Assessing the importance of individual- and colony-level variation when using seabird foraging ranges as impact assessment and conservation tools

Abstract

Knowledge of seabird distributions plays a key role in seabird conservation and sustainable marine management, underpinning efforts to designate protected areas or assess the impact of human developments. Technological advances in animal tracking devices increasingly allow researchers the movement of birds from specific colonies, to acquire such information. Nevertheless, most seabird colonies have not been subject to such tracking and another means must be found to assess their likely distribution. Consequently, foraging range data collated and summarized across other tracking studies has often been used to estimate species-level foraging distances for use within applied settings. However, generic species-specific foraging ranges must be used with caution due to the amount of variation in seabird foraging behaviour at both the individual and colony level. Specifically, while current reviews of seabird foraging ranges provide summary estimates of maximum foraging range, they typically do not assess the extent of among colony or among individual variation around such estimate. To address this, we conducted a variance component analysis of the maximum distance reached offshore from the breeding colony per foraging trip (foraging range) using multi-colony tracking datasets to estimate the degree of between-individual, between-year, and between-colony variation in foraging range in four UK breeding seabirds (Black-legged Kittiwake *Rissa tridactyla*, Common Guillemot *Uria aalge*, Razorbill *Alca torda* & European Shag *Gulosus aristotelis*). We also provide updated estimates of typical foraging ranges for each species and quantified the influence of breeding stage and colony size. Overall, between-colony variation was typically the largest variance component, explaining 20% - 30% of the observed variation in foraging range across the four species. Individual-level variation was also relatively large among Shags. Among Guillemots, Razorbills, and Shags, average foraging ranges were positively associated with colony size. In addition, Kittiwakes and Razorbills travelled further during incubation than chick rearing. More generally, our estimates of mean foraging ranges for each species were subject to a high degree of uncertainty which should be incorporated into impact assessments carried out using such data.

Keywords: between-group variation**,** GPS tracking, individual variation**,** marine conservation, movement ecology,

Introduction

Seabirds are among the world's most endangered avian groups (Croxall et al. 2012) and face a myriad of potential threats, many from an anthropogenic origin (Dias et al. 2019). Consequently, concerns about seabird conservation increasingly need to be addressed within marine spatial planning and environmental impact assessment frameworks (Soanes et al. 2013, Broadbent & Nixon 2019). Within such frameworks, knowledge of seabird distributions is often a key piece of information and often underpins efforts to identify important marine areas (Cleasby et al. 2020a), delineate suitable Marine Protected Areas (MPAs, Lascelles et al. 2016, Mallory et al. 2019), or understand the potential impacts of human activities (Clay et al. 2019, O'Hanlon et al. 2023). The rapid development of animal bio-loggers means that animal distributions can increasingly be observed directly (e.g. via the use of GPS sensors) aiding the identification of important areas of habitat (Wakefield et al. 2017, Cleasby et al. 2020a). However, most seabird colonies have not been subject to tracking studies and for more inaccessible colonies, or other logistical reasons, tracking may be unfeasible. Therefore, another means must be found to assess the likely foraging range of birds from such colonies.

In some cases, multi-colony tracking studies can provide wide-scale predictions about seabird distributions beyond the immediate colonies surveyed via species distribution modelling (Wakefield et al. 2017, Cleasby et al. 2020a, Ronconi et al. 2022). However, these models rely upon large amounts of data and are currently only available for a small subset of species. Alternatively, many seabird tracking studies report summary estimates of different measures of foraging range, often measured as the maximum distance recorded between the colony and locations observed at-sea during a given foraging trip (Thaxter et al. 2012). Therefore, for colonies lacking suitable tracking data, species-level foraging ranges are often derived from foraging range estimates collated and summarized across available tracking studies. Such estimates are often used in an applied context to determine where birds from a given colony could forage and the potential threats' they may encounter within this area (Thaxter et al. 2012, Mallory et al. 2019, Woodward et al. 2019).

However, caution is urged when using data from a limited number of years or locations when summarizing species-level foraging ranges (Thaxter et al. 2012, Mallory et al. 2019) due to the amount of variation observed in seabird foraging behaviour. For example, the distance birds travel when foraging may vary with colony size (Lewis et al. 2001), degree of competition with neighbouring colonies (Wakefield et al. 2013, Pratte et al. 2017, Bolton et al. 2019), coastal morphology (Wakefield et al. 2017), and habitat availability (Corman et al. 2016, Christensen-Dalsgaard et al. 2018), which is assumed to be a proxy for food availability. Typical foraging ranges may also vary within colonies across foraging trips due to temporal variation in prey distribution and environmental conditions (Hamer et al. 2007, Bogdanova et al. 2014, Cleasby et al. 2015a, Osborne et al. 2020), among-individual variation in behaviour, for example due to prey or habitat specialisations (Wakefield et al. 2015, Sanchez et al. 2018, Cleasby et al. 2019), and the effects of breeding stage on central place constraints (Wakefield et al. 2011, Robertson et al. 2014). However, while previous reviews have summarised seabird foraging ranges across studies (Thaxter et al. 2012, Woodward et al. 2019) they have typically do not include a detailed examination of the variation in foraging range. In part, this may be because relevant information is not reported by individual studies or due to difficulty in standardizing approaches across the literature.

Individual research studies do occasionally examine sources of variation in seabird foraging behaviour but generally focus upon among individual variation within a single colony or across a small number of colonies (Wakefield et al. 2015, Potier et al. 2015, Harris et al. 2020). Consequently, the extent of among-colony and -individual variation in foraging range may be overlooked but could represent an important source of variation when estimating foraging ranges of untracked colonies.

Within Europe, the potential impact of offshore renewables is of increasing concern as the number of such developments expands in the next 30 years (Best & Halpin 2019). For example, European Union (EU) strategy aims to increase offshore windfarm capacity from 12 GW currently to 60 GW by 2030 and to 300 GW by 2050 to meet green energy targets (European Commission 2020). Offshore developments can impact seabird populations in a variety of ways including collision mortality, and sub-lethal barrier and displacement effects (Masden et al. 2009, Furness et al. 2013). Therefore, an important step in any impact assessment is to identify which breeding populations could potentially interact with proposed developments. Distance from the colony is a key constraint on seabird foraging distributions during the breeding season, given the need to return regularly to the nest and provision young (Orians and Pearson 1979). As such, metrics summarizing maximum foraging range are often used as a screening tool to examine whether the foraging range of birds from a given colony overlaps with proposed offshore developments, potential threats, or proposed marine protection areas (Ludynia et al. 2012, Thaxter et al. 2012). For example, within the UK, foraging ranges are recommended for use during the EIA / HRA screening stage of proposed windfarm developments (APBMer 2020) by relevant statutory nature conservation bodies (SNCBs). However, the degree of between site variation in foraging ranges and the representativeness of species-level foraging ranges across different colonies has been highlighted as a concern (NatureScot 2023).

Here, we provide a variance component analysis of foraging range (defined as maximum distance reached offshore from the breeding colony per foraging trip) to quantify among-individual, -year and -colony variation in seabird foraging ranges. We use large, multi-colony tracking datasets for four UK breeding seabirds (Black-legged Kittiwake *Rissa tridactyla*, Common Guillemot *Uria aalge*, Razorbill *Alca torda* & European Shag *Gulosus aristotelis*) and provide standardized measures of between-group variance (intra-class correlation coefficients, ICC) explained by each group-level variable, allowing comparison across species (e.g. Nakagawa & Schielzeth 2010, Nakagawa et al. 2017). One advantage of the dataset used here is that all tracking data was collected as part of the same, overall research project reducing the degree of between-study heterogeneity (e.g due to differences in device attachment, handling methods etc.) simplifying variance components analysis. In addition, we quantify how foraging range varies with breeding stage and colony size. These covariates represent important contextual information on foraging range that are often readily available even for untracked colonies (BirdLife International 2010, Grecian et al. 2012, Soanes et al. 2016, Critchley et al. 2018, Patterson et al. 2022) facilitating their use in an applied context.

METHODS

Data Collection

The four study species were tracked from multiple colonies around the UK between 2010-2015 (Table S1, Figs S1 – S9). Birds were caught by hand or using a noose pole for tag deployment and were recaught using the same method to retrieve tags to download data. The sampling period covered only late incubation and early chick-rearing. Breeding status was recorded as chick-rearing if chicks were present in the nest, incubating if only eggs were present or unknown if the nest contents could not be seen.

GPS tags (Modified IgotU GT120, Mobile Action, Taiwan) were temporarily attached using Tesa® tape secured to plumage on the back where they recorded one position every 100 seconds to an accuracy of approximately 25m over a recording period of 1-9 days (All species: 1.0-9.0 days, median 2.3d, Interquartile range 1.8-3.1d; Guillemot: 1.0 - 7.1d, median 2.5d, interquartile range 1.9-3.1d; Razorbill: 1- 9d, median 2.9d, interquartile range 2.1-3.5d; Kittiwake: 1-6.0d, median 1.9d, interquartile range 1.4-2.3d; Shag: 1-6.4d, median 3.1d, interquartile range 2.5-3.9d). We previously found little evidence of device effects in any of the species tracked (Cleasby et al. 2020b, Cleasby et al. 2021). For additional details on field methodology including the number of individuals tracked per colony and more information on potential device effects see Wakefield et al. (2017) and Supporting Online Materials – Appendices S1 and S2 respectively.

Data Analysis

Data Processing

Using the track2kba r package (Beal et al. 2021), excursions >1 km from the colony or 0.2 km for Shag and comprising more than 10 GPS fixes were classed as foraging trips. Given a 100 second sampling frequency, the minimum trip duration is therefore 10 × 100 = 1000 seconds or 16.6 minutes. Due to battery failures, incomplete trips, that lacked either a clear starting time or, more typically, a clear ending time (<0.2% of all trips), were excluded from analysis. Once individual foraging trips were identified, we calculated the Haversine distance (great-circle distance) from the colony to each pair of coordinates recorded during a foraging trip. The maximum Haversine distance from the colony recorded during the foraging trip was then identified for subsequent analysis as the foraging range of that trip. The Haversine distance as calculated here represents the shortest distance between two points and may therefore involve travelling over land. Maximum distance calculated in this way is the most commonly used distance measure in the foraging range literature and is the measure generally used in windfarm impact assessment within the UK (e.g. ABPmer 2020, NatureScot 2023). However, an alternative analysis using the distance by sea between the breeding colony and offshore locations within a given foraging trip is reported in the Supporting Online Materials – Appendix S3, but results were similar regardless of how distance was measured (Tables S2 – S5).

Modelling foraging ranges

We modelled foraging ranges at the trip-level for each species, using the maximum recorded distance from the breeding colony from each foraging trip. Maximum distance from the colony per trip was modelled using a generalized linear mixed model (GLMM) with a gamma distribution and a log link function using a Bayesian modelling approach in R (R v4.1.1, R Core Team 2021) via the brms package (Bürkner 2017). The log link function ensures models cannot predict negative distances. We also tested the log-normal and Gaussian distributions as alternatives, however based upon posterior predictive checks the gamma distribution performed better in all cases (Supporting Online Material – Appendix S4).

For ease of interpretation, we initially fitted random effects only models for each species to provide a basic variance component analysis unconditioned on any additional predictors. Due to the structure of our data, we included random intercept terms nesting as follows: individual nested within site-year nested within site, where site-year is a grouping label combining the site and the year in which data were recorded (e.g. Colonsay-2010, Colonsay-2011). Results are reported along with equal-tailed 95% credible intervals (95% CRI) and a Bayesian R^2 value calculated following Gelman et al. (2019). Posterior predictive checks of the performance of the random effects only models for each species are available in the Supporting Online Material - Appendix S4.

We report intra-class correlation coefficients (ICC) for our random effects. The ICC is calculated by dividing the between-group variance (random intercept variance) by the total variance (sum of between-group-variance and remaining residual variance). ICCs normally range between 0 and 1 and can be interpreted as correlations within a class or group of data (Liljequist et al. 2019) or the proportion of the variance explained by the grouping structure applied (Hox 2002). The basic ICC formulation for a Gaussian model is:

$$ICC = \frac{\sigma_\alpha^2}{\sigma_\alpha^2 + \sigma_\varepsilon^2}$$

Where σ_α^2 represents the between-group variance and σ_ε^2 the residual variance. The sum of σ_α^2 and σ_ε^2 in the denominator therefore equals the total variance (Nakagawa & Schielzeth 2010). However, while the above formulation works when assuming Gaussian errors, defining a suitable value of σ_ε^2 for non-Gaussian data in a GLMM is more difficult. Following Nakagawa et al. (2017), we estimated the observation-level σ_ε^2 as $\psi_1(v)$ where v is the shape parameter from a gamma distribution and ψ_1 is the trigamma function (the 2nd derivative of the gamma function and a base function in the R environment).

In addition to the random effects only model, we also fitted models including additional fixed effect predictors for breeding stage (incubating, chick rearing, or unknown), and log_{10} colony size (colony size estimates taken from Mitchell et al. (2004) and further processed as described in Wakefield et al. (2017)). For models of Kittiwake foraging range, we also included a predictor denoting whether a trip was the first trip post-tag attachment or not due to a potential handling/device attachment effect (see: Supporting Online Material – Appendix S2). A previous investigation found that the first trip post-tag attachment did not differ in length from that observed in subsequent trips in the other three species (Cleasby et al. 2022).

Variance components should be interpreted as being conditioned on any predictors included in the model (Wilson 2008). Therefore, adjusted ICCs (sensu Nakagawa &

Schielzeth 2010) were calculated for models that included fixed effect predictors. For all fixed effects we used normal priors with a mean of 0 and a standard deviation of 10. For our random effect standard deviation parameters, we used a half student-t prior with 3 degrees of freedom – the default option in brms. For the shape parameter of the gamma distribution, we used a gamma prior with shape = 0.01 and scale = 0.1 which represents an uninformed prior.

Using GLMMs predictions can be produced for a member of an existing group (e.g. colony) included in the model (conditional), or for a member of a hypothetical new group (marginal). We present both marginal and conditional estimates in the results and Supporting Online Material (Appendix S5) but assume that the latter will be most appropriate for unobserved colonies.

Issues with bimodality in Shag data

Initial posterior predictive checks showed that models performed poorly when estimating foraging ranges for Shag. Observed data showed evidence of a bimodal pattern in Shag foraging ranges that was not reflected in simulated model predictions, which were unimodal. To address this, we fitted Shag data using an intercept only Gaussian mixture model. The Gaussian mixture model estimated two trip-level foraging range distributions, one with a mean of 0.34 km (95% CRI: 0.33 – 0.36) and one with a mean of 4.67 km (4.39 – 5.05). However, mixture models failed to converge when we included any additional random effects. Therefore, we created a new variable classifying foraging trips as short (max. distance < 500 m) or long (max. distance ≥ 500 m) based on the foraging range modes identified above. Whether a trip was classified as short or long was included as an additional predictor in our original model of maximum distance from the colony. We also specified that all variance parameters (between-group variances and the gamma shape parameter) should be estimated for short and long trips independently. Subsequent posterior checks showed this approach was better able to capture the bi-modal patterns seen in the original data.

RESULTS

Black-legged Kittiwake

Variance component parameters and intra-class correlation coefficients from random effects only models provided evidence for between-site and between-individual variation in foraging range for Kittiwake (Tables 1 & 2). However, the magnitude of ICC was relatively small (< 20% variance explained in each case, Table 2). The between-year ICC was smaller than either the between-site or between-individual ICC.

Models that included fixed effect predictors suggested that log_{10} colony size was positively associated with foraging range (Table 3, Fig. 1, Fig. S50). Kittiwakes were also predicted to travel slightly further from the colony (~ 9 km on average) during incubation than during chick-rearing. The foraging range of the first trip observed post tag attachment did not differ from that observed across subsequent foraging trips. When including fixed effects, adjusted ICC values for between-site and between-year variation were broadly similar to those calculated using a random effects only model (Table 4). The inclusion of fixed effects also had little impact on model R^2 values. Across the colonies tracked, the estimated mean foraging range varied from 13 km to 67 km based on conditional estimates from our model while also adjusting for log_{10} colony size which was included as a fixed effect in our model (Fig. 2, Table S7). The 95% CRI of these estimates generally overlapped to some degree across most of the colonies observed but the figure still highlights the degree of variation among sites.

Common Guillemot

ICCs from the random effects only model provided evidence for between-site variation in foraging range in Guillemots (26% variance explained, Table 2). ICCs associated with between-year and between-individual variation were lower (ICC < 10% variance explained in each case) than the estimated between-site variation.

Guillemot foraging ranges were positively associated with log_{10} colony size (Table 3, Fig. 1, Fig. S51), but there was weak evidence that foraging ranges differed between incubation or chick rearing. During incubation, the average distance travelled was ~ 4 km longer than during chick rearing, but although posterior estimates of $\beta_{\mathrm{Incubation}}$ were centred on positive values the lower 95% credible interval for this coefficient spanned 0. Adjusted ICCs were of a similar magnitude for between-individual and between-year variation, but slightly smaller for between-site variation once log_{10} colony size was included within the model (Table 4). In most cases, 95% CRI of conditional estimates of foraging range for different colonies overlapped and colony-level foraging ranges, excluding those estimated at Fair Isle, varied from 5.68 km to 21.67 km (Fig. 2, Table S8). In contrast, conditional estimates of mean foraging range at the Fair Isle colony were centred on a markedly higher values than other colonies (80.23 km) and were also estimated with relatively wide 95% CRI (see also: Fig. S51).

Razorbill

ICC values from random effects only model provided evidence for between-site and between-year variation in foraging ranges in Razorbill (Table 2). In contrast, the ICC for between-individual variation was relatively small (< 10% variance explained).

Razorbills tended to travel further during incubation than chick-rearing (~10 km, Table 6). Log_{10} colony size was not strongly associated with foraging range (Fig. 1, Table 3, Fig. S52). Excluding Fair Isle, conditional estimates of typical foraging range varied from 12.95 km to 33.00 km across the different colonies tracked (Table S9). In addition, the 95% CRI of conditional estimates generally overlapped across most colonies (Fig. 2). The one exception was estimates from the colony at Fair Isle, where mean foraging range was relatively long (121.71 km), mirroring the result seen in Guillemot at the same colony.

European Shag

For short foraging trips (< 500 metres from the colony), ICC from a random effects only model suggested individual identity was the most important source of variation examined, explaining ~29% of variance in foraging range (Table 2). In contrast, ICC values for between-site and between-year variation were relatively small (Table 2). Neither log_{10} colony size nor breeding status influenced the foraging range of shorter trips, though it should be borne in mind that, by definition, such trips could not exceed 500 metres (Table 3).

For longer foraging trips (≥ 500 metres), both site and individual identity were relatively important sources of variation in mean foraging range, explaining 38% and 21% of variation in this behaviour respectively (Table 3). In contrast, between-year differences explained little variation in mean forging range. In models which included additional fixed effects, foraging range was positively associated with log_{10} colony size but did not differ between incubation and chick rearing (Fig. 1, Table 3, Fig. S53). Estimates of mean foraging range ranged from 1.11 km to 6.75 km across tracked colonies and the 95% CRI of conditional estimates of the foraging range of longer trips generally overlapped (Fig. 2, Table S10).

DISCUSSION

Variance Components Analysis

Previous reviews have documented how, within species, seabird foraging ranges vary, sometimes substantially, among breeding sites, and across years (Thaxter et al. 2012, Woodward et al. 2019, Patterson et al. 2022). Understanding the magnitude and causes of this variation is important if we wish to use foraging ranges as tools in impact assessments (Oppel et al. 2018, Rebstock et al. 2022). The results presented here address these issues by providing a variance component analysis for four species tracked as part of a multi-colony, multi-year tracking study. Across all species examined, the largest single source of variation was between-site variation with colony-level ICCs ranging from 0.18 in Kittiwake to 0.32 in Shag in our random effects only models. In some cases, ICCs for site-level variation were adjusted downwards slightly when including log_{10} colony size in the models (Table 4), probably due its importance as a colony-level predictor explaining some between-site variation. Individual identity explained a relatively small proportion of variation in Guillemot, Razorbill, and Kittiwake foraging ranges, particularly, in the case of Kittiwake, once breeding stage (incubation or chick rearing) was included. In contrast, individual identity explained a greater proportion of variation in Shag for both shorter and longer trips. ICC values relating to between-year variation were generally small across species with the largest year-level ICC values observed in Razorbill, where among year differences explained 16% of variation. However, as our tracking data spanned at most six years within any single breeding colony, we may not be able to estimate the full extent of among-year variation accurately.

When interpreting variance components in non-normal extensions of LMMs (e.g. gamma GLMMs, log-transformation of response variable) it is important to realise that such models utilise a hierarchical structure that involves modelling traits on a latent scale.

Estimates on the latent scale are then converted, via an inverse link function, into expected values around which observed values are drawn according to the specified distribution (de Villemereuil 2020). The distribution-specific variance associated with this process will typically (i.e. for the gamma, and other standard distributional choices in GLMMs) be linked to the mean for distributions other than the Gaussian, so these models assume that there is an irreducible source of variation which therefore implies that on the original scale ICCs from GLMMs are not able to reach a theoretical value of 1.0 (de Villemereuil et al. 2016, Nakagawa et al. 2017). Moreover, the choice of distribution and link function can influence the ICCs calculated (Magnusson et al. 2019). We compared three possible distributional models (see Supporting Online Material – Appendix S4): a gamma GLMM (with log link), a Gaussian model, and a log-normal model. In all cases the log-normal distribution resulted in smaller ICCs in than a gamma distribution (Table S6), whilst the gamma and Gaussian models produced values that were closer to each other. We selected the gamma model, on the basis that it had the best overall fit and plausibility of the three models. The Gaussian model shows very poor empirical fit. The gamma and log-normal models both show good empirical fit, but the log-normal distribution was not used here as such models generated extreme predictions of foraging range in the distributions right-hand tail (e.g. foraging ranges > 1000 km in Kittiwake, Guillemot and Razorbill), far beyond that which we observed and which could influence the reliability of calculated ICCs (Magnusson et al. 2019). Moreover, consideration of which distribution best reflects observed foraging ranges per trip is important because it can, in turn, be used to generate predicted foraging range radii for untracked colonies to help understand species space use using posterior distributions (e.g. Patterson et al. 2022, see also: Supporting Online Material - Appendix S4).

Despite the potential importance of between-site variation across species and between-individual variation in the case of Shag, the individual variance components tested here typically explained, at most, ~30% of variation in mean foraging range. For context, reviews of animal personality (which focus on between-individual variation) report that on average 35% of variation in behaviour can be attributed to individual differences (Bell et al. 2009). Similarly, between-individual variation was found to explain 41% of variation in migratory timing across bird species (Franklin et al. 2022). Recently, Stuber et al. (2022) reported that individual repeatability in spatial behaviours such as home range size or habitat use was also relatively high (>50%). Therefore, the between-individual variation in foraging ranges reported here is lower than that typically observed in other animal behaviours including some related to movement. Nevertheless, from an applied perspective the between-group variation observed here may have an important influence on impact assessments. For example, the longer foraging ranges documented by auks at Fair Isle have led to suggestions that data from these colonies be removed when assessing the foraging range of Guillemot and Razorbill colonies outside of Shetland and the Orkneys (NatureScot 2023). More generally, we also observed important variation in typical foraging ranges across a relatively small number of UK colonies. For instance, conditional estimates of the average foraging range of Kittiwakes ranged from 13 km to 67 km, a 5.2-fold difference (95% CRI: 4.63 – 6.21) across the 20 colonies studied here. Similarly, outside of the UK, Mallory et al. (2019) document multiple instances where foraging ranges varied widely among breeding colonies within the Canadian Arctic across multiple seabird species.

Given the nature of foraging range as a measure of distance between the colony and the terminus of a foraging round-trip some of the between-group variation observed is likely to be generated by differences in key foraging locations across groups. For example, the longer foraging ranges of Kittiwakes observed at colonies in North Yorkshire have previously been attributed to birds selecting to forage on the Dogger Bank where there is a predictable food resource associated with a sandeel (*Ammodytes* spp.) bank located relatively far offshore from the colony (Carroll et al. 2017, Dunn 2021). Similarly, variation in foraging range across two Kittiwake colonies in Norway was driven, in part, by the proximity to a shelf break, a key foraging habitat, that was utilised by both colonies but closer to one colony than the other (Christensen-Dalsgaard et al. 2018). Such foraging sites may be relatively static and predictable across years (Neves et al. 2023), generating consist differences in foraging range between colonies across years. Alternatively, such differences may represent birds exploiting more ephemeral resources located at different distances from specific colonies that were present during a specific tracking period but may be less reliable in the longer-term (Suryan et al. 2002, Goutte et al. 2014). Such mechanisms can also operate to generate between-individual differences as, even within a colony, individuals may show fidelity to specific foraging sites or habitats (Wakefield et al. 2015, Cleasby et al. 2019, Trevail et al. 2021). Because our dataset only included colonies within the UK and Ireland it is also possible that a broader dataset including data on foraging ranges from additional colonies across a wider region, and encompassing greater environmental variability, would find even greater levels of between-group variation. That said, our marginal estimates of typical foraging range (Table 1) generally align with the summarized representative foraging ranges reported by Woodward et al. (2019) who incorporated data from colonies both within and outside the UK (Supporting Online Information - Table S11).

Alongside the variance components considered in the current study, foraging range is likely to vary considerably within individuals as this is often an important variance component in its own right for labile behavioural traits (e.g. Bell et al. 2009, Westneat et al. 2015). For instance, variation in the degree of individual specialisations in Kittiwake habitat selection in response to environmental conditions have already been documented using the tracking data analysed here (Trevail et al. 2021), which may result in individually consistent foraging ranges in some populations. Further investigation of within-individual variance and its drivers is beyond the scope of the current paper and would be better addressed by studies deploying GPS devices for longer and therefore recording more foraging trips per individual (Cleasby et al. 2015b). Nevertheless, it represents one area in which further detailed examination of foraging ranges could be directed.

Effect of colony size and breeding status on foraging range

Foraging range was positively associated with colony size in Guillemot, Kittiwake and Shag (on trips ≥ 500m) though less evidence for a clear association in Razorbill. These findings support previous research in which breeding adults from larger colonies were found to forage further afield than those from smaller colonies (Lewis et al. 2001, Ballance et al. 2009, Patterson et al. 2022). Given the apparent links between colony size and foraging range across seabirds (Jovani et al. 2016) and the availability of census data for many breeding populations (Mitchell et al. 2004, Ronconi et al. 2022) adjusting expectations of foraging range in relation to colony size may provide a way to refine foraging distance-based approaches in the absence of colony-specific tracking data. Longer foraging ranges are also likely to result in declines in the provisioning rate of chicks which can constrain chick growth at some colonies (Gaston et al. 1983).

Foraging ranges were associated with breeding stage (incubation or chick rearing) in Kittiwake, Razorbill and Guillemot, and incubating birds tended to travel slightly further than their chick rearing counterparts. A general pattern in seabirds is for longer trips pre-hatching, followed by a period of shorter trips while young chicks are brooded before foraging trips lengthen again as chicks age and become thermally independent (Oppel et al. 2018). However, it should be borne in mind that our comparisons are based on late-stage incubation and early-stage chick rearing behaviours only. Therefore, during earlier-stage incubation or later-stage chick rearing, the study species may forage further from the colony at other parts of their annual cycle than our results suggest, an uncertainty that should be incorporated into impact assessments (Busch & Garthe 2018). An individual's sex is also likely an important factor influencing foraging range (e.g. Soanes et al. 2014, Cleasby et al. 2015a) but the sex of birds in the current study was unknown so this could not be assessed.

Foraging ranges within applied settings

For any breeding colony not included within our analysis, marginal estimates (Table 1) probably represent the most suitable estimate of expected foraging range (and can be conditioned on colony size if desired) assuming colony-level tracking data from another source are not available. In each case, the 95% credible intervals around marginal estimates were quite wide, reflecting uncertainty in modelled estimates of typical foraging ranges (Tables 1 & 3, Tables S2-S5). Consequently, if using foraging range as an impact assessment tool, this uncertainty should be considered as the difference in area covered between foraging ranges extending to the estimated mean foraging range or those extending to its upper 95% CRI can be substantial. Conditional estimates from our models also demonstrate that while typical foraging ranges are similar across many colonies, certain colonies stand out. For example, the estimated foraging ranges of auks at Fair Isle are markedly longer that those observed at other colonies (Fig. 2, Tables S8 & S9). The breeding success of auks originating from Fair Isle was extremely low during the first four years of study (2010 – 2013, Fair Isle Bird Observatory Annual Reports for 2009-2010, 2011, 2012, 2013). The increased foraging ranges observed at this colony may therefore reflect birds having to travel an unusually long way to find food (Fayet et al. 2021). From a planning perspective, distant sites may only be used occasionally but may be important when foraging conditions are poor (Bogdanova et al. 2014). Regional-scale variation in foraging ranges driven by difference in foraging conditions could also be important but would require sampling multiple colonies within defined regions to assess accurately (Davies et al. 2013).

Across the seabird tracking literature the three most commonly reported foraging range summary metrics are: 1) the absolute maximum foraging range – the maximum foraging distance recorded by a given species; 2) 'mean-max' foraging range - mean of the maximum foraging range reported across a set of *n* tracked colonies; 3) mean foraging range - the grand mean of the mean foraging range reported at each of *n* colonies, possibly weighting by the number of birds tracked at each colony (see: Thaxter et al. 2012, Woodward et al. 2019). In terms of existing foraging metrics our results are akin to the global mean foraging range described in Thaxter et al. (2012). However, our modelled estimates differ in that we do not use a two-step approach whereby average foraging range is calculated per colony before a subsequent grand mean is calculated as in Thaxter et al. (2012). Instead, we used variance components for breeding site and year alongside individual identity to account for group-level variation while calculating an overall mean. Within an applied setting, the choice of which foraging range metric to use represents a balance between being suitably precautionary while also seeking to avoid including large areas of space with low seabird densities (Soanes et al. 2016). For example, during windfarm impact assessment, the mean-max foraging range + 1 SD is commonly used during the EIA / Habitats Regulations Assessment screening stage in the UK and has been recommended by relevant statutory nature conservation bodies (e.g. NatureScot 2023). Based on the current dataset, mean-max foraging range + 1 SD does indeed appear to be highly precautionary: <2% of trips exceeded this range across the four species considered (Fig. 3, see also Supporting Online Material - Appendix S7). In contrast, while estimates of mean foraging range from our models may identify areas of higher usage close to colonies, we demonstrate that the performance of generic species-level foraging ranges was not uniform across colonies (see also:), in part due to the different sources of variation examined in the current study. For example, using the upper 95% CRI of mean foraging range estimated by our models to define a foraging radius, we found that the proportion of trips included within said radius varied between tracked colonies to a greater extent than if using the recommended mean-max + 1 SD foraging range (Fig. 3). Therefore, at some colonies the use of species-level average foraging ranges resulted in an underestimation of foraging range and space use. As such, the more conservation mean-max + 1 SD may be preferred for initial screening during EIAs.

Aside from windfarm impact assessments, the overlap between species foraging ranges and other anthropogenic threats (O'Hanlon et al. 2023) or with designated or proposed Marine Protected Areas (MPAs) is also a common application of foraging range metrics (Thaxter et al. 2012, Critchley et al. 2018). However, the same issues relating to between-colony variation will be encountered. As such, this emphasizes the value of site-specific data where it is available, though there remain caveats about adequate tracking sample sizes (Thaxter et al. 2017). Using procedures outlined in Lascelles et al. (2016) the representativeness of tracking data in the current study for colonies in which ≥ 5 birds were tracked was ≥ 70% in most cases (Cleasby et al. 2018) but <50% in a few instances (eg. Kittiwake at Fair Isle and St Agnes and Guillemot at Fowlsheugh). Representativeness, as defined in Lascelles et al. (2016), does not aim to optimise estimation of maximum foraging range itself but nevertheless suggests we could make reasonable assumptions regarding seabird distributions at most tracked colonies. In general, future studies should aim for sample sizes that give the best representation of seabird densities throughout a foraging range (Thaxter et al. 2017, Shimada et al. 2021) rather than prioritising the estimation of maximum foraging range, which by itself contains relatively little spatial information.

Defining foraging range

At first glance the concept of maximum foraging range appears a relatively intuitive and understandable means of summarising seabird behaviour during the breeding season.

However, foraging range is often defined differently across different studies, hampering comparisons. Therefore, how foraging range is measured requires careful definition. Here, we report estimates of mean foraging range based upon observations of individual foraging trips. Such a metric will reflect the maximum distance birds typically travel during a foraging trip and is likely to encompass high use areas, particularly those close to colonies, but will not extend as far as other potential measures of foraging range such as the absolute maximum foraging range recorded by a species or mean-max foraging range (Fig. 3, Thaxter et al. 2012, Soanes et al. 2016). For example, using data from all foraging trips likely results in a mix of shorter and longer trips and it may be only the extent of longer trips (or their frequency) that differs among colonies. As a result, metrics that select the maximum foraging range observed per bird before calculating the average foraging range at a colony or simply select the maximum observed range at a given colony may accentuate differences among colonies to a greater extent but are also based on fewer (more extreme) observations from the right-hand tail of any foraging range distribution (see also: Patterson et al. 2022).

Our results also rely on how foraging trips themselves are defined and subsequently what behaviours they represent. The difficulty in defining a ‘foraging trip’ is exemplified by the challenges we faced when modelling trip distances in Shag. Selecting a distance of 200 metres from the colony to determine when a foraging trip began and ended resulted in a bimodal distribution of foraging ranges for Shag. If we had instead selected a distance threshold of 500 metres bimodality may have been less of an issue. Similarly, the choice of a 1 km distance threshold to define the start and end of foraging trips in other species may have reduced issues of bimodality compared to a smaller threshold distance. Our results in Shag highlight that foraging trips are not necessarily one homogenous group and support previous findings of bimodality in Shag foraging ranges (Wanless et al. 1991) as well as other seabird groups (Congdon et al. 2005, Saraux et al. 2011). The shorter trips identified in Shag may represent rafting, bathing, or roosting behaviour (Evans et al. 2016) rather than being for the sole purpose of gathering food. Researchers must then decide whether these shorter trips perhaps focussed on bathing or rafting etc. can be readily identified and, if so, how they should be included in any further analysis given they could have a large influence on summaries of foraging range. More broadly, some foraging range-based approaches have been shown to perform less well when data are multi-modal (Critchley et al. 2020). However, there are many reasons why seabird foraging ranges might exhibit a multimodal distribution including heterogeneous prey distributions (Fauchald & Erikstad 2002, Goutte et al. 214), individual site fidelity (Wakefield et al. 2015), sex-specific foraging behaviours (Soanes et al. 2014, Cleasby et al. 2015a), and diel patterns in departure times (Rishworth et al. 2014). Given we can increasingly track more individuals for longer periods of time due to the rapid development of tracking technology, multimodal foraging range distributions may be observed more frequently in the future which will need to be reflected in how foraging ranges are used as marine spatial management tools.

Conclusions

Overall, our results suggest that between-site variation explains approximately 20%-30% of the observed variation in mean foraging range across four seabird species. We believe accounting for this amount of variation within an applied setting is likely to be important and emphasizes the preference for collecting colony-specific data when possible. As tracking at larger scale becomes more practicable and habitat modelling procedures develop such methods may therefore begin to supersede simpler foraging range-based assumptions (Matthiopoulos et al. 2022, Ronconi et al. 2022). Among individual differences appeared to be relatively important in explaining variation in Shag foraging ranges but less so in the other species examined. However, because Shag generally have shorter foraging trips than the other species examined, we typically observe more foraging trips per individual during our tracking period (1-9 days). Consequently, it may be easier to estimate between-individual variation in Shag more precisely (Table S12). Colony size and breeding status were also associated with average foraging range in some cases and there was a general tendency for birds from larger colonies (Guillemot, Kittiwake, and Shag) and incubating birds (Kittiwake and Razorbill) to travel slightly further. Far from being an easy measure to work with, we found that foraging range could be summarised in multiple ways and therefore had to be defined carefully and precisely beforehand, was occasionally multi-modal, and our eventual estimates were subject to a high degree of uncertainty with wide credible intervals. Each of these are issues that should be addressed or acknowledged when using foraging range as an impact assessment tool.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1: Additional information on tracking sites and sample sizes

Table S1. Summary colony, and sample size information for GPS tracking data by species.

Fig. S1. Map showing location of colonies tracked in the current study.

Fig. S2. Map showing tracking data for each species studied.

Figs S3 – S9. Maps showing tracking data for European Shag zoomed in to specific colonies.

Appendix S2: Further details on potential device effects

Appendix S3: Results of foraging range analysis using distance-by-sea rather than Haversine distance

Tables S2 – S5. Results of random effects only models for each species using distance-by-sea rather than Haversine distance.

Appendix S4: Posterior Predictive Checks and Comparison of Model ICCs assuming a gamma, log-normal or Gaussian distribution

Figs S10 – S49. Plots of posterior predictive checks of models of foraging range for each species assuming either a gamma, log-normal or Gaussian distribution.

Table S6. Estimated Intra-class Correlation Coefficients for each species assuming either a gamma, log-normal or Gaussian distribution.

Appendix S5: Raw foraging range data and conditional estimates for each tracked colony.

Tables S7 – S10. Conditional estimates from a random effects only model of foraging range at tracked colonies for each species studied.

Figs S50 – S53. Boxplots showing the distribution of foraging ranges observed at each colony for each species.

Appendix S6. Comparison of foraging range estimates in the current study and those reported in Woodward et al. (2019)

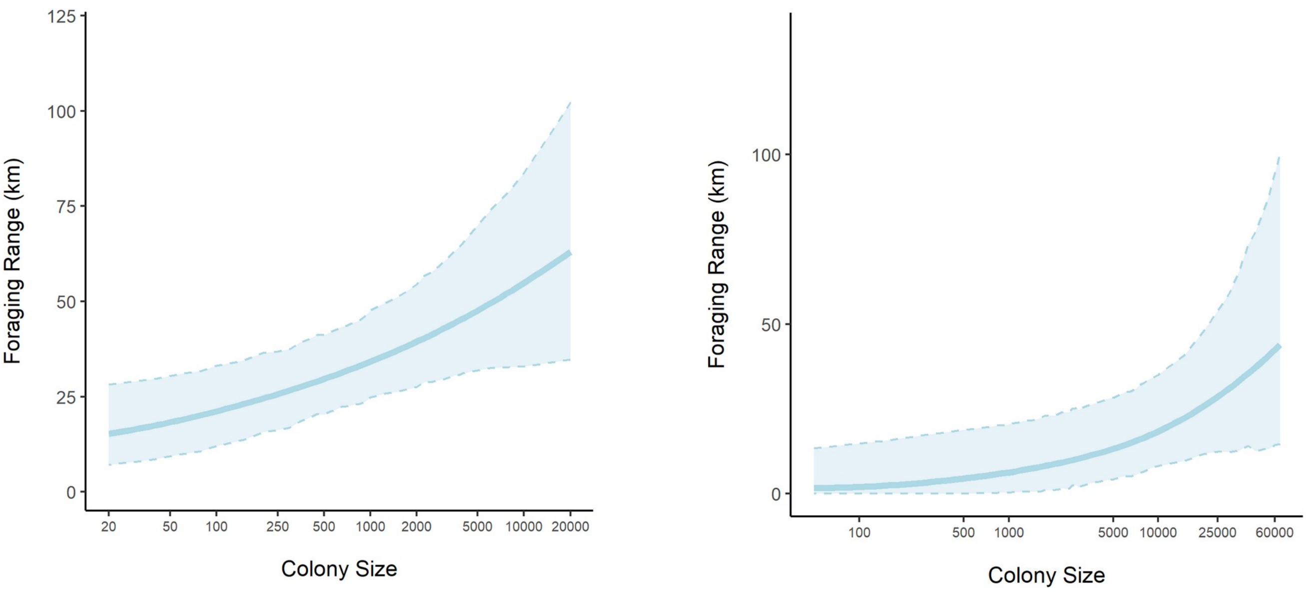
Table S11. Foraging ranges estimates reported for each species included in the current study compared to those reported by Woodward et al. (2019).

Appendix S7. Comparison of the proportion of observed foraging trips falling with different foraging range metrics

Appendix S8. Effect of sample size on variance component estimation

Table S12. Performance of variance component estimation from gamma GLMMs assuming different sample sizes.

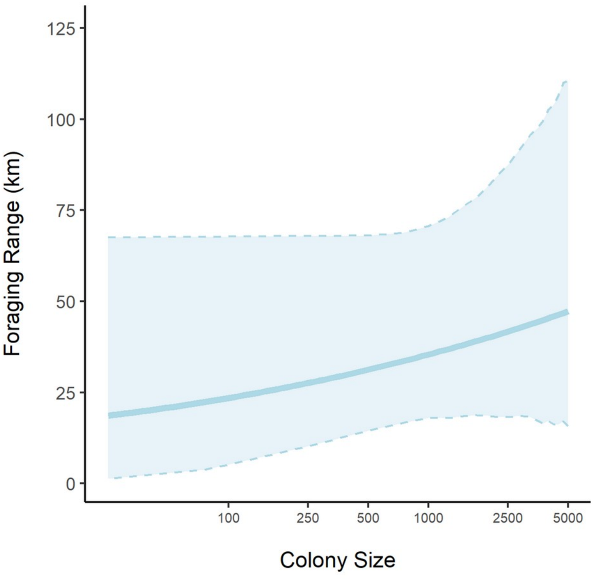
Figure 1. The relationship between *log₁₀* colony size and estimated maximum distance reached offshore from the colony per foraging trip (foraging range) for each species. Estimates represent marginal estimates from models including fixed predictors for a bird in the chick-rearing phase. Colony size is plotted on a *log₁₀* scale on the x-axis; limits of x-axis based on the range of colony sizes observed for each species in this study. The solid blue line represents the predicted slope from the model with the shaded polygon representing the extent of 95% CRI. Results for Shag are for longer trips (≥ 500 m).



Black-legged Kittiwake

Common Guillemot

Razorbill



European Shag

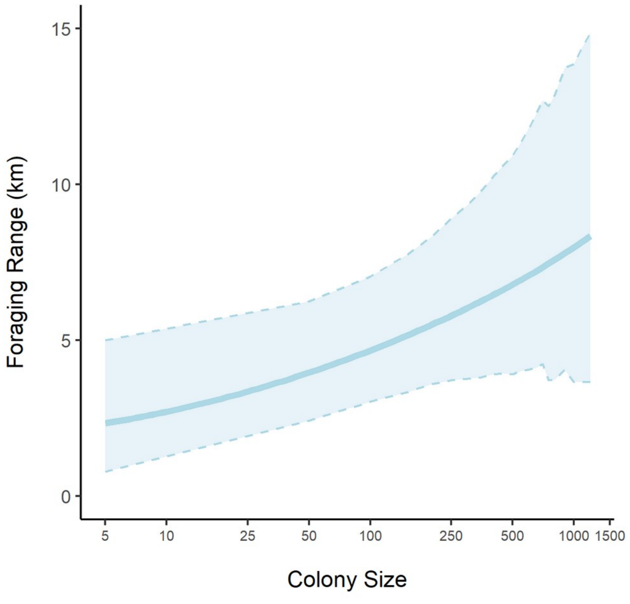
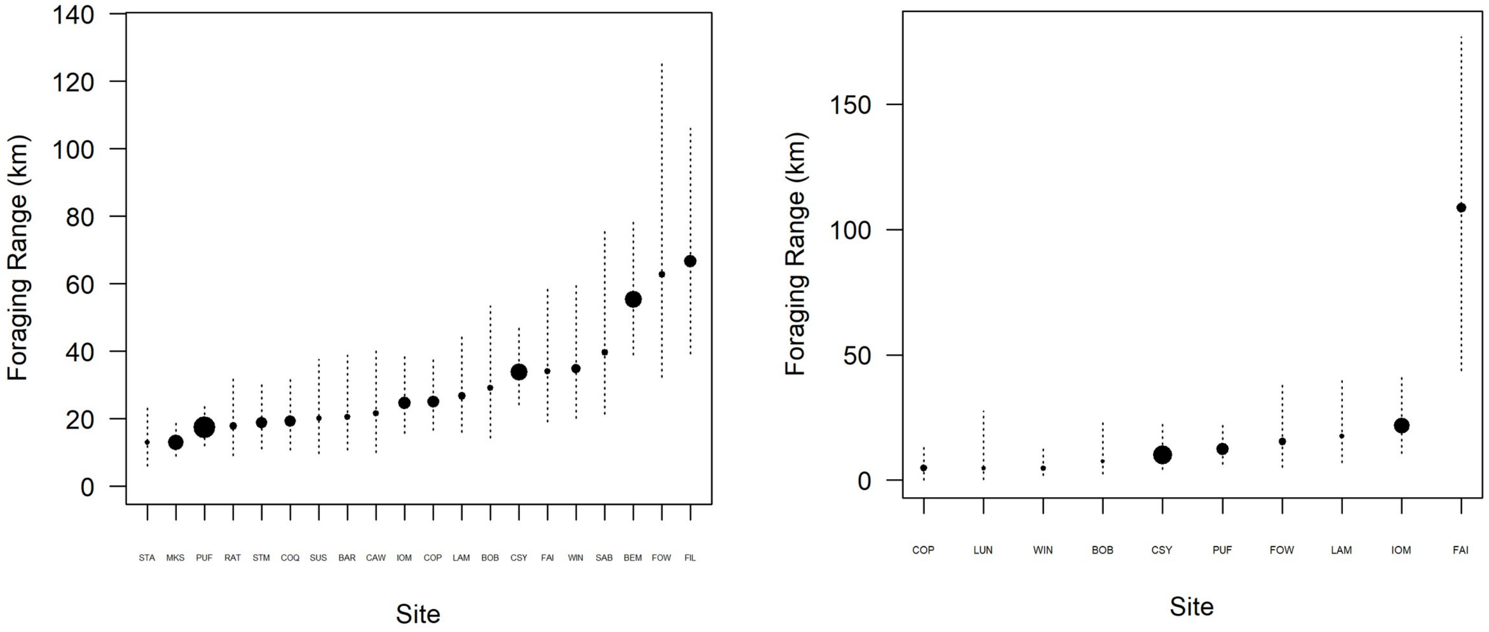


Figure 2. Conditional estimates of mean maximum distance from the colony for foraging trips in Kittiwake, Guillemot, Razorbill, and Shag (trips ≥ 500m). Estimates taken from the models reported in tables 1-4 and are also conditioned on *log₁₀* colony size. Estimates of maximum foraging distance displayed as filled black circle together with corresponding 95% CRI (dashed black lines) for each colony included within the model. Colonies are ordered on the x-axis by the estimates of max. distance from the colony to visualise the degree of between-site variation. Abbreviated site codes for each colony are presented on the x-axis, see Table S1 for details. Within each plot data points are proportional to sample size (no. trips observed) at each colony.



Black-legged Kittiwake

Common Guillemot

Razorbill

European Shag

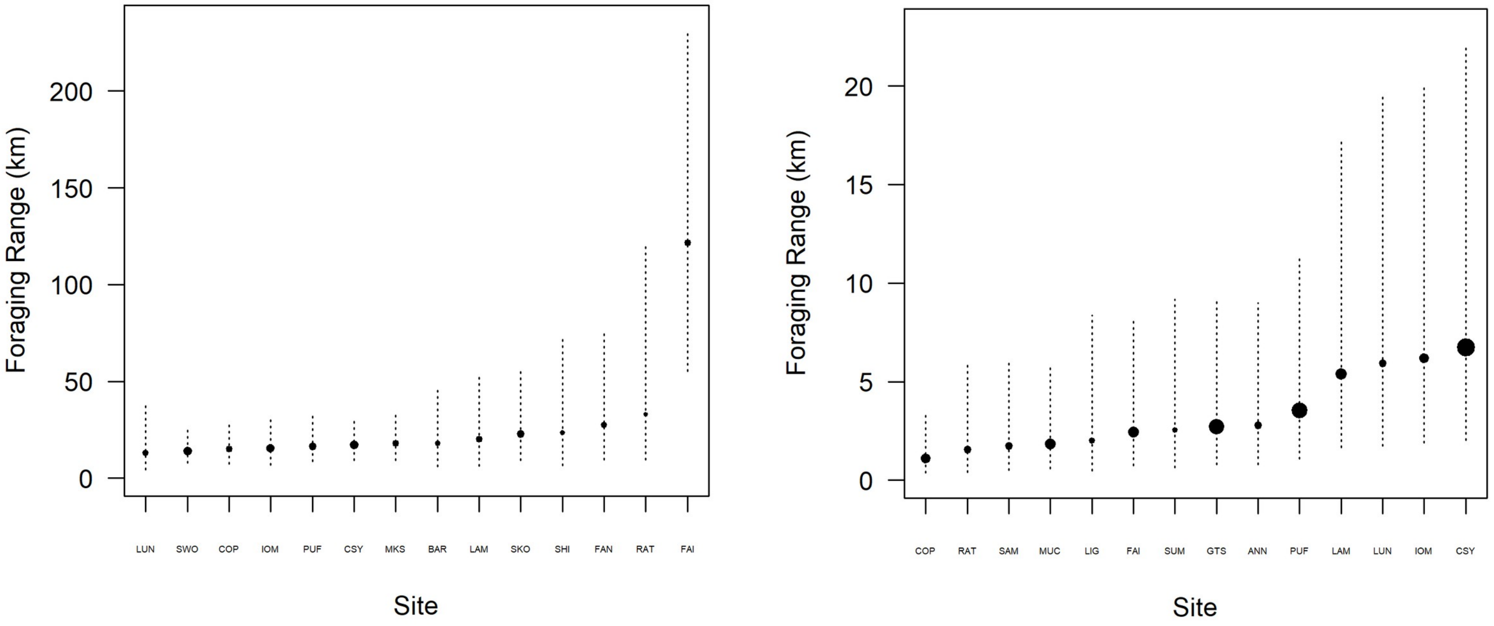


Figure 3. The relationship between different foraging range metrics and the proportion of trips within a specified foraging range at different colonies for each species. Grey lines denote the proportion of trips falling within a given foraging range along the x-axis which was calculated at regular 5 km increments or 1 km for Shag. Each grey line represents a different tracked colony. Vertical lines represent the mean-max foraging range, mean-max + 1 SD and the U95% CRI of the mean foraging range estimated from random effects only models in the main text.

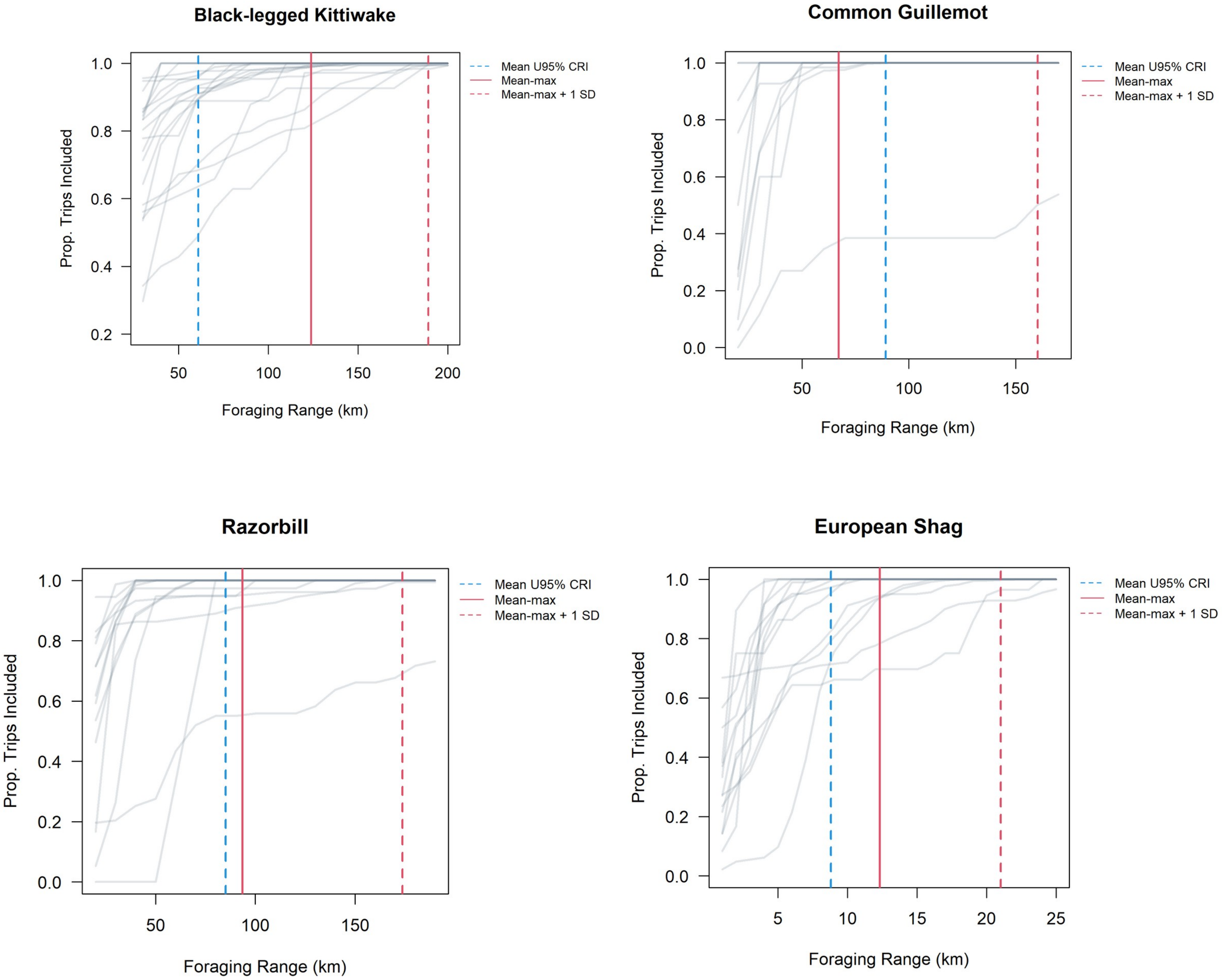


Table 1. Summary of calculated ICCs for each species based on model coefficients from a random effects only gamma model. Estimates represent median ICC values along with 95% CRI.

Intra-class Correlation Coefficient (ICC)	Species				
	Kittiwake	Guillemot	Razorbill	Shag (Trips < 500 m from colony)	Shag (Trips ≥ 500 m from colony)
σ Site	0.18 (0.059 – 0.35)	0.26 (0.071 – 0.84)	0.26 (0.10 – 0.52)	0.098 (0.002 – 0.38)	0.38 (0.19– 0.61)
σ Site : SiteYear	0.09 (0.033 – 0.17)	0.091 (0.025 – 0.28)	0.16 (0.07 – 0.29)	0.002 (0.0001 – 0.015)	0.02 (0.0002 – 0.088)
σ Site : SiteYear: id	0.17 (0.12 – 0.23)	0.043 (0.016 – 0.091)	0.065 (0.032 – 0.11)	0.29 (0.17 – 0.42)	0.21 (0.12 – 0.31)

Table 2. Results of foraging range models for each species. Model coefficients displayed were obtained from a random effects only gamma model and represent median values with corresponding 95% CRI in brackets. Model predictions of foraging range displayed onto the original scale (km) as marginal estimates from the model. Random effect variance parameters were used to calculate the ICC values in Table 1. Due to bimodality in the foraging ranges of Shag trips a single, fixed effect predictor classifying the length of foraging trips as short of long was included in the model for this species. Variance components for shorter and longer trips in Shag were estimated separately. In addition, sample sizes and model R^2 also reported separately for shorter and longer trips.

Species	Parameter	Estimate (95% CRI)	Original Scale (95% CRI)
Black-legged Kittiwake	Intercept	3.30 (2.98 – 3.62)	41.47 km (27.85 – 61.01)
n = 20 Sites, 52 SiteYears, 601 Individuals, 1930 Observations	σ Site	0.59 (0.34 – 0.92)	
	σ Site : SiteYear	0.41 (0.27 – 0.59)	
	σ Site : SiteYear: id	0.57 (0.51 – 0.65)	
R^2 = 0.44 (0.40 – 0.48)	Shape	1.36 (1.27 – 1.45)	
Common Guillemot	Intercept	2.72 (1.97 – 3.41)	29.99 km (12.55 – 86.14)
n = 10 Sites, 24 SiteYears, 203 Individuals, 779 Observations	σ Site	0.98 (0.53 – 1.74)	
	σ Site : SiteYear	0.46 (0.25 – 0.78)	
	σ Site : SiteYear: id	0.31 (0.22 – 0.40)	
R^2 = 0.47 (0.34 – 0.59)	Shape	1.50 (1.36 – 1.66)	
Razorbill	Intercept	3.15 (2.65– 3.66)	41.84 km (21.74 – 85.11)
n = 14 Sites, 41 SiteYears, 309 Individuals, 1224 Observations	σ Site	0.78 (0.45 – 1.32)	
	σ Site : SiteYear	0.61 (0.42 – 0.87)	
	σ Site : SiteYear: id	0.38 (0.30 – 0.47)	
R^2 = 0.58 (0.51 – 0.64)	Shape	3.15 (2.65 – 3.66)	
European Shag	Intercept	-1.11 (-1.18 - -1.00)	0.35 km (0.32 – 0.38)
Short Trips	Long Trip (≥ 500 m)	2.44 (2.03 - 2.81)	5.36 km (3.31 – 8.81)
n = 11 Sites,	σ Site $_{[\text{Short Trip}]}$	0.09 (0.01 – 0.19)	

26 SiteYears, 86 Individuals,	σ Site : SiteYear $_{\text{[Short Trip]}}$	0.04 (0.001 – 0.10)	
722 Observations	σ Site : SiteYear: id $_{\text{[Short Trip]}}$	0.14 (0.11 – 0.17)	
	σ Site $_{\text{[Long Trip]}}$	0.66 (0.41 – 1.06)	
R^2 = 0.35 (0.30 – 0.40)	σ Site : SiteYear $_{\text{[Long Trip]}}$	0.14 (0.01 – 0.30)	
Long Trips	σ Site : SiteYear: id $_{\text{[Long Trip]}}$	0.47 (0.41 – 0.53)	
n = 14 Sites,	Shape $_{\text{[Short Trip]}}$	28.41 (25.45 – 31.49)	
34 SiteYears, 240 Individuals,	Shape $_{\text{[Long Trip]}}$	3.08 (2.88 – 3.30)	
1787 Observations R^2 = 0.55 (0.52 – 0.59)			

Table 3. Summary of adjusted ICCs for each species based on model coefficients from a gamma model including predictors for colony size and breeding stage. Estimates represent median ICC values along with 95% CRI.

	Species				
Intra-class Correlation Coefficient (ICC)	Kittiwake	Guillemot	Razorbill	Shag (Trips < 500 m from colony)	Shag (Trips ≥ 500 m from colony)
σ Site	0.11 (0.033 – 0.26)	0.20 (0.012 - 0.57)	0.24 (0.092 – 0.52)	0.089 (0.001 – 0.39)	0.32 (0.15 – 0.58)
σ Site : SiteYear	0.072 (0.029 – 0.15)	0.10 (0.017 – 0.29)	0.17 (0.082 – 0.34)	0.031 (0.001 – 0.19)	0.013 (0.001 – 0.088)
σ Site : SiteYear: id	0.18 (0.13 – 0.23)	0.051 (0.019 – 0.10)	0.066 (0.032 – 0.11)	0.29 (0.17 – 0.46)	0.24 (0.13 – 0.32)

Table 4. Results of foraging range models for each species. Model coefficients for fixed and random effects components displayed as median values with corresponding 95% CRI in brackets. Model predictions of foraging range displayed onto the original scale (km) as marginal estimates from the model, conditioned on relevant fixed effect predictors and setting colony size (CS) at specified values for each species. Due to bimodality in the foraging ranges of Shag trips a single, fixed effect predictor classifying the length of foraging trips as short of long was included in the model for this species in two-way interactions with other predictors.

Species	Parameter	Estimate (95% CRI)	Original Scale (95% CRI)
Black-legged Kittiwake n = 20 Sites, 52 SiteYears, 601 Individuals, 1930 Observations R^2 = 0.45 (0.41 – 0.49)	Intercept	1.78 (0.71 – 2.80)	38.44 km (26.11 – 51.49) CS: 1000
	Log_{10} Colony Size	0.47 (0.14 – 0.81)	
	Breeding Status (Incubation)	0.22 (0.03 – 0.40)	8.96 km (1.51 – 20.61) CS:1000
	Breeding Status (Unknown)	-0.38 (-0.68 – -0.08)	
	First Trip Post Tag Attachment	0.02 (-0.13 – 0.10)	0.35 km (-2.62 – 3.58) CS: 1000
	σ Site	0.45 (0.26 – 0.73)	
	σ Site : SiteYear	0.36 (0.23 – 0.52)	
	σ Site : SiteYear: id	0.57 (0.50 – 0.64)	
	Shape	1.36 (1.28 – 1.45)	
Common Guillemot n = 10 Sites, 24 SiteYears, 203 Individuals, 779 Observations R^2 = 0.50 (0.34 – 0.58)	Intercept	-1.82 (-7.33– 3.73)	24.32 km (9.66 – 63.09) Colony Size = 5000
	Log_{10} Colony Size	1.07 (0.16 – 2.34)	
	Breeding Status (Incubation)	0.18 (-0.07 – 0.45)	4.31 km (-2.64 – 18.43)
	σ Site	0.63 (0.20 – 1.32)	
	σ Site : SiteYear	0.46 (0.25 – 0.78)	
	σ Site : SiteYear: id	0.32 (0.23 – 0.41)	

	Shape	1.51 (1.36 – 1.67)	
Razorbill *n* = 14 Sites, 41 SiteYears, 309 Individuals, 1224 Observations R^2 = 0.59 (0.52 – 0.65)	Intercept	1.85 (-0.91 – 4.80)	42.97 km (18.47 – 93.10) CS: 3000
	Log_{10} Colony Size	0.42 (-0.57 – 1.29)	
	Breeding Status (Incubation)	0.22 (0.01 – 0.41)	10.67 km (0.97 – 32.09)
	Breeding Status (Unknown)	0.20 (-0.38 – 0.76)	
	σ Site	0.76 (0.40 – 1.30)	
	σ Site : SiteYear	0.62 (0.42 – 0.87)	
	σ Site : SiteYear: id	0.39 (0.29 – 0.47)	
	Shape	1.36 (1.26 – 1.48)	
European Shag Short Trips *n* = 11 Sites, 26 SiteYears, 86 Individuals, 722 Observations R^2 = 0.36 (0.30 – 0.40) Long Trips *n* = 14 Sites, 34 SiteYears, 240 Individuals, 1787 Observations R^2 = 0.56 (0.52 – 0.59)	Intercept	-1.03 (-1.23 - -0.81)	0.35 km (0.31 – 0.39) CS: 500
	Long Trip (≥ 500 m)	1.07 (0.23 – 2.28)	7.12 km (3.91 – 10.93) CS: 500
	Log_{10} Colony Size	-0.02 (-0.13 – 0.09)	
	Breeding Status (Incubation)	-0.06 (-0.18 – 0.07)	-0.002 km (-0.033 – 0.036) CS: 500
	Breeding Status (Unknown)	-0.05 (-0.34 – 0.22)	
	Log10 Colony Size × Long Trip	0.62 (0.06 – 1.19)	
	Breeding Status (Incubation) × Long Trip	-0.01 (-0.25 – 0.24)	-0.46 km (-1.91 – 1.02) CS: 500
	Breeding Status (Unknown) × Long Trip	0.26 (-0.20 – 0.70)	
	σ Site $_{\text{[Short Trip]}}$	0.08 (0.01 – 0.20)	
	σ Site : SiteYear $_{\text{[Short Trip]}}$	0.05 (0.01 – 0.12)	
	σ Site : SiteYear: id $_{\text{[Short Trip]}}$	0.14 (0.11 – 0.18)	
	σ Site $_{\text{[Long Trip]}}$	0.57 (0.34 – 0.94)	

σ Site : SiteYear $_{\text{[Long Trip]}}$	0.12 (0.01 – 0.27)	
σ Site : SiteYear: id $_{\text{[Long Trip]}}$	0.47 (0.42 – 0.53)	
Shape $_{\text{[Short Trip]}}$	28.41 (25.43 – 31.54)	
Shape $_{\text{[Long Trip]}}$	3.08 (2.88 – 3.29)	