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Research Article

Sample Size Required to Characterize Area Use of Tracked Seabirds

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ABSTRACT Conflicts in resource use between humans and wildlife populations are increasingly determined through quantitative approaches. To better understand interactions between birds and human activities in the marine environment, telemetry is routinely used to characterize the area use of species, but evaluations are often based on a small number of individuals taken as representative of a local population studied. Furthermore, the relative importance of the number of animals required and for what duration they should be tracked has received little attention. We examined the central-place foraging movements of 24 lesser black-backed gulls (*Larus fuscus*) from a protected population from 1 March to 31 August during 2010–2013. Using bootstrapping and non-linear modeling, we investigated whether sample sizes were sufficient to characterize offshore area use by considering the cumulative area use for an increasing number of birds and duration of tracking. Box-and-whisker analysis suggested a minimum of 13 birds and a precautionary upper maximum of 41 birds were needed to describe 95% of the estimated area use of the population (defined by 100% occupancy). Tracking fewer birds for longer was more important than tracking more birds for less time. A period of 145 days was required to characterize area use for 13–41 birds; however, offshore areas were used primarily after May, meaning that a 97-day tracking period from May onwards was also representative. Predicted and observed areas were strongly correlated, and the predicted area of 15 birds for 151 days was 91% of the total estimated for the population. These findings suggest that the data were suitable for determining interaction with offshore developments, and were characteristic of the population. This study has revealed the power of a long-term tracking dataset, and has uncovered further complexities surrounding study design and analysis that may shape conclusions drawn. The method and considerations raised have wider applicability for other datasets where human-wildlife resource use conflicts need to be assessed. © 2017 The Wildlife Society.

KEY WORDS area occupancy, bootstrap resampling, lesser black-backed gull, non-linear modeling, offshore wind farm, sensitivity analysis, telemetry.

Telemetry has become a central tool to study the movements, behavior, and area use of animals (Ropert-Coudert and Wilson 2005, Wilson and Vandenabeele 2012). Advances in technologies are now permitting detailed understanding of where there is existing, or potential for, conflict in resource use with humans, from the largest African mammals (Graham et al. 2009) to small bats (Castle et al. 2015) and birds (Bridge et al. 2011). A central question, however, is whether the data gathered appropriately characterize the area use by a species to make robust conclusions as to the potential impacts of such activities.

The importance of sampling regimes in assessing the area use and behavior of animals has previously been highlighted (Seaman et al. 1999, Girard et al. 2002, Nicholls et al. 2005, Börger et al. 2006). A number of approaches have been adopted to quantify the veracity of data gathered, such as determining a minimum number of points per animal (Seaman et al. 1999, Girard et al. 2002, Hodder et al. 2007, Harless et al. 2010, Kolodzinski et al. 2010) and numbers of animals (Hindell et al. 2003, Börger et al. 2006) required to estimate home range. These methods have commonality because they use forms of incremental analysis, assuming that a home range will reach an asymptote with an adequate number of samples (Börger et al. 2006). Further, recent studies have provided methodological advances in investigating the power of tracking datasets for central-place foragers, such as seabirds during the breeding season (Soanes et al. 2013, 2014, 2015; Bogdanova et al. 2014; Lascelles

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et al. 2016). Indeed, telemetry has been central in revealing important foraging areas and commuting patterns in seabirds (Hamer et al. 2007, Bogdanova et al. 2014), allowing potential interactions with human marine activities to be evaluated (Langston et al. 2013, Wade et al. 2014). In one such approach, Soanes et al. (2013), allowed a sampling regime to be determined based on the number of foraging trips from the colony during the breeding season and the number of birds tracked. If an appropriate number of animals have been tracked for a suitable period, then area usage can be appropriately characterized for the study population. Correspondingly, the quantification of any potential interaction between humans and wildlife will be meaningful and representative. Although such assessments are informative as a *post hoc* test on the data collected, they can also be used to inform future studies to determine the number of devices needed to estimate area use (Soanes et al. 2013).

Within a given period, studies may record as little as only 1 foraging trip per individual from a central place, or use only the first trip to draw conclusions or make predictions on habitat use or foraging behavior (Grémillet et al. 2008, Quintana et al. 2011). Even where multiple trips are recorded, this may be only for a restricted period during the breeding season (Votier et al. 2006, Soanes et al. 2013). The foraging behavior of many species can vary considerably across the pre-breeding, breeding, and post-breeding periods when birds are associated with colonies (Thaxter et al. 2015); therefore, tracking for a short period may not adequately characterize the full extent of habitat use. Resource use by species may also vary on an inter-annual basis (Hamer et al. 2007, Thaxter et al. 2015, Warwick-Evans et al. 2016); therefore, tracking over several years may be needed to build up a coherent picture of habitat use. Bogdanova et al. (2014) reported that over a 15-year period, data from 1 year captured on average 54% of the breeding season foraging distribution of European shags (*Phalacrocorax aristotelis*) with 8 years needed to reach 90%. Where possible, tracking species for longer periods throughout the year will provide a more complete appraisal of habitat use and interactions between species and marine developments. Long-life tracking devices now permit such wider temporal investigation (Bouten et al. 2013). However, the trade-offs between tracking fewer birds for longer or more birds for shorter time have not been assessed for the entirety of life-history stages of the intra-annual cycle.

We used information collected from 24 central-place foraging lesser black-backed gulls (*Larus fuscus*) tracked within (intra-annual) the year (during the period that they were associated with their breeding colony) and across multiple years (inter-annual) using global positioning system (GPS) devices (Bouten et al. 2013). Our primary objectives were to determine how many birds needed to be tracked, and for what duration, to characterize offshore area use for the population. Further, we determined if sample sizes were deficient, how many extra birds would be needed and over what duration. Through this work, we also aimed to provide guidance on future study design and analytical thresholds.

STUDY AREA

We studied lesser black-backed gulls at a colony of 550–640 apparently occupied territories (Marsh 2013) at Orford Ness, Suffolk, United Kingdom (52°06′N, 1°35′E) over 4 consecutive years (Jun 2010–Aug 2013). Several operational, consented, or proposed offshore wind farms are located within the foraging range of breeding birds from this colony (Thaxter et al. 2015). Orford Ness forms part of the Alde-Ore Estuary Site of Special Scientific Interest and Special Protection Area (SPA), classified under the European Commission Birds Directive (79/409/EEC) for its breeding populations of Eurasian marsh harrier (*Circus aeruginosus*), lesser black-backed gull, pied avocet (*Recurvirostra avosetta*), little tern (*Sternula albifrons*), and Sandwich tern (*Thalasseus sandvicensis*), and wintering ruff (*Calidris pugnax*), avocet, and common redshank (*Tringa totanus*; Joint Nature Conservation Committee 2016). The SPA covers an area of 24.0 km^2 and comprises of temperate intertidal mud-flats, salt marsh, vegetated shingle, saline lagoons, and semi-intensified grazing marsh (Stroud et al. 2001). Orford Ness is a shingle spit, heath, and cuspate foreland habitat, which has been shaped by centuries of longshore drift and wave patterns giving rise to ridges and valleys, and was subject to recent military use, now ceased. The vegetated shingle (total of 5.7 km^2) includes specialized floral communities, including shingle heath dominated by sea campion (*Silene uniflora*) and false oat grass (*Arrhenatherum elatius*) alongside numerous lichen species. Lesser black-backed gulls breed in areas characterized as grazing marsh, influenced by historical reclamation and military activity, now left as natural succession, dominated by rough grass sea couch (*Elytrigia atherica*; National Trust 2017). The rainfall yearly total at nearby Levington climate station for 1981–2010 was 561 mm, peaking in October, with a mean annual temperature of 14.2°C and a maximum average 22.4°C in August (Met Office 2017). For the purposes of this study, data collection each year was limited to 1 March to 31 August while birds were associated with the breeding colony. This period corresponded to pre-breeding (Mar and Apr), breeding (May and Jun), and post-breeding (Jul and Aug). Although lesser black-backed gulls forage in terrestrial and marine habitats (Thaxter et al. 2015), the focus of this study was offshore area use.

METHODS

Capture Methods and Attachment of Devices

We captured birds at the nest site during early incubation using a walk-in wire mesh trap (Thaxter et al. 2014). During June 2010 and May 2011, we attached solar-powered GPS devices (University of Amsterdam, Amsterdam, Netherlands; Bouten et al. 2013) using either a leg-loop harness ($n = 3$ birds, 2010), a body harness with a breast strap ($n = 4$ birds, 2010), or a wing harness ($n = 4$ birds, 2010, 14 birds 2011; Thaxter et al. 2014, 2015). The total mass of devices (plus harness) was 21 g (<3% body mass, $\bar{x}$ weight = 851 ± 85 [SE] g, range = 710–955 g). There was no effect of harnesses on territory attendance, breeding success, or over-winter survival (Thaxter et al. 2016); therefore, behavior is considered representative. All handling of birds was in accordance with ethical protocols set out by the British Trust for Ornithology (BTO; Redfern and Clark 2001), responsible for licensing of bird ringing activities in the United Kingdom. Further licensing endorsements under individual ringing permits were approved by the Special Methods Technical Panel, an independent body reporting to the BTO Ringing Committee, and followed strict guidelines in compliance with the panel and established procedures previously used on this species (Shamoun-Baranes et al. 2011, 2017). Of the 25 tags deployed, 24 produced data; 1 bird lost its tag immediately after deployment (Thaxter et al. 2014). We used a grid-based approach (2×2 km^2) to examine area occupancy (Soanes et al. 2013) within offshore grid squares. The span of years available was too short to properly assess whether inter-annual fluctuations in movements had been fully characterized (Bogdanova et al. 2014). Following initial investigations of data from individual years, we pooled data across years for final predictions. Because the study period included months before and after breeding when birds were less restricted to central-place foraging trips, we used a measurement of days rather than trips. We numbered days from the first instance the bird was tracked (2010 and 2011), or for birds returning to the colony in subsequent years, from the first instance they were recorded in the March to August period. During breeding, GPS locations were taken every 5 minutes while birds were away from the colony and 30 minutes at the colony, whereas in pre-breeding and late post-breeding (mid-Jul onwards) periods, tags were set to 30 minutes. We interpolated GPS points to 1-second intervals to avoid birds moving across a square without contribution to the time budget. For each bird, we first calculated the time spent in each offshore square each day and averaged time across years. We assumed occupancy of grid squares to be zero for days that birds were outside the study area, including those days spent wholly inland. Further data manipulation details are provided below under the analysis section for bootstrap sampling and non-linear modeling.

Analysis

We drew from the method of Soanes et al. (2013) and developed this approach further to quantify area use in relation to the number of birds and number of days of data. Using bootstrapping, we assessed the variation in the relationship between area use, the number of birds tracked, and tracking duration. We then used non-linear modeling to predict the total area use of birds from the colony, and in turn back-predicted a number of birds needed to provide a robust characterization of this total area.

Initial starting sample sizes.—The approach of Soanes et al. (2013) uses an iterative sampling of a number of birds for a set number of trips, so that each bird has the same level of sampling effort, so as not to bias the results by individual bird behavior. This approach discards further trips for birds with more data to align all birds with the minimum shared number. We term this a starting sample, and for our case, we use number of days rather than number of trips. We selected a core starting sample of birds and days (12 birds tracked for 160 days) approximating a median sample size, alongside a lower sample (9 birds for 170 days) and an upper sample (15 birds for 151 days). We further considered all available starting samples (see Sections S1 and S2, available online in Supporting Information) to compare their separate predictions (sensitivity section); however, only samples of 5 to 17 birds that had $\geq$143 days data available were representative of the full March to August period, covering pre-breeding, breeding, and post-breeding periods.

Bootstrap sampling and non-linear modeling.—We used a bootstrapping approach to investigate the relationship between cumulatively increasing numbers of birds or days and area used (km^2), based on 100%, 95%, 75%, and 50% occupancy values; the occupancy levels chosen reflected those used in previous studies (Hamer et al. 2007, Casper et al. 2010, Soanes et al. 2013). For each starting sample of birds and days, the algorithm selected a sample of birds (providing the desired no. days needed) for an individual bootstrap. The algorithm then sequentially added birds to the sample to yield a matrix of time spent in each square each day, and then cumulatively summed the time for each square across days. We then ordered squares by the summed time spent in them (from greatest to least) such that the minimum number of squares needed to produce the desired occupancy levels could be calculated. We repeated this process for all birds sequentially added to the bootstrap for the given starting sample. Following Soanes et al. (2013), results were based on 100% occupancy (see Section S1 for consideration of 95%, 75%, and 50% occupancy). For a desired sample of birds, occasionally more individuals were available than the number required because birds sometimes had the same duration of data available; in those instances, the algorithm randomly selected the desired number of birds from all those with available data. Because of computing time and the number of samples investigated, we ran 1,000 bootstraps (Bogdanova et al. 2014). We conducted the bootstrap procedure in R (R Core Team 2014) and provide R code for bootstrap sampling algorithms in Supporting Information online.

We used non-linear modeling to fit relationships between area use and the cumulative number of birds in each bootstrap. We investigated 6 candidate models (Table 1), selecting the most parsimonious for each bootstrap using

Table 1. Non-linear models fitted to the relationship between the cumulative area use (y) and cumulative number of birds in the sample (x), for lesser black-backed gulls tracked from Orford Ness (Mar–Aug 2010–2013). Coefficients of *a*–*c* denote the shape of the curve relationship; for Michaelis–Menton and two-parameter asymptotic models, the asymptotic value of the y-axis is given by coefficient a, and for the three-parameter asymptotic and logistic models, the asymptote is denoted by coefficient b.

Type	Model structure
Michaelis–Menten	$y = (a \times x)/(b + x)$
Two-parameter asymptotic	$y = a \times (1 - \exp(-x/b))$
Three-parameter asymptotic	$y = a + (b - a)(1 - \exp(-x/c))$
Three-parameter logistic	$y = b/(1 + \exp(a \times (x - c)))$
Linear	$y = a + b \times x$
Polynomial	$y = a + x - x^2$

Akaike's Information Criterion (AIC) and considered models with $\Delta\text{AIC} \leq 2$ to be competitive. Using this best-fitting bird–area curve for each bootstrap, we estimated the area use of the population (1,280 breeding individuals; Marsh 2013) together with the back-transformed number of birds (i.e., predicted number) needed to describe 95% (Soanes et al. 2013), 90% (Bogdanova et al. 2014), or 50% estimated area use of the population. We fit curves for all combinations of increasing numbers of birds and days for each starting sample, but extrapolations for increasing numbers of birds beyond the sample size of 24 birds were based on the maximum number of days (Soanes et al. 2013). We used box-and-whisker analysis to assess the variance of the back-transformed predicted number of birds (Börger et al. 2006). If the number of birds included in the starting sample fell within or exceeded the interquartile range of the predicted number of birds, we interpreted that number as a minimum sufficient number of birds to characterize area use. We considered the upper quartile of the distribution a precautionary maximum limit required. We estimated the number of birds that would be needed to describe 95% of the predicted area use of the overall population as an upper requirement. We also calculated the 90% and 50% thresholds for equivalency to Bogdanova et al. (2014; see Section S2 for results and discussion on selecting a suitable upper limit). For core, lower, and upper starting samples, we expressed the predicted area use for each combination of birds and days as a heat-intensity plot, with values proportional to the predicted area use for the maximum number of birds and days. These plots revealed seasonal plateaus in day–area relationships, and we considered the number of days required to characterize area use to be where they reached an asymptote (see Section S1). To validate results, we predicted area use (in km^2) for the number of birds in the starting sample compared with the observed area use of the same birds used in the starting sample (for the same no. days). We conducted this comparison for core, lower, and upper starting samples and present data through boxplot analysis (median, upper, and lower quartiles) and Pearson's correlation of individual bootstraps (see Section S3, available online in Supporting Information). To provide further context when drawing conclusions, we also used boxplot statistics to assess the predicted area use for the number of birds contributing data to the study (24 birds), the precautionary maximum number of birds estimated to be required to describe area use, and the overall population. We conducted all data processing and mapping in R (version 3.1.2; R Core Team 2014) using custom-written routines, and non-linear modeling using R packages nls2 and drc.

Sensitivity analysis of starting samples.—The final predictions of numbers of birds could theoretically vary depending on what starting sample was initially chosen, and between individual birds added within the samples. Therefore, we assessed their sensitivity by comparing predictions between and within starting samples. We compared predictions from samples with more or fewer birds (and days) by assessing the relationship between the number of birds needed to predict 95% of the area use of the population, and the number of birds in each starting sample; we used jack-knifing to determine if starting samples were sensitive to the number of birds included (Efron and Tibshirani 1993). We sequentially removed birds from the maximum number in the sample, and re-calculated the number of birds needed to predict 95% of the area use of the population each time a bird was removed. These analyses were based on the maximum number of days for the starting sample, and used the same non-linear curve fitting procedure as above. We also fitted non-linear curves to relationships between the numbers of birds in starting samples and numbers of birds predicted.

RESULTS

Area use, expressed by 100% occupancy, showed an asymptotic relationship with a cumulatively increasing number of birds (Fig. 1, Section S1). For longer spans of tracking (~140 days; Fig. 1, Section S1), 2 separate increases and plateaus in area use were apparent with increasing days tracked, reflecting seasonal changes in behavior and tracking duration. Birds made few offshore movements during pre-breeding (first increase and plateau, Mar–May); thereafter birds moved farther offshore during the chick-rearing period (second increase in May–Jul, plateau in Jul–Aug [Figs. 2 and 3]). For some birds, data were only available from the first breeding season of tracking, and thus for a short period May–June onwards. Considering a reduced temporal period covering too few days meant that seasonal patterns in area use were not fully encapsulated (Section S1 and Fig. 2).

The best-fitting non-linear model was the 3-parameter logistic (Table 2, Fig. 4), followed by the Michaelis–Menten. The 3-parameter logistic allows for a more a sigmoidal curve shape, which reflected individual behavior. Birds differed greatly in their habitat use, with some foraging more inland across the study period than others. Thus, there was a high probability of selecting birds that had either more inshore distributions, or simply had much smaller area use, influencing early and late parts of the curve.

We used starting samples of 5–17 birds covering 143–176 days to derive the numbers of birds needed to describe 95% of the estimated area use of the population (Table 3). For the upper sample (15 birds), the predicted numbers of birds needed to describe 95% of the estimated area use of the population were a median of 13 (inter-quartile range [IQR] = 8–41) birds (Table 3). This was the highest prediction from those samples representative of the March–August period (i.e., ≤17 birds). The minimum sufficient number of birds was therefore 13 birds (from the median prediction above), but the precautionary upper limit was 41 birds, taken from the upper quartile value. Equivalent numbers for the lower (9 birds) and core (12 birds) samples were given as 8 birds (IQR = 4–22) and 11 birds (IQR = 7–36), respectively (Table 3). Because the use of a 95% threshold to characterize the area use of the population was subjective, we also calculated results using 90% and 50% values (Section S2).

Heat-intensity plots for core, lower, and upper starting samples suggested that 145 days were needed to characterize 95% estimated area use of the population (Fig. 5), based on

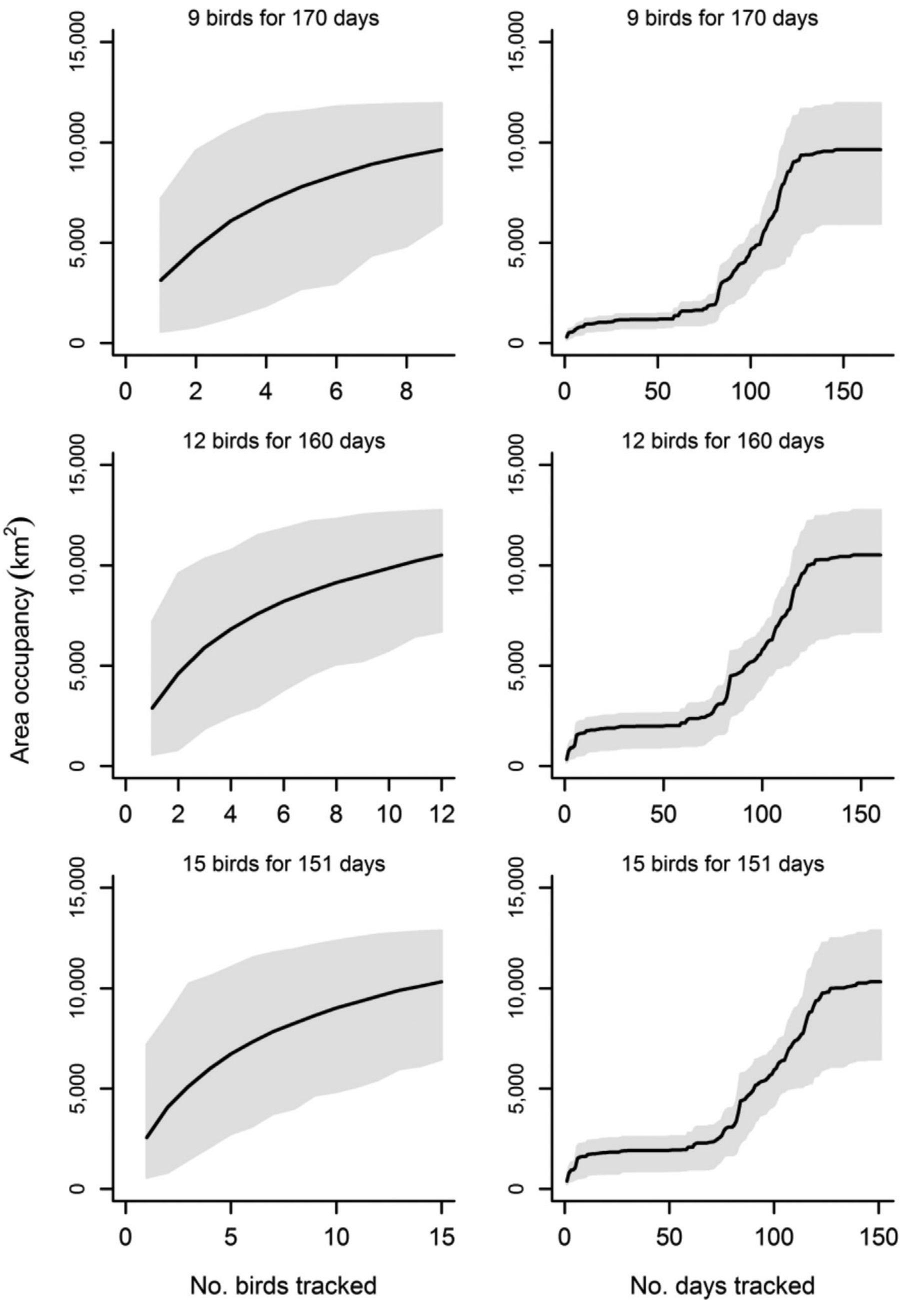

Figure 1. Relationship between cumulative area use (based on 100% occupancy) and cumulatively increasing numbers of lesser black-backed gulls tracked from Orford Ness (Mar–Aug 2010–2013) for the maximum number of days in starting samples and number of days of tracking for the maximum number of birds in starting samples. We considered samples of 9 (lower), 12 (core), and 15 (upper) birds. We show the median (black line) and 95% bootstrap confidence intervals (gray shading).

upper quartile predictions above. The initial plateau in estimated area use that occurred during pre-breeding (Fig. 2) represented 11–12% of the value for the full period, and lasted between days 10 and 58 (plateau duration of 48 days). Given that areas used during pre-breeding were also used later in the study period, these results indicate that characterization of 95% of the estimated area use of the population could be reached by tracking birds for a shorter duration of 87 days (i.e., 145–58 days) from May onwards. Some southerly locations were exclusively but infrequently used during pre-breeding. Consequently, a conservative minimum tracking duration was indicated as 97 days from May (i.e., 145–48 days), including the 10-day period before the first pre-breeding plateau.

Predicted and observed area uses were strongly correlated (see Section S3 for core, lower, and upper starting samples). Further, based on the 15-bird (151 day) sample, the area use predicted for those 15 birds was 10,635 km^2 (IQR = 8,416–11,944 km^2, max. = 13,776 km^2), compared to an observed area of 11,040 km^2 (IQR = 6,444–12,877 km^2, max. = 13,060 km^2), giving additional validation that the models were representative of the observed (measured) data.

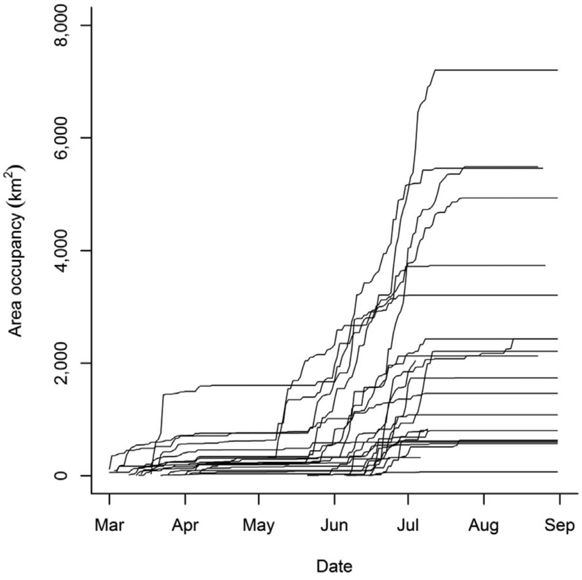

Figure 2. Cumulative increases in area use of lesser black-backed gulls tracked from Orford Ness through the March to August study period (2010–2013) for individual birds.

The total observed area use of the full sample of 24 birds (taking each bird's maximum tracking duration, 6–184 days) was 13,468 km^2, a similar value to the maximum observed area for 15 birds for 151 days above. The predicted median area for 15 birds at 151 days was 95% of the total predicted for overall population (11,662 km^2, IQR = 9,206–14,098 km^2), or 91% based on the upper quartile area prediction (see section S3). Further, using extrapolations from the 15-bird starting sample, had we obtained data across 151 days for all 24 birds tracked in this study, the upper quartile area use prediction was also predicted to have been 91% that of the total population (Table S3.1). We estimated the predicted upper quartile area at 151 days for 41 birds (i.e., the precautionary upper limit of predicted birds) to be 96% that of the population (Table S3.1).

Sensitivity analyses revealed that including more birds in initial starting samples resulted in increases in the predicted number of birds required to characterize area use (Fig. 6a,b). Non-linear models highlighted this was an asymptotic relationship (Fig. 6a,b). Up to the 12-bird sample, upper quartile predictions increased markedly to 36 birds and thereafter stabilized (32 birds predicted for the 17-bird sample). Therefore, predictions generated from starting samples with >12 birds were reliable in estimating the number of birds needing to be tracked to characterize area use.

Sensitivity analyses also indicated that with increasing numbers of birds included within samples, more birds were predicted to be required to characterize 95% of the estimated area use of the population. As above, non-linear models

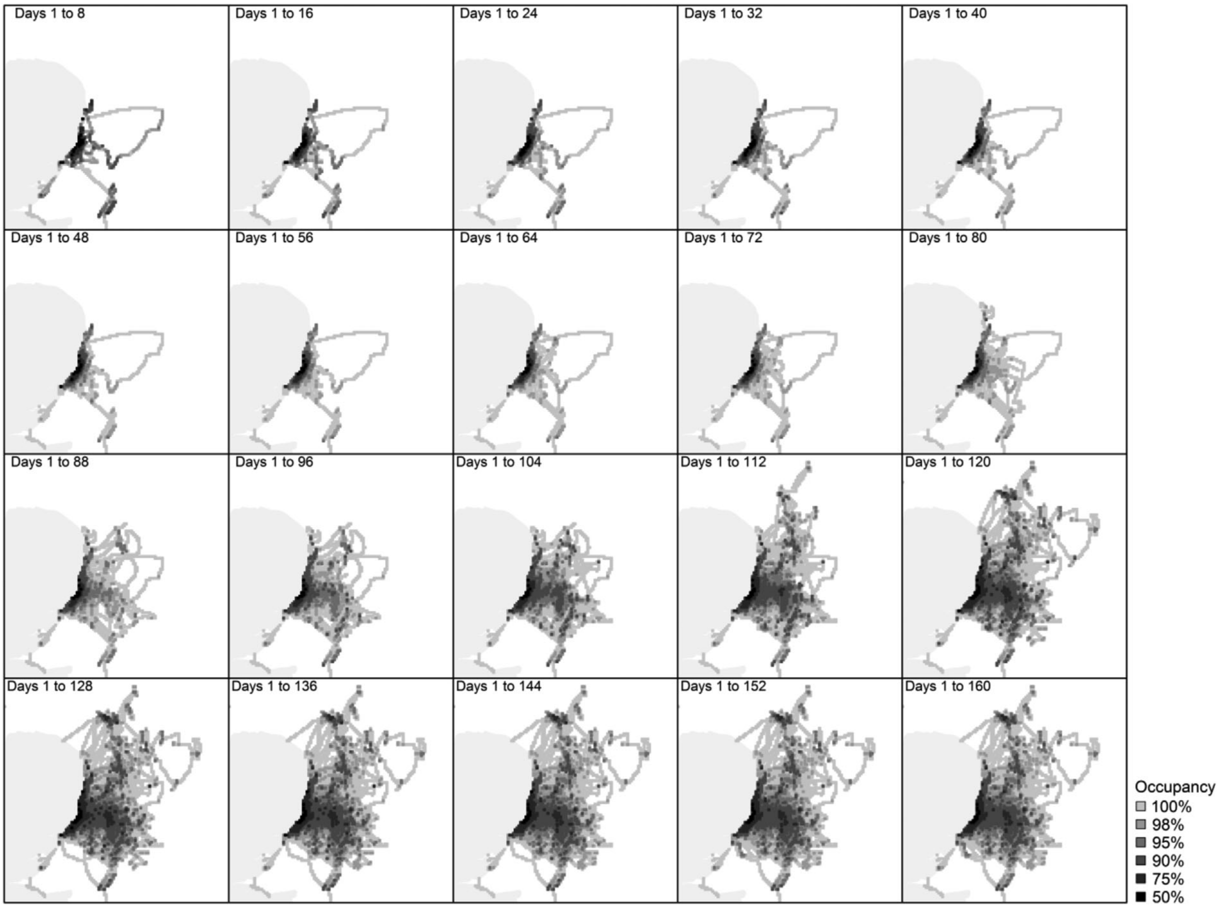

Figure 3. Example output of estimated area use for 12 lesser black-backed gulls tracked from Orford Ness (Mar–Aug 2010–2013) across 160 days; occupancy levels of 50%, 75%, 90%, 95%, 98%, and 100% are presented.

Table 2. Summary of the best models fitted to individual bootstraps for the 9-, 12-, and 15-bird starting samples, for the relationship between area use (based on 100% occupancy) and number of lesser black-backed gulls tracked from Orford Ness (Mar–Aug 2010–2013). Coefficients marked with a dagger (†) are median (lower and upper 95% confidence limit) parameter estimates representing the asymptote for respective models, and *n* represents the number of times the model type was the best-fitting relationship. Coefficients of *a*–*c* denote the shape of the curve relationship in each model.

				Coefficients		
Birds	**Days**	**Model type**	***n***	***a***	***b***	***c***
9	170	Michaelis–Menten	118	14,336.3 (6,823.0, 511,257.1)†	4.3 (0.2, 548.4)	
		Two-parameter asymptotic	74	11,513.3 (7,242.9, 17,509,010.0)†	4.3 (0.8, 16,256.1)	
		Three-parameter asymptotic	169	−9,036.0 (−114,818.9, 6,252.9)	9,548.4 (5,823.4, 14,981.8)†	1.1 (0.3, 11.9)
		Three-parameter logistic	625	−0.7 (−3.8, −0.1)	11,090.4 (5,999.3, 95,864.2)†	2.7 (−1.3, 28.7)
		Linear	13	6,269.3 (5,377.1, 6,545.2)	346.1 (68.8, 543.8)	
		Polynomial	0			
12	160	Michaelis–Menten	182	13,309.9 (7,403.8, 51,751.6)†	3.8 (0.5, 47.4)	
		Two-parameter asymptotic	74	11,528.1 (7,183.4, 969,398.2)†	4.4 (1.0, 1,420.8)	
		Three-parameter asymptotic	165	−4,613.1 (−30,613.8, 6,663.9)	11,054.3 (7,000.2, 27,668.0)†	2 (0.5, 47.5)
		Three-parameter logistic	567	−0.5 (−2.4, −0.1)	11,730.6 (7,014.0, 114,935.7)†	3.4 (−0.9, 35.7)
		Linear	11	2,930.7 (1954.3, 6745.5)	418.2 (145.6, 838.7)	
		Polynomial	0			
15	151	Michaelis–Menten	180	13,400.6 (7,870.2, 107,111.0)†	4.4 (0.6, 140.7)	
		Two-parameter asymptotic	76	11,706.0 (6,452.6, 5,165,314.2)†	4.6 (1.3, 6,561.6)	
		Three-parameter asymptotic	159	−2,157.1 (−15,759.8, 6,929.9)	11,054.3 (6,455.2, 90,061.7)†	3.3 (0.5, 157.7)
		Three-parameter logistic	573	−0.4 (−2.2, −0.1)	11,564.1 (6,690.8, 113,917.0)†	4.1(−0.7, 44.9)
		Linear	11	2,419.1 (1,381.1, 3,680.8)	536 (257.2, 689.8)	
		Polynomial	0			

indicated asymptotic relationships (Fig. 6c,d). For example, for the 16-bird sample, upper quartile predictions increased to 36 birds for 10 birds in the sample, thereafter predictions were between 36 and 40 birds (Fig. 6). Consequently, we considered conclusions based on using the maximum number of birds from starting samples to be robust.

DISCUSSION

Number of Birds and Tracking Duration Required to Characterize Area Use

A minimum of 13 birds (median prediction) and a maximum of 41 birds (upper quartile) were predicted to describe 95% of the estimated area use of the population (Table 3). Sensitivity analyses revealed these predictions to be robust among and within individual starting samples. The minimum tracking duration required to characterize 95% of the offshore area use of the population for March to August was 145 days. However, because of limited offshore area use between March and May, tracking birds for 97 days from early May onwards resulted in equal characterization of the full 145-day period.

The median estimate of 13 birds needed to describe 95% of the estimated area use of the population was smaller than the total number tracked (24 birds), and less than the number of birds considered in the starting sample (15 birds). One interpretation is that a sufficient minimum number of birds was tracked from this population (i.e., ≥13 birds for >145 days). Based on upper quartile values, however, a value of 41 birds was suggested. If the maximum number of birds tracked (24 birds) could have been studied for a full 151 days, the predicted upper quartile area was predicted to be 95% of the predicted area use of that upper quartile value of 41 birds, and 91% of the total population of the colony. The 41-bird value may therefore be considered as an upper precautionary number, and these comparisons strongly suggest the number of birds tracked was sufficient to characterize area use for this population. Conclusions on the duration of tracking and number of individuals to be tracked, however, also reflect the study design, requirements, research questions posed, and further judgements regarding the thresholds used to describe area use to assess the adequacy of sampling.

The Importance of Study Design and Analytical Thresholds

Wider study design.—Aspects of the study, including the period of interest, and questions posed at the outset are central in governing sampling protocols. A study focused on area use solely during part of the breeding period could yield different answers on the appropriate number of individuals and duration of tracking required. For example in breeding birds, the diets of adults and their chicks may differ, meaning that foraging habitat use may also vary (Wilson et al. 2004). Similarly, the sample sizes required to characterize overall area use may differ if defined areas or subsets of habitats are investigated, such as offshore area use as investigated in this study.

The extent of inter- and intra-annual spatial variation in animal movements is well known for many central-place foragers (Sharples et al. 2012, Shackleton et al. 2016),

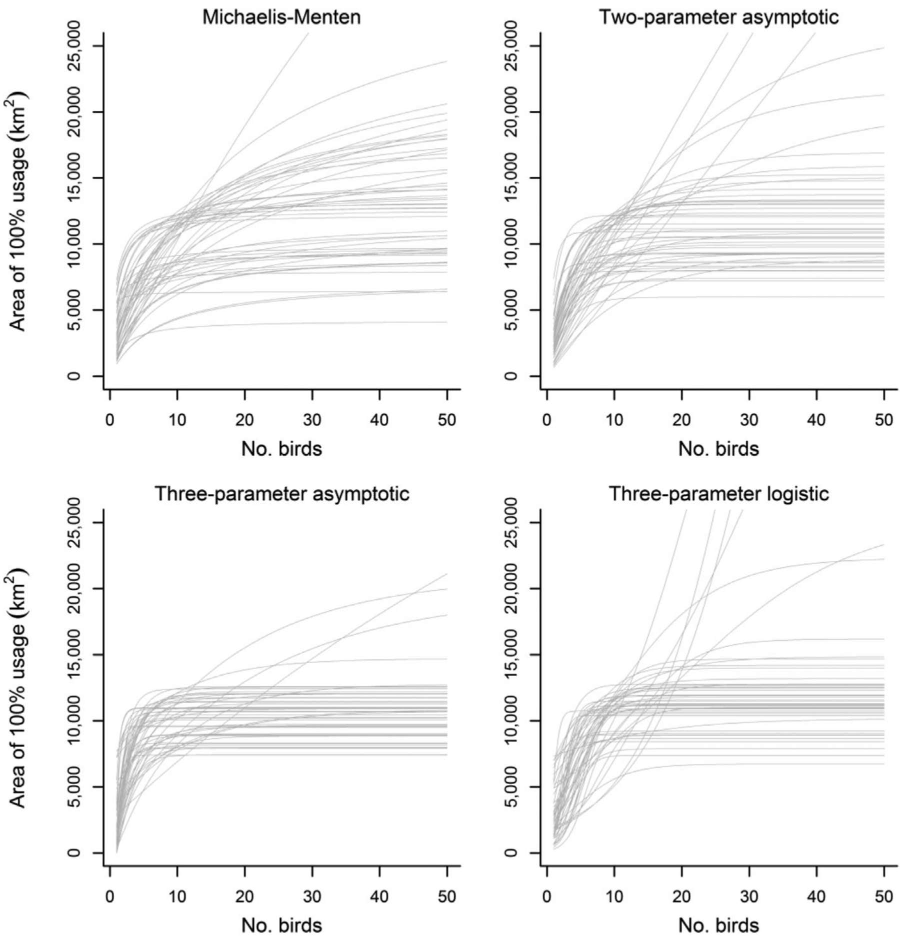

Figure 4. Example plots of the most regularly chosen models representing bootstrap relationships between area use (based on 100% occupancy) and number of lesser black-backed gulls tracked from Orford Ness (Mar–Aug 2010–2013), for the core starting sample of 12 birds over 160 days. Models are based on the maximum number of days in the sample. To show the asymptote characteristics of the curves, the first 50 models for each model type are presented and relationships are extrapolated out to 50 birds.

including seabirds (Hamer et al. 2007, Warwick-Evans et al. 2016). The extent of annual coverage in tracking studies could therefore influence final sampling protocols recommended. Although 4 years of data were available in this study, further years of data may be required to fully estimate population area use (Bogdanova et al. 2014; see individual year predictions in Section S4, available online in Supporting Information). Using upper starting samples, the number of lesser black-backed gulls that were predicted to meet 95% area use of the population in individual years varied between 21 to 47 birds (upper quartile). This range in values bounded the prediction for 4 years (41 birds), but nonetheless represented a 2-fold range. Warwick-Evans et al. (2016) reported individual northern gannets (*Morus bassanus*) foraged over a wider area in years of low food availability. It is possible that the higher asymptotes seen for lesser black-backed gulls in years of poor breeding success (2012; Thaxter et al. 2015) could reflect similar processes operating, but this requires further investigation. Given the known inter-annual variation in space use in some species, >1 year of tracking is highly recommended. Further, only partial understanding may be gleaned from shorter study periods within a season, when animals may not use a full suite of habitats. Consequently, the period of interest is likely to be a key determinant of minimum tracking durations required, as in the case for lesser black-backed gulls. Given the intra- and inter-annual variation apparent lesser black-backed gulls, the choice of solar-powered GPS tags that record over multiple years was also justified.

The devices used in relation to the research goals of the study are also central to determining eventual sampling protocols. For example, studies may commence mid-way during a breeding period when animals are trapped at the central place, such as a nest site or territory, potentially excluding periods of interest earlier in the year. For lesser black-backed gulls in this study, data for the pre-breeding period of March to May were obtained only if individuals returned the year after tag deployment with functioning tags. Not all individuals may survive to provide full temporal coverage, and tags may also malfunction. Correction for likely survival rates for study species (e.g., for lesser black-backed gulls, 91%; Wanless et al. 1996, Camphuysen and Gronert 2012) and devices deployed versus those retrieved, would also need to be applied when considering the total number of tags required at the outset. Conversely, however, given intra-annual variability, for lesser black-backed gulls

Table 3. Boxplot statistics for the numbers of birds needed to describe 95% of the estimated area use of the population, based on 100% occupancy for lesser black-backed gulls tracked from Orford Ness (Mar–Aug 2010–2013). Starting samples of birds are ranked according to the maximum number of days available (for 2010–2013). Results are described for a core (C) sample representing half the number of birds tracked, and lower and upper samples within the central third of the ranked sample sizes available: lower = 9 birds for 170 days (L), upper = 15 birds for 151 days (U), considered representative of the March to August period. Upper whisker = the maximum point falling within 1.5 × (UQ – LQ) + UQ; lower whisker = minimum point falling within LQ – 1.5 × (UQ – LQ).

No. birds[a]	No. days[a]	Lower quartile (LQ)	Median	Upper quartile (UQ)	Whisker range
5	176	2	4	15	1–35
6	173	3	6	17	1–37
7	172	4	6	17	1–36
8	171	4	7	21	1–46
9[L]	170	4	8	22	2–47
10	167	5	9	25	2–53
11	163	6	9	26	2–56
12[C]	160	7	11	36	2–80
13	158	7	11	33	2–72
14	158	8	12	31	2–66
15[U]	151	8	13	41	2–89
16	147	8	13	33	3–69
17[b]	143	9	13	33	3–69

[a] Samples <5 birds deemed too few to produce meaningful predictions (max. duration = 184 days, 2 birds).

[b] Samples >17 birds had too few days (18 birds, 78 days to 24 birds, 6 days) to allow characterization March–August.

the area use for the full March to August study period could be characterized based on data for the period from May to August alone, thus not requiring birds to return.

Analytical decisions.—Numerous judgements regarding the thresholds used to describe area use are also required. We selected 100% occupancy to characterize total area usage; however, we determined that lower occupancy levels can produce slightly different relationships between area use and the number of birds tracked and duration of tracking (Section S1). Such considerations may be species specific. For instance, lesser black-backed gulls use marine and terrestrial environments and this population exhibited a relatively small 50% occupancy area.

The percentage deemed appropriate to describe area use of the population is another important consideration in determining the number of individuals to be tracked and the duration of tracking. For example, is a 95% value acceptable (Soanes et al. 2013, this study) or is a 90% value (Bogdanova et al. 2014) more suitable (Section S2)? For lesser black-backed gulls, we ascertained the number of birds and days tracking that were needed at different threshold levels through graphical representation of the proportion of the total population area use plotted with respect to increases in the numbers of birds and days in the sample (Fig. 5). We estimated the predicted number of birds needed to describe 95% of the estimated area use of the population at 13 (IQR = 8–41) birds. By comparison, 90% and 80% thresholds (the latter as used in standard power analysis) provided predictions of 10 (IQR = 7–25) birds and 8 (IQR = 5-16) birds, respectively.

We used boxplot analyses to derive median, lower, and upper values of numbers of individuals that would be required to estimate a proportion of total area use of the population. However, the choice of percentage quantiles of the distribution can lead to very different conclusions. Such decisions can be informed by comparing the predicted area use for the chosen sample to that of the total population. For instance, in this study the upper quartile of the predicted area use for 41 birds was 96% that of the full population (Table S3.1), suggesting this upper value was precautionary. Taking even higher quantiles, for example out to the upper whisker of the boxplot (89 birds), was therefore likely to be overly cautious.

In our study, a grid size of 2 × 2 km^2 was deemed sufficient to characterize area occupancy. The scale of the analysis, however, is an important element in determining the power of data from spatial analyses (Soanes et al. 2015); larger cells, or comparatively more smoothed utilization distributions from kernel density approaches (Worton 1989), require smaller samples (Soanes et al. 2015). Therefore, further consideration of grid size resolutions would be valuable.

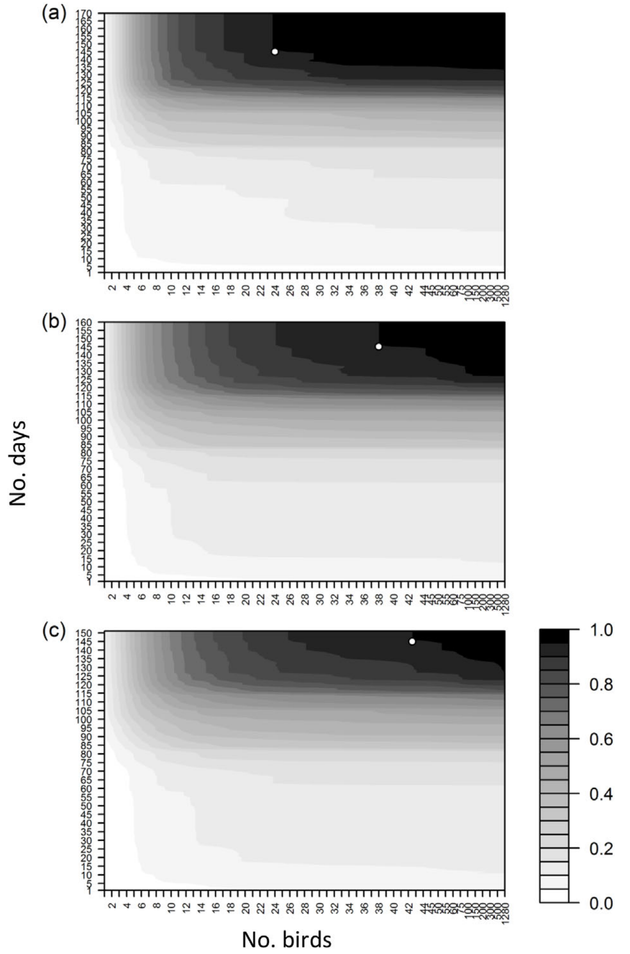

Figure 5. Heat-intensity plot demonstrating the trade-off between the number of lesser black-backed gulls tracked from Orford Ness (Mar–Aug 2010–2013) and number of days considered in estimating the area use for the population. We present starting samples of a) 9 (lower), b) 12 (core), and c) 15 (upper) birds. We present graphs for the upper quartiles of the bootstrap distribution and show the minimum tracking duration needed to describe 95% of the estimated area use of the population (white circles). Proportions are scaled in relation to the estimated area use of the total population at the maximum number of days per sample (max., 1.0).

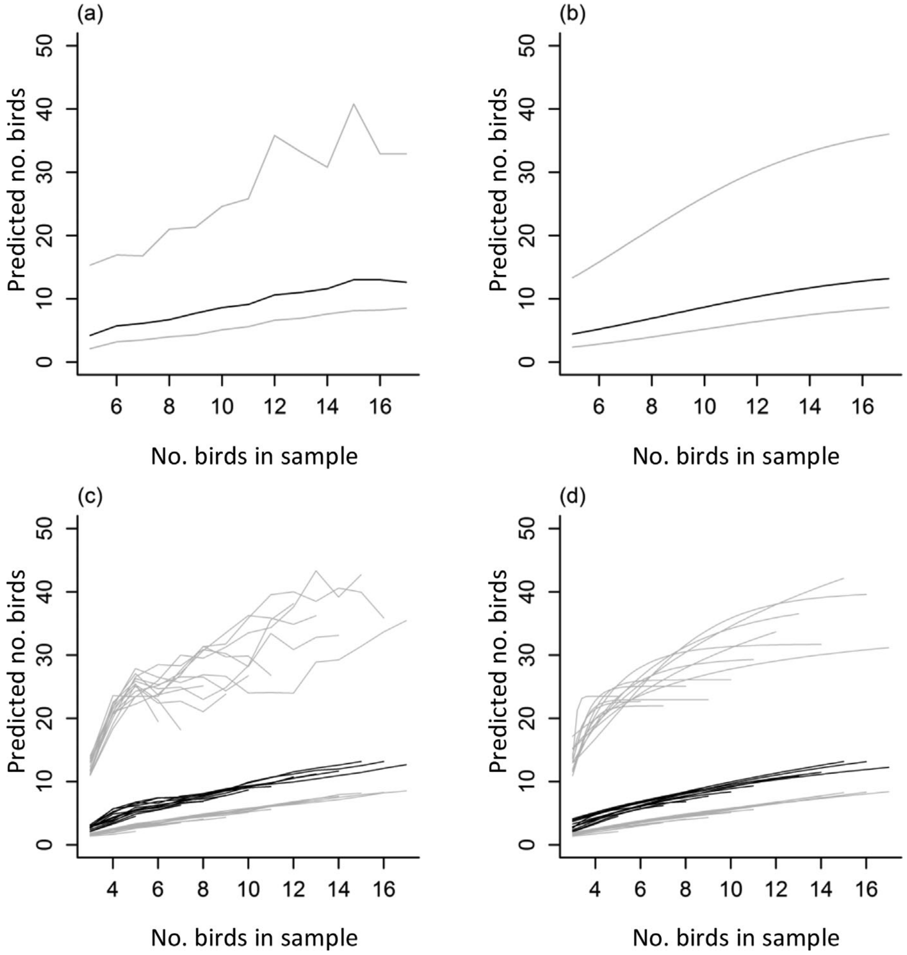

Figure 6. Sensitivity of starting samples to increasing numbers of lesser black-backed gulls tracked from Orford Ness (Mar–Aug 2010–2013) included in samples, shown by predictions of numbers of birds needed to characterize 95% of the area use for the population for different samples (a) and corresponding modeled non-linear relationships (b). We also present sensitivity of starting samples to birds that they contained as shown by predictions of numbers of birds needed to describe 95% of the area use for the population following sequential removal of birds from samples (c), and corresponding modeled non-linear relationships for each sample (d). In all cases, plots include the upper and lower quartiles (gray lines) and medians (black lines).

The adequacy of the initial starting sample used, central to the Soanes et al. (2013) approach, is an issue that has not previously been scrutinized. In our study, we obtained the highest predictions from the 15-bird sample, upon which we based final conclusions. However, the choice of different starting samples of birds and days (Table 3, Section S2) influenced the final conclusions. Sensitivity analysis was therefore required to determine robustness of starting samples. The selection of a starting sample covering too few individuals or too short a duration may present difficulties when subsequently drawing conclusions. Ultimately, the method in this study is somewhat circular in that the conclusion on an appropriate number of individuals tracked and duration of tracking is dependent upon the selection of starting sample. Consideration of all combinations of individuals and days represents the most logical solution.

Wider Applications and Considerations

The techniques employed in this study are transferable to other systems where high precision telemetry data, such as from GPS devices, have been gathered, and particularly when those data are relied upon for monitoring potential human-wildlife impacts (Roeleke et al. 2016). Although we focused on area use of a species' during pre-breeding, breeding, and post-breeding periods, the approach of using a number of days as a sampling unit means the techniques are not restricted to central-place foraging telemetry studies.

With the availability of affordable, short-lived devices, a central question is whether area use can be estimated over a short period through tracking a large number of individuals. Constraints on feasibility, time, labor, and cost may drive a portion of the study design. The availability of study individuals and appropriate places for catching animals will always dictate the feasibility of marking. However, our study has highlighted the relative greater importance of tracking fewer individuals for longer periods of time, than tracking a larger number for less time. Such a finding may dictate the type of device and attachment methods to use, potentially with associated cost implications if using more expensive devices to record for longer periods. Assessing whether such a trade-off of birds versus days holds for other species with similar datasets would be useful. Frequently, however, telemetry studies have not scrutinized the power of data gathered in this way. Correspondingly, the sampling methods are perhaps still in their relative infancy and require further investigation. For instance, we conducted our analysis on individuals followed across the defined study period over several years, rather than separate cohorts of individuals in different years. This additional trade-off needs further study. Sub-sampling protocols (e.g., recording positional information every 5 or 10 days) may also be an efficient means of increasing the battery life of tags and widening the temporal period studied. This may be important for species with large intra-annual variation in behavior, but disentangling the relative importance of monitoring for a consecutive number of days, versus covering greater temporal variation in movements, requires further validation.

MANAGEMENT IMPLICATIONS

The sampling approach used indicated that an adequate number of lesser black-backed gulls were tracked over a suitable duration to appropriately characterize area use of breeding birds from the Orford Ness colony. By extension, our results implied that the telemetry dataset was suitable for assessing interactions of lesser black-backed gulls at Orford Ness with nearby offshore wind farms (Thaxter et al. 2015). For birds and marine mammals, GPS-telemetry data are now regularly used to inform Environmental Impact Assessments for proposed offshore wind farms (Bailey et al. 2014) and may have considerable leverage in assessing the potential impacts on populations and the associated mitigation of such effects (Cleasby et al. 2015). Study populations of species, however, may show very different patterns in area use, for example, linked to habitat availability, requiring specific assessments in each case, alongside consideration of study-specific aspects and analytical thresholds as highlighted. This study provides both the example of how tracking data is being used to understand potential impacts of anthropogenic resource use on wildlife populations, and guidance for applying the methodology to other datasets where human-wildlife resource use conflicts need to be assessed.

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