ECON
Ecological Consultancy Ltd

Analysis of JNCC visual tracking data





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Executive summary

The Joint Nature Conservation Committee (JNCC) carried out a programme of visual tracking of four tern species – common *Sterna hirundo*, Arctic *S. paradisaea*, Sandwich *S. sandvicensis* and roseate *S. dougallii* – at specific colonies across the UK between 2009 and 2011. These data were used within habitat modelling to identify important at-sea foraging areas for breeding birds to inform the identification of possible marine SPAs (Special Protection Area).

This report aimed to assess how representative the sample of tracked terns was of the whole population using the most data-rich examples available of each species. These were common tern at Imperial Dock, Leith and Arctic tern Sandwich tern and roseate tern all at Coquet Island, Northumberland. Data from two or three breeding seasons and across incubation and chick-rearing was pooled to provide the most representative measure of flight distributions.

The method of Soanes *et al.* (2013) was used to investigate the relationship between sample size (tracks) and 'areas of use' based on time spent in individual predefined grid cells. All cells visited represented the 'total area of use', whereas the first 95% and 50% of cells, from ranked cumulative frequency distributions of time spent in cells, were used to represent the 'active' and 'core' areas of use respectively. Repeated random sub-sampling with replacement and bootstrapping provided mean areas of use and confidence intervals for increasing sample size (e.g. n=1, n=2, n=3 etc.) for each species and area of use (i.e. total, active and core).

Michaelis-Menten models (R^2 values between 0.988 and 0.999) were fitted to the data and the asymptotic values provided estimates for the predicted total, active and core areas of use. The proportions of these areas represented by the achieved sample sizes were calculated and the samples sizes required to predict 50% and 95% of the core and active areas of use were estimated. As in Soanes *et al.* (2013), the models were then adjusted to respective colony sizes, with the asymptotic values being reached at the whole colony population size, to assess how well the achieved samples performed relative to estimates for the colony.

Model asymptotic values for the total area of use were highest for Arctic tern (891 km^2), followed by Sandwich tern (595 km^2), common tern (465 km^2) and roseate tern (166 km^2). The asymptotic values for core areas of use were much smaller at around 65 km^2 for Arctic and common tern, 47 km^2 for Sandwich tern and only 12 km^2 for roseate tern. The differences between species are likely a result of variations in colony population size, foraging ranges, patterns of foraging behavior, and/or habitat variability. Based on existing foraging range information from the literature the size of estimated areas was unexpectedly high for Arctic tern, lower than expected for Sandwich tern and much lower than expected for roseate tern, especially relative to its sympatric congeners.

The areas derived from the sample sizes achieved were highly representative, capturing >70% of the core areas of use by all the populations. For common tern at Leith, which had the largest number of available tracks (*n*=121) both the active and total areas of use were also reasonably well estimated (71% and 66% of the areas estimated respectively). However, for the other species at Coquet Island the areas estimated by the available sample sizes were lower at 48-57% for active use and 43-50% for the total area of use. The potential for birds to forage in all directions from this island colony, coupled with the large range of both Arctic and Sandwich terns may have partly responsible.

The sample sizes achieved for all species were sufficient to describe >50% of the area of active use, but the predicted sample sizes required to describe 95% of the area of active use were very high, ranging from 715 (roseate tern) to 2002 (Sandwich tern). This would appear to be an impractical goal, even for visual tracking where relatively larger sample sizes may be achieved (compared to remote tracking via bird-borne devices) by the systematic selection of one individual after another. The nature of an asymptotic model results in rapidly diminishing returns relative to effort and it would be beneficial to consider cost/benefits in relation to an appropriate target of the level of use to be described at the outset of the study.

Soanes *et al.* (2014) have now recently demonstrated that increasing cell size has a considerable effect on the analyses, reducing the sample sizes required to describe predetermined areas of use. Thus, application of a larger cell size in this study is likely to have yielded rather different results and further increased confidence in the dataset. A more traditional application of the home range concept (e.g. use of Minimum Convex Polygons, MCPs) may also have a provided a less stringent, but equally valuable means of assessing the adequacy of available sample size.

Contents

1 Introduction

Tracking is being increasingly used as a tool to delineate key habitats, important migratory pathways and understanding specific behavioural traits of seabirds. Such research can provide information which can be used to support policy, planning and conservation objectives. For example, tracking studies have already aided in the evaluation of Marine Protected Areas or MPAs (Garthe & Skov 2006, Harris *et al.* 2007, Louzao *et al.* 2006, Burger *et al.* 2008, Louzao *et al.* 2008, Gremillet & Boulinier 2009, Wakefield *et al.* 2009, Wilson *et al.* 2009, Yorio 2009).

The Joint Nature Conservation Committee (JNCC), working with the four Statutory Nature Conservation Bodies, has carried out visual tracking (simply following a bird using a high-speed rigid-hulled inflatable boat rather than using tags – see Perrow *et al.* 2011) of a number of tern species *Sterna spp.* at specific colonies across the UK, with the aim of identifying important foraging areas during the breeding season. Ultimately, this will inform the selection of areas that might be suitable for designation as marine Special Protection Areas (SPAs) designated under the EC Birds Directive (2009/147/EC).

The tracking data gathered has been used within habitat models to investigate the distribution of birds in relation to potential explanatory variables. However, there is uncertainty regarding the power of the sample sizes achieved to describe the areas of use by the populations and thus how representative the data from tracks is when used within the habitat models.

Without good *a priori* knowledge of the area that may be used by a specific population it is difficult to estimate suitable sample size requirements before undertaking tracking. Such studies are invariably resource limited, with the bulk of these resources taken by equipment hire or purchase and particularly human resources. Coupled with methodological difficulties, tracking studies thus tend to produce limited datasets. The ability to extrapolate or infer general trends from the pool of data generated may therefore also be limited. Hebblewhite & Haydon (2010) examined the suitability of sampling regimes and suggested that tracking studies can focus too closely on providing detail rather than adhering to good study design. The numbers of different individuals within a population that are tracked, and the numbers of trips each individual is tracked for, will contribute to the capacity of the dataset to provide an accurate representation of the spatial distribution of all birds at the colony as a whole.

The metrics used to delineate the area of use by a bird population can vary in terms of the methods used to define it (e.g. minimum convex polygons MCP or kernel density methods - see Kie *et al.* 2010 for a review of methods). However, an assessment of the representativeness of sample size would likely take the same form in all cases: calculate the areas of use represented by different sample sizes of tracking data, fit a model and extrapolate to the point where no further gain in area is achieved through the addition of extra data (see Gilbert *et al.* 2005).

Soanes *et al.* (2013) recognised the importance of understanding the power of sample size in tracking studies, especially given their use in policy and planning, and sought to define how many individual birds need to be tracked to define a home range for breeding seabirds. They used the examples of black-legged kittiwake *Rissa tridactyla* and European shag *Phalacrocorax aristotelis* at colonies on Puffin Island in Wales, with a sample was comprised of 19 shags and 21 kittiwakes tracked over multiple foraging trips in a single breeding season using GPS data loggers.

The method of Soanes *et al.* (2013) used the additive time spent by tracked birds in pre-defined grid cells to quantify areas of use (i.e. cells visited for quantities of time). All of the cells visited were used to represent the area of active use (after Casper *et al.* 2010), whilst other fractions of the area can be determined by ranking cells in order of the amount of time spent within them, for example the top 50% of cells (according to time spent within them) was used as the core foraging area (Ford 1979). Using sub-sampling of individuals within the pool of available track data, they investigated the relationship between the numbers of birds tracked and the areas of use (e.g. total or core foraging areas) derived from the data. Models fitted to the resultant data described the relationships and, when extrapolated to respective colony populations, allowed the evaluation of the sample sizes achieved and their predictive capability. Increasing the numbers of trips (made by individuals) included in the analyses increased the estimates of areas used by the birds. It was also suggested that the number of individuals required to predict the home range of the colony decreased with increasing numbers of trips included per individual. Soanes *et al.* (2013) concluded that all tracking studies should aim to conduct similar analyses to determine the reliability of home-range are predictions.

2. Aim

This short investigation aims to provide an indication of whether the numbers of tracks of terns obtained provide representative coverage of the extent of the areas used by whole colony populations. Limited resources meant that it was not possible to test the suitability of a number of different methods or to analyse all species tracked at all colonies.

Rather, as agreed with JNCC, the most data-rich examples for each of the four species of tern - Sandwich tern *Sterna sandvicensis*, common tern *S. hirundo*, roseate tern *S. dougallii* and Arctic tern *S. paradisaea* – were analysed using the methods of Soanes *et al.* (2013)

3 Methods

Given its specific relevance to the data in question and its recent publication in a highly respected ecological journal, the method of Soanes *et al.* (2013) was thought to provide a suitable platform for analysing the datasets generated by the visual tracking of terns. Louise Soanes kindly provided a basic example of the code used in their analyses, which was then modified to allow the analysis of the much larger datasets described here.

3.1 Raw data

Raw data were supplied by the JNCC for the four species of tern at two separate colonies, namely common tern at Imperial Dock, Leith and Arctic tern, Sandwich tern and roseate tern all at Coquet Island, Northumberland. These represented the most data-rich colonies for the respective species. Data were provided in Excel spreadsheets containing GPS fix locations at 1 second time intervals for each track of each species with identifiers for year, date and period (i.e. incubation or chick rearing). All track fixes, including non-foraging data were used to assess how representative the raw data was of the overall areas used by the populations at individual colonies. For each species, data were pooled across sample periods and years, ultimately providing 187,496 fix locations for common tern, 119,500 for Arctic tern, 114,483 for Sandwich tern and 20,997 for roseate tern. This corresponds to total tracking times of 52.08 hrs for common tern, 33.19 hrs for Arctic tern, 31.81 hrs for Sandwich tern and 5.83 hrs for roseate tern.

Prior to analysis the data was filtered for any anomalies and to ensure that the correct information and data structure was present to allow compatibility with the analytical software. In a number of instances the tracks were shorter than 1 minute in length (often only a few seconds), largely because visual contact was lost soon after commencing tracking. These tracks (*n* = 31 in total) were excluded from analysis. In addition, there were a number of birds that had breaks in their tracks, where position co-ordinates were not provided in a continuous manner, often losing several minutes of information. This was a result of problems with the GPS equipment during specific tracking bouts. Although data could have been interpolated during these periods of missing data, it could not be guaranteed that the interpolations would be representative of what the bird actually did and so these tracks (*n*=12 in total) were also removed from the datasets.

All tracks were included in the analysis, whether they were complete (i.e. if birds were tracked from the colony and back again) or incomplete (i.e. birds were lost part way through their trip). Potential sample bias arising from any form of selectivity in the tracking protocol or conditions leading to the loss of birds (e.g. conditions becoming adverse to tracking further offshore) could not therefore be taken into account, although it is known that care was taken to randomly sample birds departing from the colony in all directions.

A breakdown of the final numbers of tracks used in the analyses is presented in Table 1. A total of 379 tracks were used in analysis, with 121 for common tern, 91 for Arctic tern, 117 for Sandwich tern and 50 for roseate tern. Each track is assumed to be of a different individual as a result of an extremely low probability of encountering any individual more than once.

Table 1. Summary of numbers of common, Arctic tern roseate and Sandwich terns tracked from respective colonies during the breeding season in different years. Also shown are the numbers of tracks excluded from the analyses as a result of being shorter than one minute in length and due to missing data.

Colony	Tern species	Year	No. of birds tracked	No. of tracks < 1 min	No. of tracks missing data	No. of tracks used	Total tracks used in analysis
Imperial Dock, Leith	Common	2009	114	9	7	98	121
		2010	23	-	-	23	
Coquet Island	Arctic	2009	41	7	4	30	91
		2010	14	-	-	14	
		2011	49	2	-	47	
Coquet Island	Sandwich	2009	49	9	1	39	117
		2010	8	-	-	8	
		2011	71	1	-	70	
Coquet Island	Roseate	2009	21	3	-	18	50
		2010	1	-	-	1	
		2011	31	-	-	31	
Totals			422	31	12	379	379

All analyses were conducted in the statistical software R (R Development Core Team 2008) with some data manipulations carried out using macros in Microsoft Excel.

3.2 Calculating areas of use from tracking data

The analysis looked to evaluate the 100% 'total area of use' (i.e. the area encapsulated by all cells being visited by tracked birds), 95% 'area of active use' (based on the top 95% of cells from a ranked cumulative frequency distribution based on time) and the 50% 'core area of use' (based the first 50% of cells from a ranked cumulative frequency distribution based on time). This is subtly different to Soanes *et al.* (2013), who defined all the cells visited as the 'area of active use' (although referring to this earlier as the 95% home range) and the first 50% of the cumulative frequency distribution as the 'core foraging area'. The interpretation used in this study uses the top 95% of the cells by time as the active area rather than all cells which may otherwise contain some spurious outliers (accounted for in the total area of use).

Following the preparation of the datasets, the time spent in predefined grid cells of 0.25 km^2 by individuals was calculated using the 'trip' package in R (Sumner 2011). Grid cells of 500 x 500 m were used to mimic the resolution at which JNCC's habitat modelling was carried out (although see later discussion in Section 4.3). This was first performed for all individuals and then sampling was carried out to examine the time spent in cells by 1 individual (each individual separately), 2 individuals, 3 individuals, and so on. The time spent in cells was calculated within 'trip' by simply summing the time spent (1 second intervals) in each of the predetermined grid cells.

For each of the species at the specified colony, individuals were selected randomly (using a random sampling function within R) from the pool of all individuals and analyses were run the same number of times as there were tracks in the respective pools. The total number of cells in which birds had spent time was counted and multiplied by the cell area (0.25 km^2) to calculate the total area of use for each of the samples of individuals.

The resultant datasets were then ranked to provide a list of cells in which decreasing amounts of time were spent by the sampled birds. This list was then converted to cumulative percentage and the number of cells comprising the first 50% and 95% of the total time recorded during the tracking was counted and multiplied by the cell area (0.25 km^2). Thus, for each species and set of repeated samples (based on random sampling at different sample sizes), areas were calculated for the total, active and core datasets.

Bootstrapping with replacement was used to draw 10,000 samples, enabling mean, upper (97.5%) and lower (2.5%) percentile values (or 95% confidence intervals) to be calculated for the areas of use at each sample size using the R package 'boot' (Canty & Ripley 2011).

3.3 Fitting models and evaluating sample sizes

Asymptotic *Michaelis-Menten* models (Equation 1) were fitted to the data.

$$\text{Equation 1: } y = \frac{a*x}{(b+x)}$$

where a = the asymptotic value of the y axis, and b = the value of x at which half of the maximum response is attained.

Following Soanes *et al.* (2013), two and three parameter-asymptotic models were also fitted and the best model was selected based on fit and Akaike information criterion (AIC) scores. *Michaelis-Menten* models always outperformed the 2 Parameter-asymptotic models, but the performance of the 3 parameter-asymptotic models was good or even slightly better in some cases as also noted by Soanes *et al.* (2013). But these produced spurious results when attempting to estimate the numbers of tracks required to estimate various percentages of the areas of use and following Soanes *et al.* (2013) only the *Michaelis-Menten* models were used.

The percentages of the total, active and core areas of use predicted by the actual numbers of bird tracks were calculated to provide an estimate of sample performance. Further, the numbers of tracks required to determine both 50% and 95% of the active and core areas of use were derived for each species to provide a further indicator of sampling requirements.

These models were then adjusted, based on colony specific population estimates as the sample size for each species, to determine new model asymptotic values (areas of use). This was undertaken to provide an indication of the likely areas of use based on the tracking of a sample reflective of respective colony sizes. The percentage of the areas of use of the population of the whole colony represented by the actual samples was calculated to indicate how well the tracking activities had performed. The numbers of tracks required to estimate 50% and 95% of the adjusted predicted active and core areas of use was then calculated as described above for the original model.

Colony populations used to calculate the numbers of birds required were derived from the latest counts (either 2010 or 2012) present in the Seabird Monitoring Programme (SMP) database (http://jncc.defra.gov.uk/smp/).

4 Results

4.1 Areas of use

Figure 1 provides a comparison of the mean total, active and core areas of use for each species based on the numbers of individuals sampled from the pool of available data. These results suggest Arctic tern tracks consistently produced the largest areas of use. Common and Sandwich tern appeared to have similar areas of use in terms of the total and active areas of use (Figure 1 a & b). However the tracking data seem to suggest that common tern at Leith occupy a larger core area relative to the Coquet Island Sandwich tern (Figure 1 c). Roseate terns had the smallest areas of use throughout, at all sample sizes.

4.2 Modelled relationships & sample performance

Model predictions for each of the four species are illustrated in Figure 2 and the associated parameters are detailed in Table 2. Figure 3 illustrates the variation in model asymptotic values between species and across the three levels of ranked track data used (i.e. total, active and core areas). In all cases visual checks and high r^2 values (minimum of 0.98), suggested the *Michaelis-Menten* model fitted the data well, thereby supporting the use of an asymptotic model (Table 2).

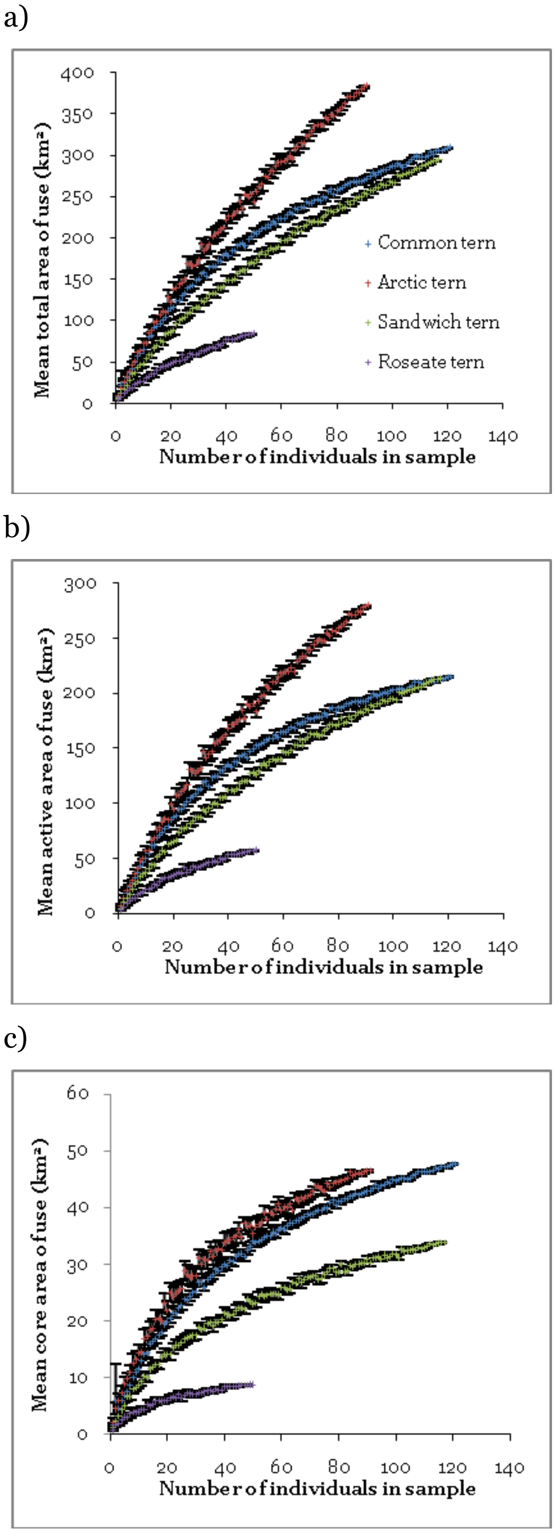

Figure 1. Mean areas of use derived from different numbers of track samples for: a) total, b) active and c) core areas of use for each tern species. Error bars represent the upper (97.5%) and lower (2.5%) confidence intervals derived from bootstrapped data.

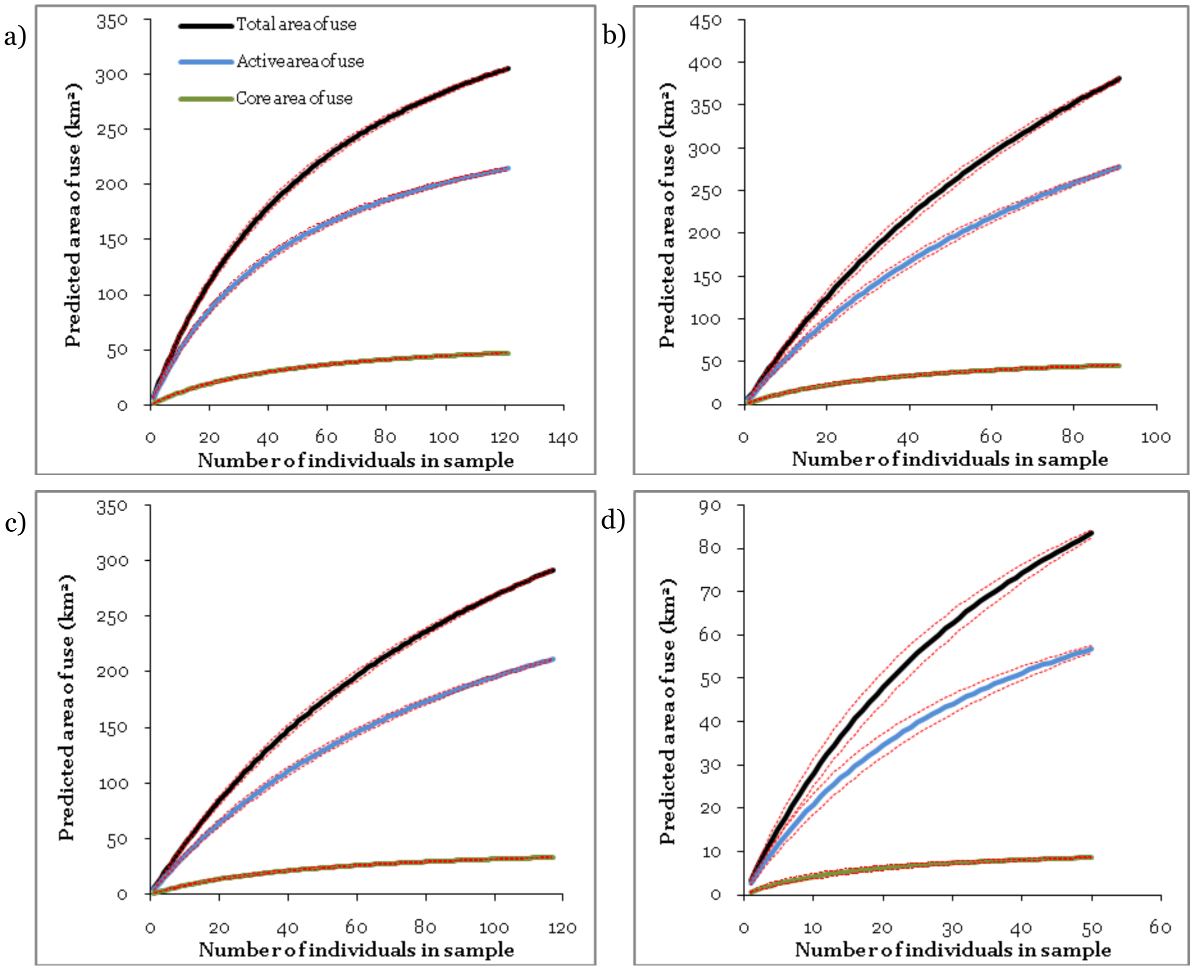

Figure 2. *Michaelis-Menten* model fits to the total, active and core areas of use estimated for different track sample sizes for: a) common tern, b) Arctic tern, c) Sandwich tern and d) roseate tern. Upper (97.5%) and lower (2.5%) confidence intervals are represented by dashed lines.

Removal of the cells comprising the lowest 5% of time spent by tracked birds, to represent the area of active use, resulted in a marked reduction in the model asymptotic values (Table 2 & Figure 3). The further reductions in model asymptotic values for the core areas (after the removal of the cells comprising the lowest 50% of time spent by tracked birds) were far greater. The narrow confidence intervals around the model estimates suggested limited variability in the areas used by individuals at different sample sizes. The models fitted to the roseate tern data (Figure 2 d) had slightly larger confidence intervals than the other datasets, which is likely to be a result of the relatively small areas of use and available sample size *(n* = 50) for this species.

The largest model asymptotic value for the total area of use was produced by the Arctic tern model (891 km^2), followed by Sandwich tern (595 km^2), common tern (466 km^2) and a much smaller area associated with roseate tern (166 km^2). Core area model asymptotic values were more consistent between species, ranging from 12 km^2 (roseate tern) to 66 km^2 (common tern). Arctic and common tern shared similar asymptotic values for the core area of use models at 65 and 66 km^2 respectively.

Table 2. Parameter estimates from *Michaelis-Menten* models used to predict the total, active and core areas of use of the four tern species at the respective colonies. The coefficient *a* represents the area of use at the asymptote of the model and *b* the sample size at which half the maximum response is attained. R^2 values (coefficient of determination) are provided for each of the models. Upper (97.5%) and lower (2.5%) confidence intervals are provided in parentheses.

Area of use	Parameter	Common tern (Leith)	Arctic tern (Coquet)	Sandwich tern (Coquet)	Roseate tern (Coquet)
Total area of use	*a*	465.7 (454.9-475.8)	890.8 (808.9-992.5)	595.1 (560.6-634.3)	165.9 (146.5-193.7)
	b	63.6 (58.4-68.9)	121.9 (101.2-148.0)	121.6 (107.0-138.4)	49.2 (36.9-67.4)
	r^2	0.999	0.998	0.999	0.995
Area of active use	*a*	304.1 (298.8-309.6)	578.5 (534.3-633.0)	401.8 (381.0-425.6)	99.6 (90.4-112.5)
	b	50.6 (46.6-54.9)	98.6 (82.9-118.1)	105.4 (93.0-119.7)	37.6 (28.5-50.5)
	r^2	0.999	0.998	0.999	0.995
Core area of use	*a*	65.8 64.3-67.4)	64.5 (61.9-67.6)	47.0 (45.6-48.6)	11.6 (10.8-12.7)
	b	47.8 (43.3-52.6)	36.4 (30.3-43.8)	48.8 (42.5-56.0)	17.3 (11.9-25.1)
	r^2	0.998	0.996	0.996	0.988

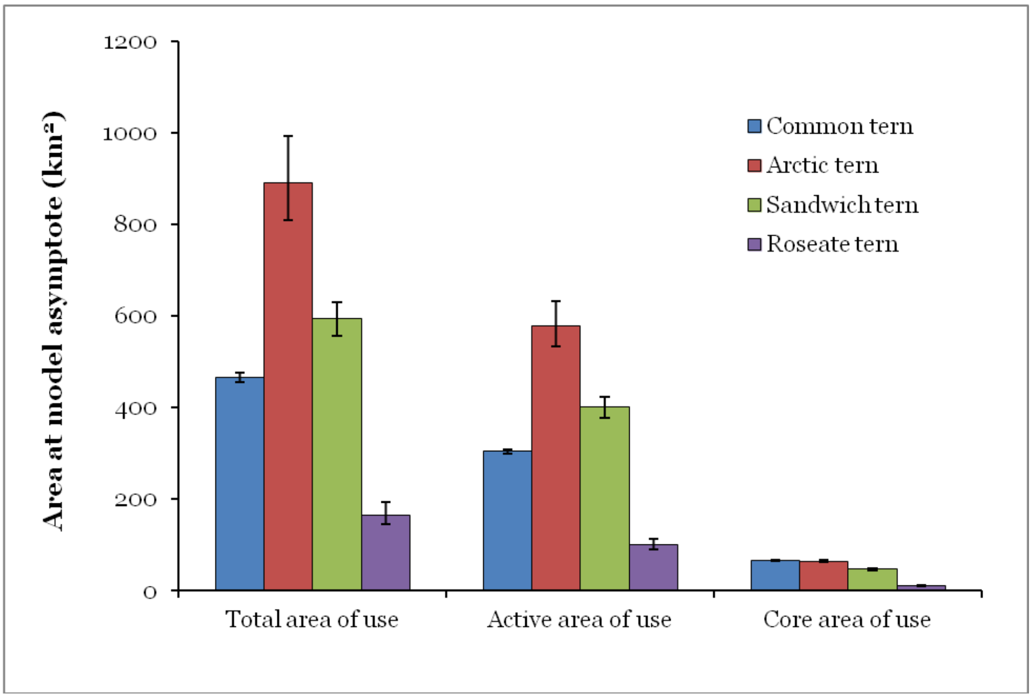

Figure 3. *Michaelis-Menten* model predicted asymptotic values representing the total, active and core areas (km^2) of use. Error bars represent upper (97.5%) and lower (2.5%) confidence intervals.

Sample sizes at which half of the maximum response was attained (represented by *b* in Table 2) for the core area of use, varied between 17 tracks (roseate tern) and 49 tracks (Sandwich tern). In contrast, between 49 (roseate tern) and 122 tracks (Arctic tern) were required to achieve half of the maximum total areas of use. These figures provide an indication of the between species/population variability in the potential numbers of tracks required to delineate the areas used by these birds.

Table 3 provides the percentages of the estimates of the sample sizes required to predict the total, active and core areas of use derived from the models. All actual sample sizes represented greater than 70% of the core areas of use, with a maximum of 74% for roseate tern. Between 43% (Arctic tern) and 66% (common tern) of the total areas of use were captured by the available sample sizes. The common tern sample size produced relatively consistent percentages for the core and active areas of use, suggesting little variation in the rate at which the asymptotic values were approached. In contrast, the percentages dropped by around 20% between the core and active areas for the other species, suggesting a much greater difference in the relative number of samples required to represent these areas.

Table 3. Percentages of the predicted total, active and core areas (km^2) of use achieved using the actual number of tracks obtained for each species. Upper (97.5%) and lower (2.5%) confidence intervals are provided in parentheses.

Tern species	Sample size	% of total area of use	% of active area of use	% of core area of use
Common (Leith)	121	65.5 (63.7-67.4)	70.5 (68.8-72.2)	71.7 (69.7-73.7)
Arctic (Coquet)	91	42.7 (38.1-47.3)	48.0 (43.5-52.3)	71.4 (67.5-75.0)
Sandwich (Coquet)	117	49.0 (45.8-52.2)	52.6 (49.4-55.7)	70.6 (67.6-73.3)
Roseate (Coquet)	50	50.4 (42.6-57.6)	57.1 (49.7-63.7)	74.3 (66.6-80.7)

The analysis of the sample sizes required to represent 50% and 95% of the active and core areas of use supported the view that much larger numbers of tracks would be required to capture a greater proportion of use (Table 4). However, common tern required similar numbers of tracks for both the core and active areas of use, whereas for the other species, more than double the numbers of tracks needed for the core area were required to predict similar percentages of the active areas.

Table 4. Sample sizes required to represent 50% and 95% of the active and core areas (km^2) of use for each species based on individual model parameters. Upper (97.5%) and lower (2.5%) confidence intervals are provided in parentheses.

Tern species	Sample size	Active area of use		Core area of use	
		50%	95%	50%	95%
Common (Leith)	121	51 (47-55)	962 (885-1043)	48 (43-53)	909 (822-999)
Arctic (Coquet)	91	99 (83-118)	1872 (1575-2244)	36 (30-44)	692 (575-833)
Sandwich (Coquet)	117	105 (93-120)	2002 (1767-2274)	49 (43-56)	927 (808-1065)
Roseate (Coquet)	50	38 (29-51)	715 (542-960)	17 (12-25)	329 (227-477)

4.3 Colony size adjusted estimates & sample performance

The adjusted model asymptotic values, based on the colony populations, are shown in Table 5. The percentages of these areas represented by the actual track sample sizes is shown in Table 6 and the numbers of tracks required to represent 50% and 95% of the respective active and core areas of use are given in Table 7. The adjusted asymptotic values remained very similar to (i.e. the confidence intervals intersected), but were always smaller than the original model estimates (see Table 2 & Table 5); as a result of the sample size constraints.

Table 5. Model predicted asymptotic values representing the total, active and core areas of use (km²) based on sample sizes consistent with the respective colony populations being sampled. Upper (97.5%) and lower (2.5%) confidence intervals are provided in parentheses.

Tern species	Colony population	Predicted total area of use	Predicted area of active use	Predicted core area
Common (Leith)	1636 (2010)	448 (439-457)	295 (290-300)	64 (63-65)
Arctic (Coquet)	2550 (2012)	850 (778-938)	557 (517-605)	64 (61-66)
Sandwich (Coquet)	2578 (2012)	568 (538-602)	386 (368-407)	46 (45-48)
Roseate (Coquet)	142 (2012)	123 (116-131)	79 (75-83)	10 (10-11)

The percentages of the areas of use represented by the tracking effort were therefore also similar to, but slightly larger, than those calculated from the unadjusted models (see Tables 3 & 6). However, the sample sizes for roseate tern appeared to perform much better in relation to the colony adjusted predicted areas relative to the other species (e.g. an increase from the original 74% to 83% of the core area of use). This is a function of the very small colony size (142 individuals) relative to the number of tracks (*n*=50).

The numbers of tracks required to represent 50% of the active and core areas of use based on the colony adjusted models were very similar to those from the original models (see Tables 4 & 7). However, the numbers required to define 95% of these area were reduced greatly, again reflecting the constraints placed on the sample sizes.

Table 6. Percentages of the colony adjusted total, active and core areas (km²) of use achieved using the actual number of tracks obtained for each species. Upper (97.5%) and lower (2.5%) confidence intervals are provided in parentheses.

Tern species	Sample size	% of total area of use	% of active area of use	% of core area of use
Common (Leith)	121	68.1 (66.4-69.8)	72.7 (71.1-74.3)	73.8 (72.0-75.6)
Arctic (Coquet)	91	44.8 (40.3-49.2)	49.9 (45.5-54.0)	72.4 (68.6-75.9)
Sandwich (Coquet)	117	51.4 (48.3-54.4)	54.8 (51.7-57.7)	71.9 (69.1-74.6)
Roseate (Coquet)	50	67.9 (62.8-72.5)	72.2 (67.4-76.5)	83.3 (78.4-87.5)

Table 7. Number of individual tracks required to represent 50% and 95% of the active and core areas (km²) of use for the four species based on the size of the colony and model fits to respective data. Upper (97.5%) and lower (2.5%) confidence intervals are provided in parentheses.

Tern species	Sample size	Active area of use		Core area of use	
		50%	95%	50%	95%
Common (Leith)	121	48 (44-51)	594 (564-624)	45 (41-49)	574 (538-608)
Arctic (Coquet)	91	91 (78-108)	1056 (954-1165)	35 (30-42)	538 (465-620)
Sandwich (Coquet)	117	97 (87-110)	1102 (1027-1179)	47 (41-54)	673 (608-742)
Roseate (Coquet)	50	25 (20-30)	113 (108-118)	14 (10-19)	96 (85-105)

5 Discussion

5.1 Was the sample size of tracks adequate?

The methods of Soanes *et al.* (2013) were successfully applied to the visual tracking data of terns undertaken by the JNCC. Judging by the very high R^2 values the fitted *Michaelis-Menten* models performed well and illustrated substantial differences in the predicted total, active and core areas of use (i.e. model asymptotic values) between species (Figure 2). Arctic tern generally had the largest areas of use, Sandwich and common tern were smaller but similar to each other, and roseate tern apparently used much smaller areas.

The relative scope of the derived areas for each species do not reflect the reported foraging ranges for each in the review by Thaxter *et al.* (2012), as Sandwich tern has by far the largest range with a maximum of 54 km (mean maximum ± 1SD value of 49 ± 7.1 km and mean ± 1SD value of 11.5 ± 4.7 km). The maximum range values for Arctic, common and roseate terns are all the same at 30 km, although the mean maximum ± 1SD values, but not necessarily mean ± 1SD values, are higher for Arctic (mean maximum of 24.2 ± 6.3 km and mean of 7.1 ± 2.2 km) compared to roseate (mean maximum of 16.6 ± 11.6 km and mean of 12.2 ±-12.1 km), with common having the smallest range (mean maximum of 15.2 ± 11.2 and mean of 4.5 ± 3.2 km). The level of confidence assigned by Thaxter *et al.* (2012) to their assessments of range based on the number and quality of studies (i.e. direct tracking or indirect inference) is moderate for Sandwich, Arctic and common terns but low for roseate tern. The tracking undertaken may thus simply indicate that roseate tern does have a smaller range than currently suggested.

Moreover, the review of information of foraging ecology of all UK tern species by Eglington & Perrow (2014) concludes that the considerable variation in range shown by all species, both between and within colonies on both annual and seasonal scales, may result from differences in the abundance and distribution of prey (and suitable habitat) overlain by possible interference competition from sympatrically nesting conspecifics. The apparently small range of roseate tern at Coquet may be linked to the presence of other species leading to partitioning of resources (habitat, prey type and size) in one way or another (see Safina 1990, Shealer 1998, Hall *et al.* 2000, Monticelli *et al.* 2006, Black & Diamond 2005, Rock *et al.* 2007). Indeed, a parallel study using the Coquet Island 2011 data showed that Arctic and common terns, breeding on Coquet Island, used similar foraging areas (63% overlap) and portioned resources by diet while in contrast, roseate terns differed from both Arctic and Common tern in relation to foraging areas (0% and 41% overlap respectively) and diet (Robertson *et al.* 2014).

Importantly, variation in the range and foraging behavior of a species from a colony means that it may be more difficult to sample effectively, and a greater sample size would be required using the methods of Soanes *et al.* (2013). For example, in many cases the wide-ranging Sandwich tern travels in direct lines to pre-determined foraging locations, compared to common terns that may show a quartering or zig-zag search pattern and shift areas of search perhaps in response to conspecifics (Perrow *et al.* 2010). In this simple illustration, a Sandwich tern on a foraging trip may cross relatively little of its potential range (i.e. number of cells in the analysis) whereas a common tern, for the same length of trip, may cross much more.

Range length and the pattern of foraging could explain the differences in the relationships between sample size and area used between species, with much steeper slopes for Arctic tern and Sandwich tern than common and roseate tern. This initially suggests that many more samples would be required to describe the full range of the former two species, but yield more information for each further track gained than would be the case for common and roseate tern.

This leads to the key question of the study of whether enough birds were tracked to be representative of the areas used by all birds within the population of the colony. Despite the overall differences in slope between species for the larger areas, the core area models were all very similar in form for all species, rapidly rising toward the asymptotic values within the range of the sample sizes collected (Figure 2). Thus, around 70% of core area of use was captured for all species by the tracking. It would seem reasonable to conclude that the tracking effort was broadly sufficient to describe the main areas used by the population, especially since this incorporates some inter-annual variation as a result of pooling samples taken from 2-3 years. As such, this provides confidence that the tracking data could be used for other purposes as in the modeling of habitat relationships, with the caveat this may in fact be undertaken on a substantially smaller dataset of foraging events alone, rather than all the fixes used here.

Furthermore, the percentages of the total and active areas of use did not decrease substantially for common tern at Leith with 66% to 71% being described respectively, clearly showing the asymptotic values was approached by the sample size achieved. It is of note that the number of tracks of common tern was the highest achieved (*n*=121) and coupled with the foraging behavior of common terns (see above), the lack of sympatric congeners and perhaps restricted but productive habitat around the colony in an industrial dockland may all have contributed to the ability of the tracks to describe well the areas of active and total use of common tern at this colony.

In contrast, for all the species tracked at Coquet, there was a marked reduction in the ability of the tracks to describe the active area of use (48-57%) and the total area of use (43-50%). Confidence in the ability of the tracking data to represent the entire population is reduced accordingly, as only around half of the total area that could be used is represented in the dataset.

The similar pattern of decline in the area described across species irrespective of the difference in sample size, foraging behavior and pattern of tracks could conceivably be linked to the fact that Coquet is an island, with the potential of birds to forage in all directions. A few tracks in a different direction, coupled with a few long tracks in the case of Arctic and Sandwich terns, may have a considerable influence on the area used and the ability of tracking to capture the habitat use.

Approaching the question of the adequacy of the sample size gained from another perspective, the analysis of sample sizes showed that to describe 50% of both the active and core areas of use, between 17 (roseate tern) and 105 (Sandwich tern) tracks would be required. The required number was, in fact, achieved for all species. However, to achieve 95% of the active area of use the number of tracks required was extremely large from *n*=715 for roseate tern and *n*=2002 for Sandwich tern, slightly more than required for Arctic tern (*n*=1872) despite the fact that Arctic tern appeared to use a larger area. This again likely reflects the variability in individual foraging ranges and how the habitat is used.

Using the original model, more tracks would be required than there were birds in the colony for roseate tern. Even for common tern, where 71% of active area of use was estimated by the sample size achieved (*n*=121), an extremely large sample (*n*=962) was required to estimate 95% of it. The fact that a fraction of the tracks required (13%) achieves 71% of the area clearly illustrates the prospect of diminishing returns. In other words, a great deal more effort would quickly reach a point where the benefits would be outweighed by the resource costs. The impracticality of the sample sizes apparently is further illustrated by the colony adjusted models that suggest the equivalent of 36%, 41%, 43% and 80% of the common, Arctic, Sandwich and roseate tern colonies respectively would need to be tracked to define 95% of the respective active areas of use.

5.2 Improvements to the modelling approach

Application of the methods of Soanes *et al.* (2013) to the tracking data gathered by the JNCC reach similar conclusions to those for radio-telemetry data; that much larger numbers of birds should be tracked than is initially perceived and that the number of birds required to represent the full area used by the population may be so large to be impractical. This tends to generate a sense that tracking is less useful than perceived, despite the data delivered being generally far more informative than other methods. Even a single track can offer considerably more insight than the experiences of a number of surveys that are restricted in time and space for example. However, there are a number of methodological issues with the analysis as used by Soanes *et al.* (2013) that, if resolved, may change the conclusions reached.

First, there is confusion over the concept of home range as applied by Soanes *et al.* (2013). Powell and Mitchell (2012) discuss the question of ‘what is a home range?’ and illustrate how the concept is often fundamentally misunderstood whilst focus is placed on the ‘best’ methods for delineating a representative area. Home range was formally defined by Burt (1943) as the “*area traversed by the individual in its normal activities of food gathering, mating and caring for young*”. For the purposes of analysis, Kenward (2001) suggests a convenient definition “*as an area repeatedly traversed by an animal*”. In this context, it is clear that the use of ‘home range’ in the title of the paper by Soanes *et al.* (2013) is misleading as the authors actually attempted to quantify areas of use through the time spent by tracked birds in pre-defined grid cells. This is a far more precise or stringent, and thus more difficult to achieve, measure than a more standard measure of home range, which is not dependent on the ‘infill’ within the range used by the birds depending on the means of defining it. A minimum convex polygons (MCP) for example would simply connect the outliers of the location fixes from the birds, whereas some form of kernel density or contour method would seek to incorporate the frequency of occurrence of location fixes to capture zones of more important use thereby reducing the importance of outliers. The data discussed here simply provide an indication of the areas visited by different samples of birds from respective colonies. The alternative method of (MCPs) could be used to generate different areas (e.g. 100% and 95% MCPs) encompassed by the different sample sizes with associated variability. It would clearly be useful to compare the performance of this approach to the one of Soanes *et al.* (2013).

Second, in the analysis of tracks conducted here, many predefined cells including those close to a colony or between tracks were not included in the analysis as none of the tracked birds visited them. Cell size is clearly an important variable. In recognition of this, Soanes *et al.* (2014) recently provided an example of its effects in relation to the habitat use of Brown boobies *Sula leucogaster*. Here an increase in the cell size from 1 km to 20 km resulted in a large drop in the numbers of birds required to predict different areas used by the birds. For example to predict the 95% utilization distribution 345 birds would need to be tracked given 1 km^2 cells, 340 birds at 5 km^2, 275 birds at 10 km^2 and 220 birds at 20 km^2 . The study concluded that increasing the spatial scale of the analysis increases the representativeness of the sample size.

In this study, a small cell size of 0.25 km^2 (500 m x 500 m) was used to provide good spatial resolution and because it was representative of the cell sized used in the habitat modelling carried out by the JNCC. Retrospectively, a different cell size, perhaps similar to the 1 x 1 km cell size used by Soanes *et al.* (2013, 2014) may have been less stringent and reduced the occurrence of blank cells, although it could also have led to loss of spatial resolution and lumping of data. Whatever the case, a different cell size seems likely to yield rather different results and it would be useful to test its effects.

Although not specifically affecting its performance, the models were adjusted to a sample size consistent with the individual colony population sizes as used by Soanes *et al.* (2013) to extrapolate the areas (referred to as ‘home range’) to the colony. This is perhaps an unnecessary step for this study, as it only serves to illustrate that the outputs from both approaches are generally very similar (compare Tables 3 and 6) which is indicative of the asymptotic model used. In real terms, collecting the same number of tracks as there are birds in the colony does not mean that each individual bird is sampled and each individual would be likely to make many trips possibly to very different locations. Thus the original model, without the constraints, probably provides the best indication of how suitable the sample size is in relation to describing the areas used by the birds.

Finally, it was originally hoped that the analyses could be segregated to assess inter-annual variations in relationships, as such an analysis would provide further insight into the importance of the length and intensity of survey activities. However, given the time consuming processor intensive steps involved in the analysis, it was only possible to examine the full datasets from the combined years. Further development of the method and refinement of the analytical code is required to significantly reduce the resources required to perform the analyses on large datasets.

6 Concluding summary

Within this report the relationships between visual tracking sample size and derived areas of use for four species of tern (common, Arctic, Sandwich and roseate) from specific colonies (Leith for common tern and Coquet Island for the others), have been evaluated. The methods described by Soanes *et al.* (2013) were applied successfully to the largest available JNCC visual tracking datasets allowing assessment of the relationship between sample size and areas used by the birds.

The models served to estimate the areas of use by the four species at their respective colonies and illustrated the variations between the parameters. The differences between the sizes of the predicted areas of use likely results from variations in foraging ranges, patterns of foraging behaviour and habitat variability (as tackled within the habitat modelling). It was noted that, given the relative foraging range estimates, the apparent size of areas used was unexpectedly high for Arctic tern, lower than expected for Sandwich tern and much lower than expected for roseate tern, especially relative to its sympatric congeners.

The numbers of tracks obtained were found to be highly representative (>70%) of the core areas of use by all the populations. For common tern at Leith, the larger number of tracks achieved, provided a similarly reasonable estimation of both the active and total areas of use. However, for the other species, much larger samples were required to describe these larger areas with confidence. Arctic and Sandwich tern did not perform particularly well when describing the active areas of use, probably due to the larger colony populations and larger foraging ranges relative to common and roseate terns.

Describing a high percentage of the active area of use by the colonies is a somewhat unrealistic goal given the results of this investigation, with very large sample sizes often being required to represent 95% of the area (over 2000 tracks in some cases). Such a number of tracks would generally be an unrealistic target unless spread over a sustained sampling campaign with considerable resources. Such study targets are likely to be unrealistic and could limit the undertaking of studies such as this, which provide unique insights into the behavior and ecology of important bird species. Ultimately, increased quantities of data will provide greater confidence in results, but the costs and benefits must be carefully weighed against each other.

It has recently been acknowledged by Soanes *et al.* (2014) that increasing cell size has a considerable effect and reduces the sample sizes required to adequately describe the areas of use. Application of a different cell size in this study is likely to have yielded different results. It is also noted that a more traditional application of the home range concept (e.g. use of MCPs) would also have a provided a less stringent, but equally valuable means of assessing the value of available sample size.

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