated and that the data collected across these sites are standardised to help overcome any challenges associated with statistical power. This should not be seen as a barrier to collecting additional data at sites where circumstances allow.

Analyses of flight height

Regardless of whether flight heights are estimated using GPS or altimeters, an important first step in the analysis is to calibrate these data based on points at which behavioural classification indicates birds are floating on the sea-surface. In the case of altimeters, this will provide an indication of pressure at the sea surface in any given location which can then be used to calibrate modelled estimates from elsewhere (e.g., ECMWF ERA5). In the case of GPS estimates, this will help determine whether there is any systematic error in the flight height estimates due to errors in estimating mean sea level from the geoid. Regardless of the methodology used to estimate species flight heights, it should be recognised that there will be uncertainty around them due to error, bias, differences in precision and individual variability. Consequently, these data should be modelled to produce continuous flight height distributions, rather than presented as individual point estimates. Where appropriate, and data allow, distributions can be generated for different behaviours (e.g., foraging or commuting flight), locations or conditions.

Analyses of flight speed

Whilst instantaneous estimates of speed are not routinely reported in the output from all tag types, this should in theory be possible. Tag manufacturers may facilitate requests to record and output these data if researchers raise this prior to placing an order. Subsequent analyses of flight speed from tagging data should be based on these instantaneous measurements of speed, rather than estimated from distance travelled between fixes, an approach which may systematically under-estimate speed. As with flight height, flight speed estimates can be partitioned for foraging and commuting flight and/or analysed in relation to location and local conditions.

Integrating GPS data into assessments of collision risk

GPS tags offer data on flight height, flight speed and levels of nocturnal activity, all of which are potentially of value in relation to assessing collision risk. Indeed, in many cases, these may reflect the best available data. However, integrating these data into collision risk models may not be straightforward.

At present, avoidance rates used for the Band collision risk model are based on comparisons of observed and predicted collision rates. The predicted collision rates are generally based on generic data (e.g. Alerstam et al., 2007), meaning that these data contribute to the model error that is incorporated in the avoidance rates. Using GPS data, which may have been collected at a site-specific level, may alter the predicted collision rates used to estimate avoidance rates and account for some of this model error, with implications for the estimated avoidance rate.

Before incorporating GPS data into collision risk models, there will need to a careful consideration of the implications for the avoidance rate. This could be investigated by comparing collision rates in the absence of avoidance predicted using site-specific GPS data and generic data. If there is a substantial difference between the two predicted collision rates, this may indicate a need for a more fundamental assessment of the model to enable it to incorporate data from sources such as GPS which were not widely available at the time it was developed.

References

Alerstam, T., Rosén, M., Bäckman, J., Ericson, P. G. P., & Hellgren, O. (2007). Flight Speeds among Bird Species: Allometric and Phylogenetic Effects. *PLoS Biology*, *5*(8), e197. https://doi.org/10.1371/journal.pbio.0050197

Babcock, M., Aitken, D., Lloyd, I., Wischnewski, S., & Barratt. (2018). *Flamborough and Filey Coast SPA Seabird Monitoring Programme 2018 Report*.

Band, B. (2012). Using a collision risk model to assess bird collision risks for offshore wind farms. Retrieved August 23, 2017, from https://www.bto.org/sites/default/files/u28/downloads/Projects/Final_Report_SOSS02_Band1ModelGuidance.pdf

Band, W. (2012). Using a collision risk model to assess bird collision risks for offshore windfarms. SOSS, The Crown Estate, London, UK.

Band, W., Madders, M., & Whitfield, D. P. (2007). Developing field and analytical methods to assess avian collision risk at Wind Farms. In M. de Lucas, G. F. E. Janss, & M. Ferrer (Eds.), *Birds and wind farms: risk assessment and mitigation*. Madrid: Quercus.

Bivand, R., & Lewin-Koh, N. (2021). maptools: Handling Spatial Objects. R package version 1.1-2. Retrieved from https://cran.r-project.org/package=maptools

Bodey, T. W., Cleasby, I. R., Bell, F., Parr, N., Schultz, A., Votier, S. C., & Bearhop, S. (2018). A phylogenetically controlled meta-analysis of biologging device effects on birds: Deleterious effects and a call for more standardized reporting of study data. *Methods in Ecology and Evolution*, *9*(4), 946–955. https://doi.org/10.1111/2041-210X.12934

Borkenhagen, K., Corman, A.-M., & Garthe, S. (2018). Estimating flight heights of seabirds using optical rangefinders and GPS data loggers: a methodological comparison. *Marine Biology*, *165*(1), 17. https://doi.org/10.1007/s00227-017-3273-z

Brooks, M. E., Kristensen, K., van Bentham, K. J., Magnusson, A., Berg, C. W., Nielsen, A., … Bolker, B. M. (2017). glmmTMB Balances speed and flexibility among packages for zero-inflated Generalized Linear Mixed Modelling. *The R Journal*, *9*, 378–400.

Chamberlain, D. E., Rehfisch, M. R., Fox, A. D., Desholm, M., & Anthony, S. J. (2006). The effect of avoidance rates on bird mortality predictions made by wind turbine collision risk models. *Ibis*, *148*, 198–202.

Chivers, L. S., Lundy, M. G., Colhoun, K., Newton, S. F., Houghton, J. D. R., & Reid, N. (2012). Foraging trip time-activity budgets and reproductive success in the black-legged kittiwake. *Marine Ecology Progress Series*, *456*, 269–277. https://doi.org/10.3354/MEPS09691

Cleasby, I. R., Morrissey, B. J., Bolton, M., Owen, E., Wilson, L., Wischnewski, S., & Nakagawa, S. (2021). What is our power to detect device effects in animal tracking studies? *Methods in Ecology and Evolution*, *12*(7), 1174–1185. https://doi.org/10.1111/2041-210X.13598

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 wind farms. *Journal of Applied Ecology*, *52*(6), 1474–1482. https://doi.org/10.1111/1365-2664.12529

Clewley, G. D., Clark, N. A., Thaxter, C. B., Green, R. M., Scragg, E. S., & Burton, N. H. K. (2021). Development of a weak-link wing harness for use on large gulls (Laridae): methodology, evaluation and recommendations. *Seabird*, *33*, 18–34.

Cook, A.S.C.P., Ward, R. M., Hansen, W. S., & Larsen, L. (2018). Estimating Seabird Flight Height Using LiDAR. *Scottish Marine and Freshwater Science*, *9*(14). Retrieved from https://data.marine.gov.scot/dataset/estimating-seabird-flight-height-using-lidar

Cook, A S C P, Humphreys, E. M., Masden, E. A., & Burton, N. H. K. (2014). *The Avoidance Rates of Collision Between Birds and Offshore Turbines*. Edinburgh. Retrieved from http://www.gov.scot/Resource/0046/00464979.pdf

Cook, Aonghais S.C.P., Humphreys, E. M., Bennet, F., Masden, E. A., & Burton, N. H. K. (2018). Quantifying avian avoidance of offshore wind turbines: Current evidence and key knowledge gaps. *Marine Environmental Research*, *140*, 278–288. https://doi.org/10.1016/J.MARENVRES.2018.06.017

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. https://doi.org/10.1007/s10336-014-1094-0

Evans, T. J., Young, R. C., Watson, H., Olsson, O., & Åkesson, S. (2020). Effects of back-mounted biologgers on condition, diving and flight performance in a breeding seabird. *Journal of Avian Biology*, *51*(11). https://doi.org/10.1111/JAV.02509

Fijn, R. C., & Gyimesi, A. (2018). Behaviour related flight speeds of Sandwich Terns and their implications for wind farm collision rate modelling and impact assessment. *Environmental Impact Assessment Review*, *71*, 12–16. https://doi.org/10.1016/J.EIAR.2018.03.007

Forsythe, W. C., Rykiel, E. J., Stahl, R. S., Wu, H., & Schoolfield, R. M. (1995). A model comparison for daylength as a function of latitude and day of year. *Ecological Modelling*, *80*(1), 89–75.

Furness, R. W., Garthe, S., Trinder, M., Matthiopoulos, J., Wanless, S., & Jeglinski, J. (2018). Nocturnal flight activity of northern gannets Morus bassanus and implications for modelling collision risk at offshore wind farms. *Environmental Impact Assessment Review*, *73*, 1–6. https://doi.org/10.1016/J.EIAR.2018.06.006

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. https://doi.org/10.1016/j.jenvman.2013.01.025

Garriga, J., Palmer, J. R. B., Oltra, A., & Bartumeus, F. (2016). Expectation-Maximization Binary Clustering for Behavioural Annotation. *PLOS ONE*, *11*(3), e0151984. https://doi.org/10.1371/JOURNAL.PONE.0151984

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*(4), 724–734.

Garthe, Stefan, & Huppop, O. (2004). Scaling possible adverse effects of marine wind farms on seabirds: Developing and applying a vulnerability index. *Journal of Applied Ecology*, *41*(4), 724–734. https://doi.org/10.1111/j.0021-8901.2004.00918.x

Hartig, F. (2022). DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models. R Package version 0.4.5. Retrieved from https://cran.r-project.org/package=DHARMa

Harwood, A. J. P., Perrow, M. R., & Berridge, R. J. (2018). Use of an optical rangefinder to assess the reliability of seabird flight heights from boat-based surveyors: implications for collision risk at offshore wind farms. *Journal of Field Ornithology*. https://doi.org/10.1111/jofo.12269

Johnson, D. S., London, J. M., Lea, M. A., & Durban, J. W. (2008). CONTINUOUS-TIME CORRELATED RANDOM WALK MODEL FOR ANIMAL TELEMETRY DATA. *Ecology*, *89*(5), 1208–1215. https://doi.org/10.1890/07-1032.1

Johnston, A., & Cook, A. S. C. P. (2016). *How high do birds fly? Development of methods and analysis of digital aerial data of seabird flight heights. BTO Research Report No. 676*. Thetford. Retrieved from https://www.bto.org/research-data-services/publications/research-reports/2016/how-high-do-birds-fly-development-methods

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*(1), 31–41. https://doi.org/10.1111/1365-2664.12191

Johnston, D., Thaxter, C., Boersch-Supan, P., Humphreys, E., Bouten, W., Clewley, G., … Cook, A. (2021). Investigating avoidance and attraction responses in lesser black-backed gulls Larus fuscus to offshore wind farms. *Marine Ecology Progress Series*. https://doi.org/10.3354/MEPS13964

Klaassen, R. H. G., Hake, M., Strandberg, R., & Alerstam, T. (2011). Geographical and temporal flexibility in the response to crosswinds by migrating raptors. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1710), 1339–1346. https://doi.org/10.1098/RSPB.2010.2106

Largey, N., Cook, A. S. C. P., Thaxter, C. B., McCluskie, A., Stokke, Bå. G., Wilson, B., & Masden, E. A. (2021). Methods to quantify avian airspace use in relation to wind energy development. *Ibis*. Blackwell Publishing Ltd. https://doi.org/10.1111/ibi.12913

Lenth, R. V. (2022). emmeans: Estimated Marginal Means, aka Least-squares means. R package version 1.7.2.

Mallory, M. L., & Gilbert, C. D. (2008). Leg-loop harness design for attaching external transmitters to seabirds. *Marine Ornithology*, *36*, 183–188. Retrieved from http://www.marineornithology.org/content/get.cgi?rn=788

Masden, E. A. (2015). *Developing an avian collision risk model to incorporate variability and uncertainty*. Edinburgh: Scottish Government.

Masden, E. A., & Cook, A. S. C. P. (2016). Avian collision risk models for wind energy impact assessments. *Environmental Impact Assessment Review*, *56*, 43–49. https://doi.org/10.1016/j.eiar.2015.09.001

Masden, E. A., Cook, A. S. C. P., McCluskie, A., Bouten, W., Burton, N. H. K., & Thaxter, C. B. (2021). When speed matters: The importance of flight speed in an avian collision risk model. *Environmental Impact Assessment Review*, *90*, 106622. https://doi.org/10.1016/j.eiar.2021.106622

Masden, E. A., McCluskie, A., Owen, E., & Langston, R. H. W. (2015). Renewable energy developments in an uncertain world: The case of offshore wind and birds in the UK. *Marine Policy*, *51*, 169–172. https://doi.org/10.1016/j.marpol.2014.08.006

McClintock, B. T., & Michelot, T. (2018). momentuHMM: R package for generalized hidden Markov models of animal movement. *Methods in Ecology and Evolution*, *9*(6), 1518–1530. https://doi.org/10.1111/2041-210X.12995

McGregor, R., King, S., Donovan, C. R., Caneco, B., Webb, A., Webb, A., & Wilson Marine Scotland Science JaredWilson, J. (2018). *A Stochastic Collision Risk Model for Seabirds in Flight Authorisations Responsibility Name Signature Date Distribution List Name Organisation Email Address*. Retrieved from https://www.gov.scot/Resource/0053/00536606.pdf

Pennycuick, C. (1997). Actual and "optimum" flight speeds: field data reassessed. *Journal of Experimental Biology*, *200*(17).

Péron, G., Calabrese, J. M., Duriez, O., Fleming, C. H., García-Jiménez, R., Johnston, A., … Shepard, E. L. C. (2020). The challenges of estimating the distribution of flight heights from telemetry or altimetry data. *Animal Biotelemetry*, *8*(1), 1–13. https://doi.org/10.1186/s40317-020-00194-z

Ross-Smith, V. H., Thaxter, C. B., Masden, E. A., Shamoun-Baranes, J., Burton, N. H. K., Wright, L. J., … Johnston, A. (2016). Modelling flight heights of lesser black-backed gulls and great skuas from GPS: a Bayesian approach. *Journal of Applied Ecology*, *53*(6), 1676–1685. https://doi.org/10.1111/1365-2664.12760

Schaub, T., Klaassen, R. H. G., Bouten, W., Schlaich, A. E., & Koks, B. J. (2019). Collision risk of Montagu's Harriers *Circus pygargus* with wind turbines derived from high-resolution <scp>GPS</scp> tracking. *Ibis*, ibi.12788. https://doi.org/10.1111/ibi.12788

Searle, K., Butler, A., Mobbs, D., Trinder, M., McGregor, R., Cook, A., … Daunt, F. (n.d.). *Study to examine how seabird collision risk, displacement and barrier effects could be integrated for assessment of offshore wind developments*.

Seward, A., Taylor, R. C., Perrow, M. R., Berridge, R. J., Bowgen, K. M., Dodd, S., … Bolton, M. (2021). Effect of GPS tagging on behaviour and marine distribution of breeding Arctic Terns Sterna paradisaea. *Ibis*, *163*(1), 197–212. https://doi.org/10.1111/IBI.12849

Skov, H., Heinänen, S., Norman, T., Ward, R. M., & Méndez-Roldán, S. Ellis, I. (2018). *ORJIP Bird Collision and Avoidance Study. Final report*. United Kingdom.

Thaxter, C. B., Johnston, D. T., Clewley, G. D., Humphreys, E. M., & Cook, A. S. C. . (2019). *Improving our understanding of seabird behaviour at sea*.

Thaxter, Chris 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: A case study of lesser black-backed gull Larus fuscus in the UK. *Biological Conservation*, *186*, 347–358. https://doi.org/10.1016/j.biocon.2015.03.027

Thaxter, Chris B., Ross-Smith, V. H., Clark, J. A., Clark, N. A., Conway, G. J., Marsh, M., … Burton, N. H. K. (2014). A trial of three harness attachment methods and their suitability for long-term use on Lesser Black-backed Gulls and Great Skuas. *Ringing and Migration*, *29*(2), 65–76. https://doi.org/10.1080/03078698.2014.995546

Thaxter, Chris B., Ross-Smith, V. H., Clark, J. A., Clark, N. A., Conway, G. J., Masden, E. A., … 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*(2), 279–290. https://doi.org/10.1111/ibi.12340

Tjomlov, R. S., Skov, H., Armitage, M., Barker, M., Cuttat, F., & Thomas, K. (2021). *Resolving key uncertainties of seabird flight and avoidance behaviours at offshore wind farms. Annual Report for April 2020 to October 2020. Report to AOWFL.*

Toke, D. (2011). The UK offshore wind power programme: A sea-change in UK energy policy? *Energy Policy*, *39*(2), 526–534. https://doi.org/10.1016/j.enpol.2010.08.043

Wakefield, E. D., Owen, E., Baer, J., Carroll, M. J., Daunt, F., Dodd, S. G., … Bolton, M. (2017). Breeding density, fine-scale tracking, and large-scale modeling reveal the regional distribution of four seabird species. *Ecological Applications*, *27*(7), 2074–2091. https://doi.org/10.1002/eap.1591

Wischnewski, S., McCluskie, A., Bouten, W., Adlard, S., Babcock, M., & Wright, L. J. (n.d.). Plasticity in offshore space-use and behaviour across time governs the susceptibility of seabirds to offshore wind farms.

Wischnewski, S., Sansom, A., McCluskie, A., Bouten, W., Adlard, S., Aitken, D., … Wright, L. J. (n.d.). Temporal and spatial patterns in the offshore behaviour and distribution of kittiwakes: Lessons for Marine Spatial Planning.

Scottish Government
Riaghaltas na h-Alba

This publication is available at **www.gov.scot**

Any enquiries regarding this publication should be sent to us at

The Scottish Government
St Andrew's House
Edinburgh
EH1 3DG

ISBN: 978-1-83521-271-4 (web only)

Published by The Scottish Government, October 2023

Produced for The Scottish Government by APS Group Scotland, 21 Tennant Street, Edinburgh EH6 5NA
PPDAS1344943 (10/23)