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Executive Summary

- The aim of this project was to review the potential issue of 'turnover' of individual seabirds at sea during the breeding season and to assess how this may lead abundance estimates derived from boat or aerial surveys to underestimate the total number of birds that use an area during the course of the breeding season. We estimate turnover rates in species for which sufficient data were available.

- The following candidate species were identified for inclusion in the project: red-throated diver, common guillemot, razorbill, black guillemot, Atlantic puffin, European shag, common eider, northern gannet, black-legged kittiwake and northern fulmar. Turnover was estimated in four species for which sufficient data were available: common guillemot; razorbill; Atlantic puffin and black-legged kittiwake, using the Forth/Tay region as the study area. A literature review on input parameters required to estimate turnover was undertaken on the remaining species to establish data gaps.

- We defined turnover as the total number of birds that will use a particular area of sea at any point during the breeding season, divided by the number of birds that will be present in that area at a particular snapshot in time.

- We estimate turnover using modelled foraging densities of the Forth-Tay area derived from real GPS data (as produced and described in Searle *et al.*, 2014) to simulate the daily foraging locations of individual birds on individual days throughout the breeding season. By assuming that birds rest at their foraging locations, and travel in a straight line between the colony and foraging location, these simulations can also be used to evaluate the locations that are associated with foraging, commuting and resting at sea.

- We then use empirical data on the daily activity budget of birds as a basis for simulating the number of birds that would be seen performing each behaviour (foraging, commuting, resting at sea) within each wind farm footprint during a "snapshot" survey of the entire footprint area. This allows us to produce a direct estimate of turnover.

- Foraging site fidelity will clearly affect estimates of turnover, however, it is not well understood or parameterised in these species. We have, therefore, estimated turnover under a number of different scenarios regarding the extent of site fidelity: both in terms of the level of the site fidelity, as well as the spatial scale associated with it.

- As well as being contingent upon particular levels and scales of foraging site fidelity, the calculations also depend heavily upon the accuracy of the input data (bird density and time activity) and upon a number of other simplifying assumptions: that birds will only visit one foraging location on a day, that they

will rest at the same location as they feed, and that they will travel to this location in a straight line from the colony.

- Our results indicate that: (a) turnover decreases as site fidelity increases; (b) turnover decreases as birds exhibit site fidelity at finer spatial scales; (c) turnover is typically much higher for "commuting" behaviour than for "foraging" or "resting at sea" behaviours; (d) variation in turnover between the simulated snapshot surveys is generally very substantial. The results also highlight more subtle differences between individual species and wind farm footprints.

- In general, kittiwake and razorbill had higher levels of turnover than did guillemots or puffins. This is true for both foraging and resting at sea. For all wind farm footprints, kittiwake and razorbill had estimates of turnover between approximately 100 and 150 with a site fidelity level of zero, in comparison to guillemot and puffin that had estimates between approximately 60 and 100. These differences may, in part, be explained by variation in the foraging ecology of each species (foraging range and observed time activity budgets).

- Within a species, there was variation in estimates of turnover between wind farm footprints. Guillemots displayed the lowest variation in turnover estimates between the different footprints. Razorbills also exhibited relatively low variation in turnover estimates between wind farm footprints. Kittiwakes displayed a similar pattern in relation to variation amongst wind farm footprints as seen for razorbills, although overall turnover estimates for kittiwake were slightly higher than those estimated for razorbills, for both foraging and resting at sea. While puffins had the lowest overall estimates of turnover for both foraging and resting at sea of the four species, they did have noticeably higher estimates of turnover for foraging birds at the NnG and Bravo wind farm footprints in comparison to the other wind farm footprints.

- Turnover is calculated in relation to a "census snapshot", thereby assuming that it is possible to survey the entire population within an area completely and instantaneously. This is a useful approach, because it separates out the effects of turnover from those of other effects (e.g., non-detection). However, in order to relate the results of this work directly to the output from at-sea or aerial surveys it is important to account for the fact that these types of data will typically constitute a sample rather than a census, and that they will not take place instantaneously.

- **Conclusions:** This project provides relevant information to assist Marine Scotland Science with identifying knowledge gaps that may benefit from further data collection. It will also enable Marine Scotland Licensing Operations Team and Marine Renewables Developers to make more informed assessments of the potential impacts of development projects as part of the required environmental evaluations. The project, therefore, has

significant strategic relevance for site characterisation and monitoring in Scotland and beyond. Turnover is clearly only one factor that will need to be considered when assessing the risks to seabird populations from offshore developments. A related task will involve quantifying the fate of birds that lie within the development footprint. Further work is needed in order to understand whether higher levels of turnover lead, all else being equal, to higher or lower estimates of development-related mortality.

1. Introduction

The Scottish government has set a target of 100% of Scottish demand for electricity to be met by renewable sources by 2020 and an interim target of 50% by 2015. Offshore wind will be a key contributor to the renewable portfolio, and a Marine Plan identifies areas of development in the short term (up to 2020) and medium term (beyond 2020; Marine Scotland 2011; Scottish Government 2013). Some of these areas host important populations of seabirds that are protected by the EU Birds Directive. Offshore renewable developments have the potential to impact on protected seabird populations, notably from collisions with turbine blades and through displacement from important habitat.

In undertaking assessments of potential impacts of offshore wind farms on seabirds, interest lies in estimating the number of birds that will be present in a particular area of sea (e.g., the footprint of a proposed offshore wind farm) at a particular time, relative to the total number of birds that will use that area of sea at any point during the breeding season. This relative use of an area at a given time in relation to the rest of the breeding season is termed 'turnover', relating to the turnover of individual birds using a particular area over time. Estimating turnover is important because estimates of the number of birds that may be affected by offshore renewable energy developments typically involve a limited series of at-sea surveys of fixed areas (potential wind farm footprints). These surveys effectively provide a snapshot estimate of the number of birds using that area at different times during the breeding season. Therefore, there is a need for better understanding of the extent to which these snapshot estimates underestimate the total number of birds using the area over the entire breeding season. This project, (1) reviews input parameters required to estimate turnover for remaining key species to establish data gaps; and (2) estimates turnover within selected areas (wind farm footprints) within the Forth/Tay offshore wind farm development area for selected species with sufficient data. To do so, we build upon previous work conducted in a larger project estimating the effect of displacement on breeding birds in this region (Searle *et al.* 2014).

In this project we consider how the turnover of birds varies by species (black-legged kittiwake *Rissa tridactyla*; common guillemot *Uria aalge*; razorbill *Alca torda*; Atlantic puffin *Fratercula arctica*), and with other biological and methodological parameters. Inevitably, the degree of turnover of individuals using an area over the breeding season will be influenced by the extent to which birds tend to return to the same foraging location repeatedly through time (termed 'site fidelity'), and the spatial scale over which fidelity to particular foraging locations operates (termed 'spatial scale of site fidelity'). We explore how estimates of turnover are influenced by the level of

site fidelity – with individuals displaying behaviours along a scale ranging from no site fidelity (foraging locations are selected independently on each day) to complete site fidelity (the same foraging location is used throughout the breeding season). This necessarily raises the question as to how we define the appropriate spatial scale over which site fidelity operates. The spatial scale of site fidelity will vary by species, and is likely to vary seasonally in response to environmental conditions. However, empirical data on the spatial scale of site fidelity for foraging birds is scarce, so in this project we consider a range of scales over which it is assumed fidelity to foraging sites operates in each species.

We also consider how the scale and location of survey effort affects estimates of turnover. To do so, we vary both the location and size of potential wind farm footprints over which observations of individuals occur. In addition, when at sea, boat or aerial surveys are conducted, observed birds are classified as far as possible according to behaviour – either as resting on the sea surface, foraging, or flying over the area. These distinctions are important as different behaviours may influence risk of collision. To estimate turnover for a specific area, we, therefore, need to partition the activity of birds into each category to provide an estimate of turnover specific to each behaviour. Outputs from this project may then be compared to at-sea survey data that classifies observed individuals into these three behavioural categories.

Care must be taken in relating the outputs of this work to at-sea survey data. In this project we estimate turnover in relation to a complete "census snapshot" survey of the footprint, thereby assuming that the number of birds present in the survey area can be known exactly at a particular instant in time. The idea of the "census snapshot" is that we have data on the location of all birds within the survey area (e.g., the wind farm footprint) at the exact time of the survey, and that we know the behaviour of each of these birds. The survey is, therefore, assumed to be comprehensive (e.g., a census) and to take place instantaneously (a snapshot). This assumption represents an idealised situation – in reality, survey data will typically not be a complete census (because only part of the population in the area will be counted), and will typically not be instantaneous (it will take some time for the survey to be conducted). The biases associated with the actual observation process (up-scaling, non-detection) are also important in at-sea surveys, and need to be considered when translating survey data into an estimate of the overall population using a site (Thomas *et al.* 2010). However, none of these factors are directly related to turnover. The key motivation for our formulation as a "snapshot census" is to separate out the quantification of turnover (which is a property of the population itself) from the quantification of observation error (which is a property of the survey method). The latter issue is beyond the remit of this project, and its effect will differ

between different survey methodologies. However, it must be considered when relating estimates of turnover to the outputs from at-sea survey data.

When assessing turnover, we consider the following Special Protected Areas (SPAs): Buchan Ness to Collieston Coast SPA, Fowlsheugh SPA, Forth Islands SPA and St Abb's Head to Fastcastle SPA. Four recently consented wind farms are considered - Neart na Goithe (NNG), Inch Cape (IC), Seagreen Alpha (Alpha), and Seagreen Bravo (Bravo; full details are in Searle *et al.* 2014). To explore the effect of the size of a wind farm footprint on estimates of turnover we also consider 'artificial' footprints of fixed size, centred on the geographical coordinates of the recently consented footprints.

Data on bird distributions for the four species (kittiwake, guillemot, razorbill and puffin) were taken from GPS loggers that had been deployed on individual birds from the four SPAs in the region of the recently consented wind farms during chick-rearing periods in 2010, 2011 and 2012. GPS tracking data enable us to estimate the relative spatial densities of birds that have come from a specific SPA. For each species, bird densities were estimated from the filtered GPS tracking data using a Binomial generalized additive model (GAM). The GAMs provide an estimate of the predicted bird density (of breeding individuals during the chick rearing period) for each species-by-SPA combination (for more details see Searle *et al.* 2014). Our approach is based on the use of tracking data from birds of known breeding origin, and would not be directly applicable for sites and species where such data are not available. However, the use of GPS technologies is becoming increasingly affordable, and collecting tracking data to estimate at-sea turnover of individuals from data deficient SPAs should be prioritised in any future research.

We modify the simulation of locations to vary the extent to which birds display site fidelity to foraging locations because we expect this to be crucially important when considering turnover. In so doing we make two simplifying assumptions regarding how site fidelity is expressed by foraging birds. These assumptions are made partly for reasons of computational speed, and partly because of a lack of relevant empirical data to inform more realistic representations of site fidelity. Firstly, we assume that there is complete fidelity within a time-step (24-36 hours depending on the species), such that each bird visits only one foraging location for each day (or 36 hour period) of the breeding season – although the bird may visit this site more than once. The second assumption is that site fidelity operates in relation to the cells of a regular grid (0.5 km x 1.0 km) used to model the density of foraging birds, and not to other spatial areas such as irregular shaped areas that may better represent foraging hotspots.

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Finally, we categorise the activity of birds into each behavioural category by using empirical data from bio-loggers for each species to estimate the proportion of time birds spend in each activity during a time period of 05:00 to 20:00 hours. This time period was chosen to coincide with the part of the day over which at-sea surveys typically take place (Camphuysen *et al.* 2004). We also investigate an alternative methodology in which activity budgets were derived from the outputs of a foraging model developed in a previous project (Searle *et al.* 2014).

2. Literature Review

2.1. Methodology

We conducted a review of the published literature relevant to estimating turnover in species included in the project but for which modelling was not carried out (red-throated diver, black guillemot, European shag, common eider, northern gannet and northern fulmar). We focused on studies (both UK and beyond) that provide estimates of parameters considered relevant to estimating turnover during the breeding season, such as time activity budgets, foraging trip characteristics and foraging site fidelity. The literature search was carried out in the Web of Science (all databases, 1950-2015) using the following search terms in combination with the species name: 'foraging range', 'foraging trip', 'foraging trip duration', 'site fidelity', 'foraging site fidelity' and 'foraging area fidelity', 'foraging and consistency', 'nest attendance', 'time activity budget' and 'activity budget'. Due to the limited time available and majority of the literature being focussed on the chick rearing period, the search was restricted to this stage of the breeding season.

Mean and standard deviation (SD) were extracted for each parameter (where available), with the exception of foraging site fidelity where either various metrics or only qualitative information are reported in the literature. This parameter was, therefore, presented as a categorical variable, with two levels ('high'/'low') that directly reflect the interpretation of the authors of the original papers as to what constitutes a high or low measure of fidelity; details of the different fidelity metrics, however, are available within the cited references. In most cases parameter values were provided directly by the cited studies; in a few cases other relevant information was available which allowed us to derive the values of our parameters of interest. Derived values are presented in square brackets. Where data were available for more than one colony, estimates for each colony are presented separately; the only exceptions are two review studies (Langston 2010 and Thaxter *et al.* 2012) where estimates are averaged across multiple colonies and years. Where data were available for the same colony in multiple years, averaged values are presented;

annual estimates, however, can be found within the cited references. Sample size of birds in each study is provided as an indication of reliability of the data; note also that estimates from recent studies are likely to be more accurate compared to those from older studies, as a result of the use of advanced bio-logging technologies in particular.

2.2.   Results

Estimates of foraging trip characteristics (range, duration and frequency) were available for most species, and in many cases data for these parameters were available from multiple colonies (Table 1.2). In contrast, there was lack of information or only qualitative information available on foraging site fidelity for most species (Table 1.2). Data on daily activity budgets were of variable quality and often incomplete (Table 1.2). To fill these knowledge gaps, targeted field data collection involving the deployment of bio-logging devices and/or analysis of existing tracking datasets should be considered.

The most data-rich species was the Northern gannet, followed by the European shag. For these species parameter estimates from multiple colonies and years were typically available (Table 1.2). For the northern fulmar a reasonable amount of information was available regarding foraging trip characteristics but we found very little information on foraging site fidelity and daily activity budgets. Note also that in this species foraging behaviour of the adults changes substantially between the early (when chicks are brooded) and later (when chicks are not brooded) stages of offspring rearing which is why foraging trip characteristics are provided separately for these stages (Table 1.2). For the red-throated diver and black guillemot no recent data and very little older data were available for any of the parameters of interest (Table 1.2). Clearly, if turnover of individuals at sea is to be investigated in these species, new data collection would need to be prioritised as a first step. Due to the biology of the common eider, where females take their chicks to water soon after they hatch and do not return to the nest thereafter, the concept of a 'foraging trip' by a central-place foraging individual during chick rearing is not applicable. Linked to this, the cited estimates of foraging range indicate the general area used by the females and young once they have moved away from the nest site. Furthermore, male eiders take no part in offspring care and in the summer use different, generally more distant areas compared to females, where they initiate moult (Diéval *et al.* 2011). Therefore, to estimate turnover in this species, the approach to data collection would need to be sex-specific and may require (at least in females) relatively long-term deployments of the latest tracking technology (such as GPS-

GSM tags, accelerometers) to obtain information of the birds' use of areas at sea at appropriate temporal and spatial scales.

Table 1.2

Parameters relevant to estimating turnover of individuals at sea during the breeding season (data from chick rearing period only; 'NA' = not available; '-' = not applicable; values in square brackets are derived based on information within the cited references – see Methods for details).

Parameter	N birds	Mean	SD	Reference
a) Red-throated diver (*Gavia stellata*)				
Foraging range (km)	9	11.1	NA	Langston 2010
	NA	4.5	NA	Thaxter *et al.* 2012
Maximum foraging range (km)	9	12.2	NA	Langston 2010
	NA	9.0	NA	Thaxter *et al.* 2012
Foraging trip duration (h)	6	1.0	NA	Reimchen and Douglas 1984
	16	0.9	0.6	Eriksson *et al.* 1990
Foraging trip frequency/day	6	5.5	NA	Reimchen and Douglas 1984
	16	7.0	NA	Eriksson *et al.* 1990
Foraging site fidelity	16	high	-	Eriksson *et al.* 1990
Daily time at nest (h)	NA	NA	NA	NA
Daily resting time (h)	NA	NA	NA	NA
Daily foraging time (h)	16	[3.8]	NA	Eriksson *et al.* 1990
Daily commuting (flight) time (h)	16	[1.4]	NA	Eriksson *et al.* 1990
b) Black guillemot (***Cepphus grylle***)				
Foraging range (km)	56	0.7	0.5	Cairns 1987
	38	5.0	NA	Langston 2010
Maximum foraging range (km)	56	2.0	NA	Cairns 1987
	38	12.0	NA	Langston 2010
Foraging trip duration (h)	NA	[~4.0]	NA	Cairns 1987; Gaston 1985
Foraging trip frequency/day	NA	4.4	NA	Cairns 1987
	NA	5.0	NA	Gaston 1985
Foraging site fidelity	NA	NA	NA	NA
Daily time at nest (h)	NA	0*	0	Gaston 1985
Daily resting time (h)	NA	7.0	NA	Gaston 1985
Daily foraging time (h)	NA	15.5	NA	Gaston 1985
Daily commuting (flight) time (h)	NA	1.5	NA	Gaston 1985
c) European shag (Phalacrocorax aristotelis)				
Foraging range (km)	29	7.0	1.9	Wanless *et al.* 1991
	29	6.5	NA	Langston 2010
	29+	5.9	4.7	Thaxter *et al.* 2012
Maximum foraging range (km)	29	16.4	NA	Langston 2010
	29+	14.5	3.5	Thaxter *et al.* 2012
	320	9.0	3.8	Bogdanova *et al.* 2014
	57	4.0	3.7	Soanes *et al.* 2014
Foraging trip duration (h)	10	1.8	0.5	Wanless and Harris 1992
	5	2.0	1.3	Gremillet *et al.* 1996
	57	1.5	1.0	Soanes *et al.* 2014
Foraging trip frequency/day	10	2.8	0.4	Wanless and Harris 1992
Foraging site fidelity	NA	NA	NA	NA
Daily time at nest (h)	10	18.8	NA	Wanless and Harris 1992

Daily resting time (h)	10	1.4	NA	Wanless and Harris 1992
Daily foraging time (h)	10	2.5	NA	Wanless and Harris 1992
Daily commuting (flight) time (h)	10	1.3	NA	Wanless and Harris 1992
d) Common eider (*Somateria mollissima*): females only				
Foraging range (km)	10	9.3	NA	Langston 2010
	NA	2.4	NA	Thaxter *et al.* 2012
Maximum foraging range (km)	55	72.0	NA	Bustness and Erikstad 1993
	10	38.3	NA	Langston 2010
	NA	80.0	NA	Thaxter *et al.* 2012
Foraging trip duration (h)	-	-	-	-
Foraging trip frequency/day	-	-	-	-
Foraging site fidelity - repeatability in foraging area in successive years (proportion of birds in area)	12	High	-	Bustness and Erikstad 1993
Daily time at nest (h)	NA	0	0	Waltho and Coulson 2015
Daily resting time (h)	20	[20.6]	NA	Pelletier *et al.* 2008; Guillemette and Butler 2012
Daily foraging time (h)	20	[3.2]	NA	Pelletier *et al.* 2008; Guillemette and Butler 2012
Daily commuting (flight) time (h)	20	0.2	0.2	Pelletier *et al.* 2008
e) Northern gannet (*Morus bassanus*)				
Foraging range (km)	17	164.0	101.0	Hamer *et al.* 2000
	62	140.1	NA	Langston 2010
	169+	92.5	59.9	Thaxter *et al.* 2012
Maximum foraging range (km)	5	89.0	49.0	Hamer *et al.* 2001
	20	100.0	35.0	Grémillet *et al.* 2006
	53	238.2	108.0	Hamer *et al.* 2007
	62	308.4	NA	Langston 2010
	169+	229.4	124.3	Thaxter *et al.* 2012
	17	106.0	43.0	Soanes *et al.* 2013
Foraging trip duration (h)	3	13.0	NA	Garthe *et al.* 1999
	5	11.9	6.7	Hamer *et al.* 2001
	20	17.7	8.5	Grémillet *et al.* 2006
	75	28.2	12.8	Lewis *et al.* 2005; Hamer *et al.* 2007
	23	25.1	17.0	
	17	17.6	6.5	Votier *et al.* 2010 Soanes *et al.* 2013
Foraging trip frequency/day	5	[2.0]	NA	Hamer *et al.* 2001
	20	[1.4]	NA	Grémillet *et al.* 2006
	75	[0.8]	NA	Lewis *et al.* 2005; Hamer *et al.* 2007
	23	[1.0]	NA	
	17	[1.4]	NA	Votier *et al.* 2010 Soanes *et al.* 2013
Foraging site fidelity - repeatability in destination among successive trips (bearing and max distance)	5	Low	-	Hamer *et al.* 2001
	53	High	-	Hamer *et al.* 2007
	15	High	-	Soanes *et al.* 2013
	18	High	-	Patrick *et al.* 2014
	13	High	-	Patrick *et al.* 2014
	15	Low	-	Soanes *et al.* 2013
- repeatability in duration of successive trips	18	Low	-	Patrick *et al.* 2014
	13	Low	-	Patrick *et al.* 2014
Daily time at nest (h)	3	~10.7	NA	Garthe *et al.* 1999

	22;53;12	[13.6]	NA	Lewis *et al.* 2004; Hamer *et al.* 2007; Ropert-Coudert *et al.* 2009
Daily resting time (h)	3	[~6.3]	NA	Garthe *et al.* 1999
	22;53;12	[5.4]	NA	Lewis *et al.* 2004; Hamer *et al.* 2007; Ropert-Coudert *et al.* 2009
Daily foraging time (h)	3;22	[~0.6]	NA	Garthe *et al.* 1999; Lewis *et al.* 2004; Ropert-Coudert *et al.* 2009
	22;53;12	[0.5]	NA	Lewis *et al.* 2004; Hamer *et al.* 2007; Ropert-Coudert *et al.* 2009
Daily commuting (flight) time (h)	3	~6.4	NA	Garthe *et al.* 1999
	22;53;12	[4.5]	NA	Lewis *et al.* 2004; Hamer *et al.* 2007; Ropert-Coudert *et al.* 2009
f) Northern fulmar (*Fulmarus glacialis*)				
Foraging range (km)	51	69.4	NA	Langston 2010
	14+	47.5	5.9	Thaxter *et al.* 2012
Maximum foraging range (km)	51	311.4	NA	Langston 2010
	14+	400.0	245.8	Thaxter *et al.* 2012
Foraging trip duration (h)				
- early chick-rearing (brooding)	14	<10	NA	Furness and Todd 1984
	4	10.2	4.0	Weimerskirch *et al.* 2001
	50;48	11.2	NA	Ojowski *et al.* 2001
- mid-/late chick-rearing (post-brooding)	23	28	NA	Furness and Todd 1984
	NA	24	NA	Hamer *et al.* 1997
	14	31.0	NA	Phillips and Hamer2000
	50;48	20.4	NA	Ojowski *et al.* 2001
Foraging trip frequency/day				
- early chick-rearing (brooding)	NA	NA	NA	NA
- mid-/late chick-rearing (post-brooding)	23	0.8	NA	Furness and Todd 1984
	NA	[0.9]	[0.2]	Hamer *et al.* 1997
	28	0.8	NA	Phillips and Hamer 2000
Foraging site fidelity	4	Low	NA	Weimerskirch *et al.* 2001
Daily time at nest (h)	28	~1.0	NA	Phillips and Hamer2000
Daily resting time (h)	NA	NA	NA	NA
Daily foraging time (h)	NA	NA	NA	NA
Daily commuting (flight) time (h)	NA	NA	NA	NA

* from 5 days after hatching no brooding occurs (Gaston 1985)

3.   Definition of Turnover

Turnover represents the value that a "snapshot" census of the population at any particular time would need to be multiplied by in order to obtain an estimate of the total population of birds using the area at any point during the breeding season. For example, if a snapshot census identifies 100 birds using the area, a turnover value of 10 would mean that 1000 birds are estimated to use the area during the entire breeding season. More precisely, we define the "turnover" associated with behaviour *B* (resting at sea, foraging, or flying) and spatial area *A* to be:

(Number of birds that perform behaviour *B* within area *A* at any point during the entire breeding season)/(Mean across time-points of the number of birds that perform behaviour *B* visiting area *A* at each time-point *t*)

Turnover, therefore, represents the ratio of the number of birds that use the area throughout the breeding season to the number of birds that would typically be seen if a comprehensive census survey was conducted at a particular time. Note that the definition is intrinsically linked to a particular spatial area *A* and a particular behaviour *B*. The area *A* typically corresponds to the footprint of an offshore wind farm.

In mathematical terms, the definition of turnover can be expressed as:

$$T_{AB} = \frac{x_{AB}}{\frac{1}{m}\sum_{t=1}^{m} y_{ABt}}$$

where x_{AB} represents the number of birds that perform behaviour *B* in area *A* at any point during the breeding season, and y_{ABt} represents the number of birds performing behaviour *B* in area *A* at time *t* and $t = 1,...,m$ are an appropriately selected set of representative times.

Individual-based simulations are used to estimate both of these numbers. The survey at time, *t*, is assumed to be a complete snapshot census of the population within area *A*, and is assumed to occur instantaneously (i.e. providing a complete "snapshot" of all the birds using area *A* during that time) – the possibility that birds will leave or enter area *A*, or will change behaviour during the course of the survey, is disregarded. This sort of "snapshot" survey is an idealised construct, because actual survey methods do not allow for a full census of birds to be collected instantaneously over such a large area. However, most survey techniques are designed to attempt to estimate such a snapshot of the population. Whilst they may

not be able to achieve this for logistical reasons, they are designed to approximate the result that would have been obtained from an actual census snapshot survey. Therefore, in this project, we consider an idealised full census "snapshot" survey of the breeding individuals using area *A* at time *t* so that we may disentangle the effects of turnover from the effects of survey error and/or bias. The results that we obtain in this project regarding the effects of turnover will, therefore, be general, and not tied to a particular survey methodology.

In the following Sections, 3.2 to -3.4, we detail the species for which turnover is assessed, and describe the different scenarios considered within the project for capturing the level and spatial scale of fidelity, as well as the spatial location and extent of surveys. We then provided more detailed methodology for the implementation of these scenarios in Sections 3.5 to 3.6.

3.2.   Choice of Species

The choice of the four species (black-legged kittiwake, common guillemot, razorbill and Atlantic puffin) for which turnover is assessed in this project follows on from the four main species considered in a previous project regarding the effects of displacement on foraging birds in the breeding season (Searle *et al.* 2014). The Northern gannet, *Morus bassanus,* was not considered here because the very large foraging range of this species would render estimating turnover a very computationally intensive task that would not have been possible to complete within the tight timescale of the current project. However, for gannet and five other species identified by Marine Scotland to be of interest (red-throated diver, *Gavia stellata*, black guillemot, *Cepphus grille*, European shag, *Phalacrocorax aristotelis*, common eider, *Somateria mollissima* and northern fulmar, *Fulmaris glacialis*) we have conducted a review of the published literature relevant to estimating turnover (for details see Section 2.1 and 2.2 above). For data rich species, we have provided input parameters for potential future turnover modelling work that could be conducted using the framework presented in this project; for data poor species, we have highlighted knowledge gaps and future data collection needs.

3.3.   'Level of Site Fidelity' and 'Spatial Scale of Site Fidelity'

(a)   Level of Site Fidelity

The level of site fidelity within this project is set to vary between zero (representing the situation in which foraging locations are selected independently on each day) and one (representing complete site fidelity where the same foraging location is used

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throughout the breeding season). Because empirical data on the level of site fidelity is not readily available for these species, we estimate turnover at five arbitrary intervals along this continuum from zero to complete fidelity to capture a range of effects (0.0, 0.5, 0.67, 0.83, 1.0). These values for the level of site fidelity were chosen to best capture the change in estimated turnover at medium to high levels of turnover – where the greatest change in turnover per unit of site fidelity occurs (see Figures below; Section 4). The results will, therefore, demonstrate how the degree of turnover changes for each species as site fidelity increases. It follows that when fidelity is assumed to be complete (individuals forage and rest at the same location throughout the breeding season), turnover will approach a value close to one (when the spatial scale of site fidelity is at the resolution of a single grid cell; see below). In all simulations, central place foraging by breeding birds is assumed to take place.

(b)   Spatial Scale of Site Fidelity

The spatial scale of site fidelity refers to the spatial extent of the area over which birds return to a previously used foraging location, thereby displaying site fidelity. As agreed by the Steering Group, we chose to consider turnover at three different scales of site fidelity:

- 1 x 1 grid cell or 0.5 km*1.0 km
- 20 x 10 grid cells or 10 km*10 km
- 100 x 50 grid cells or 50 km*50 km

3.4.   Choice of Spatial Areas

We focus in this project upon four specific spatial areas *A* – the footprints that are associated with four recently consented wind farms in the Forth-Tay area of the east coast of Scotland - Neart na Goithe (NNG), Inch Cape (IC), Seagreen Alpha (Alpha), and Seagreen Bravo (Bravo); (Figure 3.1; full details are in Searle *et al.* 2014). These footprints each incorporate a 1 km buffer around the recently consented developments.

Figure 3.1: Map of study area showing SPAs and recently consented wind farms.

We also investigate the effect of the spatial scale of the survey area by considering "artificial" wind farm footprints centred on the median latitude and longitude of each recently consented wind farm (Figure 3.1). These "artificial" wind farms are assumed to be square, with a range of possible areas – 10 km^2, 40 km^2, 100 km^2 and 200 km^2. This covers the range of project scales that are commonly encountered and should provide an indication of the sensitivity of outputs to the area under consideration.

3.5. Choice of Behaviours

Studies of daily time budgets of birds during chick-rearing demonstrate that adults divide their time into four main activities – colony attendance, commuting flight to and

from the foraging areas, foraging, and resting on the sea surface (Daunt *et al.* 2002). At-sea surveys classify birds into the latter three behavioural categories; therefore, in this project we consider turnover for birds in flight (commuting), foraging, or resting at sea. We also consider turnover for combined groupings of behaviours: (a) birds in flight or foraging, (b) birds that are foraging or resting, and (c) birds that undertake any of the three behaviours. This was done due to the difficulty that can exist during at sea surveys in distinguishing between foraging and resting behaviour of auks, or foraging and commuting behaviours of kittiwake.

3.6.   Estimating Turnover

3.6.1. Defining Times

The level of turnover will depend on the time of day at which the survey is undertaken. In practice, surveys take place at a range of different times, so we simply assume that the survey time is randomly distributed between the earliest time that surveys typically occur (05:00 hours) and the latest time at which they typically occur (20:00 hours). We select $R = 100$ random survey times from within this interval for each of the D days in the breeding season. The choice of $R = 100$ is intended to balance accuracy (taking larger values of R reduces the stochastic noise associated with choosing individual survey times at random) and computational speed (the calculations become very slow if R is large).

3.6.2. Simulating Locations

We simulate the foraging locations and individual flight trajectories of birds from each of the SPAs within the vicinity of the recently consented wind farms using methods developed from GPS tracking data for each species (see Searle *et al.* 2014 for details). A percentage of the total population was simulated for each SPA (approximately 5,000 - 10,000 birds per species), following Searle *et al.* (2014). Briefly, for each species, bird densities were estimated from filtered GPS tracking data using a Binomial generalized additive model (GAM). The GAMs provide an estimate of the predicted bird density for each species-by-SPA combination, which are then used to select daily foraging locations for each bird in the simulation. We assume that each bird will visit exactly one foraging location on each day (although it may do so more than once). Foraging locations are restricted in this way because it is very difficult to distinguish between different foraging locations from the tracking data. This assumption also avoids significant complexities associated with estimating turnover for individuals using multiple foraging locations per day, and is consistent with the previous approach used in Searle *et al.* (2014).

We assume that resting at sea occurs at the same location as foraging, and that each bird travels in a straight line between its colony and chosen foraging location. In reality there are likely times when the birds rest at locations different from the locations where they forage, however, it is not possible to separate foraging from resting behaviours with any certainty from GPS data alone. By making these assumptions we may then evaluate whether the bird travelled through the survey target area A to reach its selected foraging site.

In previous work (Searle *et al.* 2014), the foraging locations for each bird were originally simulated independently from day to day. However, this assumption disregards the possibility that birds are faithful to a particular site or spatial region (site fidelity) when foraging over a breeding season. While this is not critically important when assessing broad-scale effects (e.g. the displacement effect from wind turbines), it is important when estimating turnover. We, therefore, modified the original simulation of foraging locations by assuming there is a spatial scale of site fidelity (represented by a regular spatial grid of one of three pre-determined spatial resolutions; 1 x 1 grid cell or 0.5 km*1.0 km; 20 x 10 grid cells or 10 km*10 km; and 100 x 50 grid cells or 50 km*50 km) that defines the extent of the area over which site fidelity operates. We also assumed there is a level of site fidelity, ϕ, which operates within this spatial area - a value of $\phi = 1$ corresponds to complete site fidelity at the level of the regular spatial grid (i.e. a bird will always return to the same cell on this spatial grid, although it will then choose locations within this spatial grid independently from day to day), whereas a value of $\phi = 0$ corresponds to an independent choice of location on each day (sensu Searle *et al.*, 2014). Note that $\phi = 0$ does not correspond to a crude definition of "no site fidelity", because birds may return to the same spatial areas on multiple days. Rather it corresponds to "no more site fidelity than that which would arise by chance, based on independent choices on each day". Full details of the approach are given in Appendix A.

Our approach assumes that birds displaying foraging site fidelity go back to the same grid square, rather than assuming that they go back to a location that is within a particular distance of the original foraging location – so fidelity does not operate as a continuous function of distance away from the original foraging location. The regular spatial grid is used for convenience: the boundaries of grid cells are arbitrary, and are unlikely to correspond to the boundaries of actual foraging areas, but it is computationally tractable and provides a useful mechanism to explore how the spatial scale of fidelity affects turnover. We expect that turnover is likely to be more closely related to the level of fidelity and to the spatial scale of fidelity, than to the exact location or shape of the foraging areas used by birds.

To assess how estimates of turnover are influenced by the level of site fidelity (ϕ) and the spatial scale of site fidelity we consider levels of site fidelity ranging from zero to one (0.0, 0.5, 0.67, 0.83, 1.0), and spatial scales of fidelity ranging from 0.5 km*1.0km to 50 km*50 km.

3.6.3. Time Activity Budgets

The simulations in Section 3.6.2 create the foraging, resting-at-sea and flight locations for each bird on each day, from which we determine whether each bird is exhibiting behaviour *B* within survey target area *A*. In order to translate these into the locations that are visited at a specific time, *t*, we need to account for daily time budgets of birds.

We do this through the use of "empirical activity budgets". A sample of breeding adults from each species have been deployed with a variety of data loggers from which daily time activity budgets were derived (i.e. the proportion of time per 24 hours spent on each of the four principal activities of foraging, flying, resting on the sea surface and colony attendance; details are provided in the following papers: Daunt *et al.* 2002; 2006; Enstipp *et al.* 2006; Harris *et al.* 2012; Thaxter *et al.* 2013). We used these data to estimate the mean proportion of time that birds spent undertaking each of the four principal activities between 05:00 and 20:00 hours. By focusing on the period during which surveys take place we are able to account for diurnal patterns in activity.

The key potential issue with the empirical approach is that it assumes that all birds have, apart from random stochastic variation, the same time activity budget, and that this budget is the same for all foraging locations. This means, for example, that the time spent foraging may not be related to the estimated prey density at each simulated foraging location, as would be expected under optimal foraging theory. An alternative approach is to estimate the daily time budget using output from a mechanistic model, rather than empirical data. We investigated two possible ways of doing this, using the optimal foraging model of Searle *et al.* (2014) but after investigation (full details are given in Appendix B) we concluded that the empirical approach provides substantially more reliable estimates of overall time budgets than the model-based approach (which was not designed to accurately replicate the empirical activity budgets of birds), and we, therefore, only use the results of the empirical approach within this study.

3.6.4. Simulating Behaviour in a Snapshot

The times (Section 3.6.1), locations (Section 3.6.2) and behaviours (Section 3.6.3) allow us to simulate, for a given bird at a particular time t on a particular day:

(a)   its location; and

(b)   the behaviour it is performing.

By calculating the locations and behaviour of all birds it is then straightforward to derive an estimate of turnover using the definition given in Section 3.1.

4.   Results

4.1.   Estimates of turnover

For each species we present graphs of the level of site fidelity (ϕ) against estimated turnover for each of the four species and each of the five recently consented wind farm footprints (the footprints of the four individual wind farms, and the combined footprint of Alpha and Bravo). Turnover is estimated across multiple levels of site fidelity for each behavioural category (foraging, resting at sea, flying), for each spatial scale of fidelity (0.5 km*1.0 km; 10 km*10 km; 50 km*50 km).

The results are shown in Figures 4.1.1 to 4.1.20. As expected, as the level of site fidelity increases for each species and footprint (x-axis in each Figure) the corresponding estimate of turnover decreases. This is because as birds display more faithfulness to foraging sites the total number of foraging sites they visit within the breeding season decreases. This means that birds make more repeat visits to a survey area over the breeding season, so the proportion of the total population observed in a snapshot survey will increase, causing turnover to decrease.

This decrease in the estimate of turnover with increasing levels of site fidelity occurs less sharply as the spatial scale of site fidelity increases for all species and footprints (comparing the orange, red and blue lines in the Figures). This is because as the spatial area over which birds express site faithfulness increases, they are less likely to return to a foraging location within the spatial extent of the snapshot survey. Although birds are being site faithful, the spatial area of the 'site' ultimately becomes sufficiently large such that fidelity to the site does not equate to fidelity to the footprint (i.e. they may return to the same "site", but nonetheless swap from being in a location that is within the footprint to one that is outside, or vice versa).

Turnover is generally much higher for commuting behaviour than for either foraging or resting. This is primarily because birds spend (according to empirical time activity budgets) a small proportion of their time each day commuting. However, it is also because the time that they do spend will be spread across a much wider spatial area than the time that they spend foraging or resting (so that site fidelity in terms of commuting will effectively be much lower than that for foraging or resting).

Uncertainty in turnover (captured by the confidence intervals on each Figure) is much lower for puffin than for the other three species (for which it is generally large). The reason for this is unclear: it may be because the estimated foraging locations of puffin are more clustered spatially than for the other species, or it may be an artefact (possibly relating to the very small amounts of GPS data that were used to construct the estimated foraging density maps for puffin).

The estimates of turnover, and associated confidence intervals, do not always decay as site fidelity increases. We suspect that this simply reflects stochastic variation between sets of simulated locations. The effect is most pronounced for Bravo – this is likely to be due to high levels of both stochasticity and spatial heterogeneity associated with this footprint (the stochasticity relates to the fact that relatively few birds actually visit this footprint, leading to noise in the resulting estimates of turnover; the heterogeneity relates to the presence of a bird density "hot spot" on the edge of the Bravo footprint).

Figure 4.1.1: Plot of fidelity against turnover for kittiwake in relation to the Inchcape footprint. Colours denote the spatial scale at which site fidelity is assumed to operate (0.5 x 1 km: blue; 10 x 10 km: red; 50 x 50 km: orange). 95% confidence intervals are shown as dotted lines.
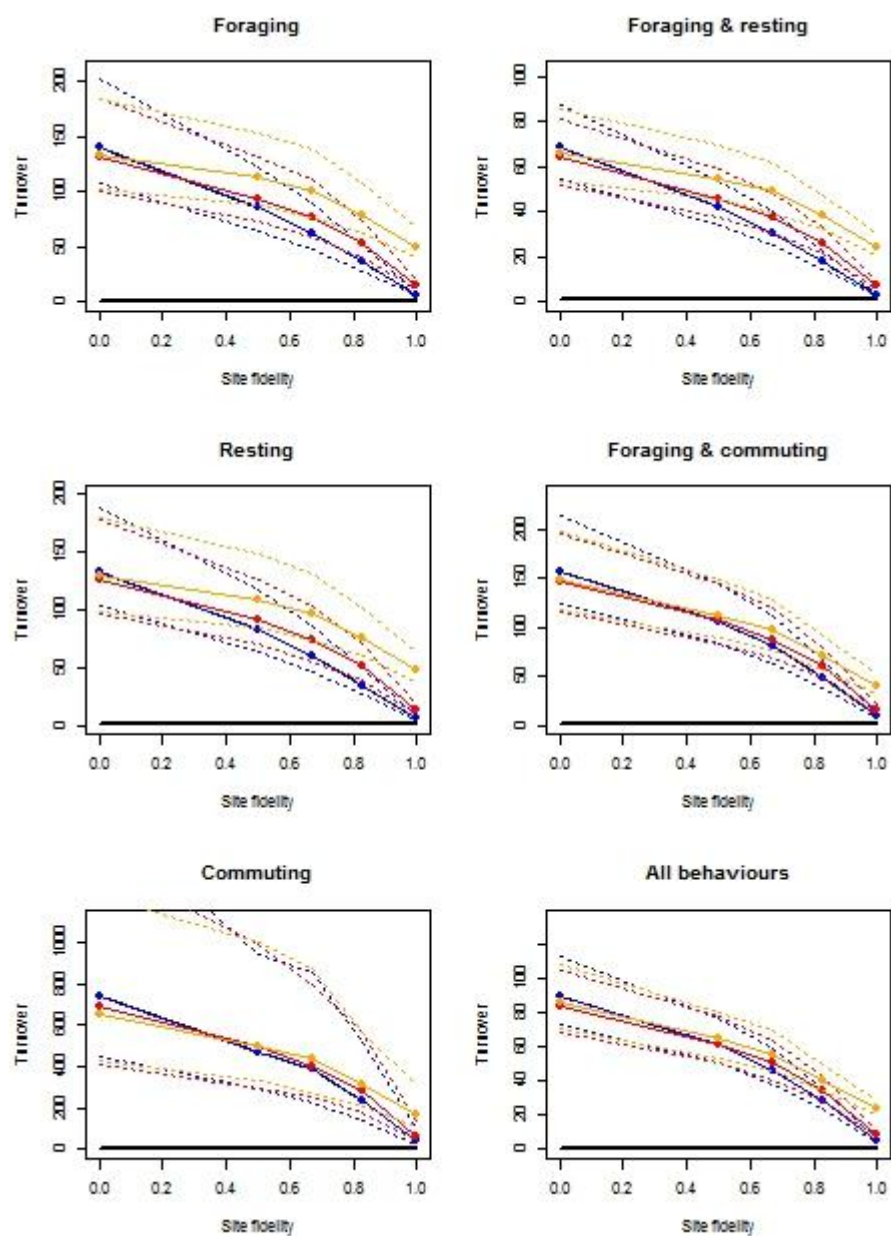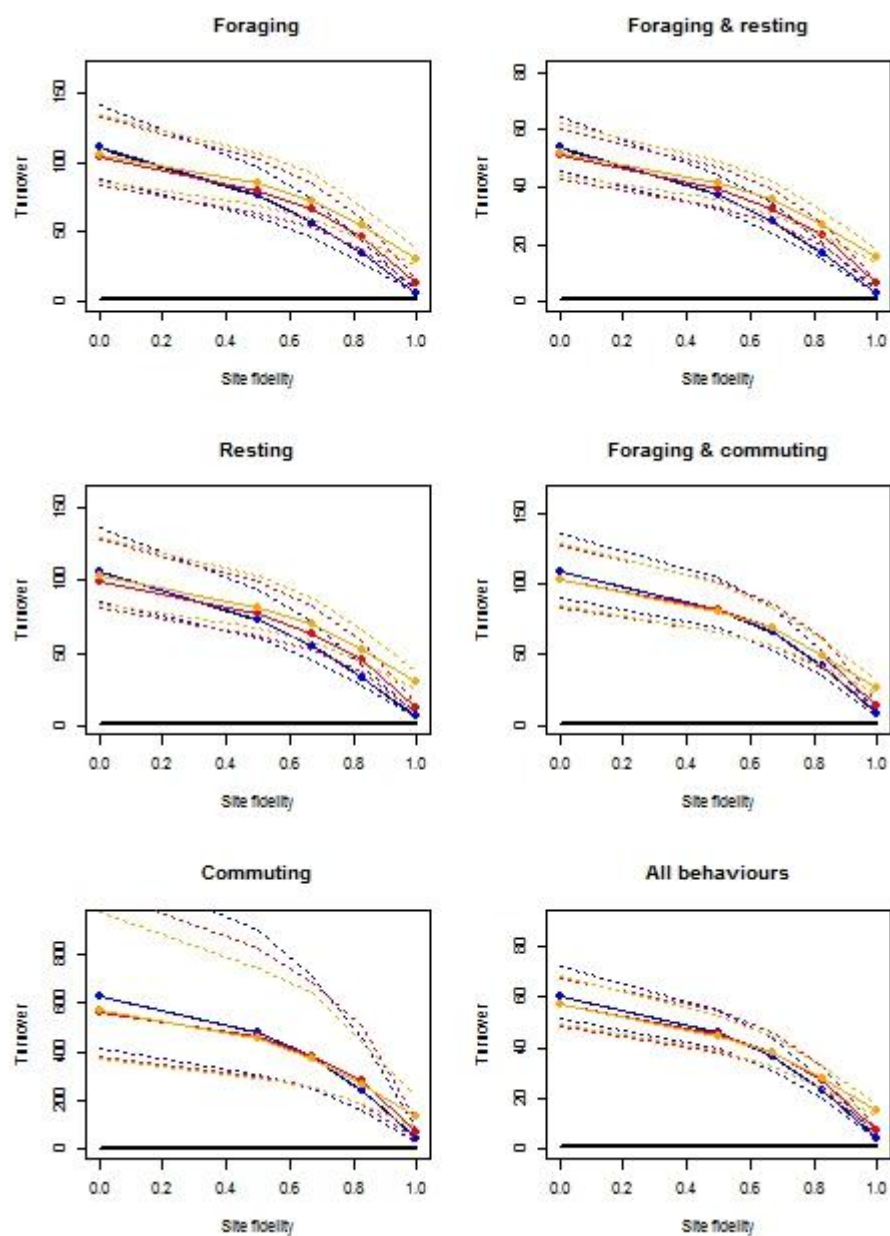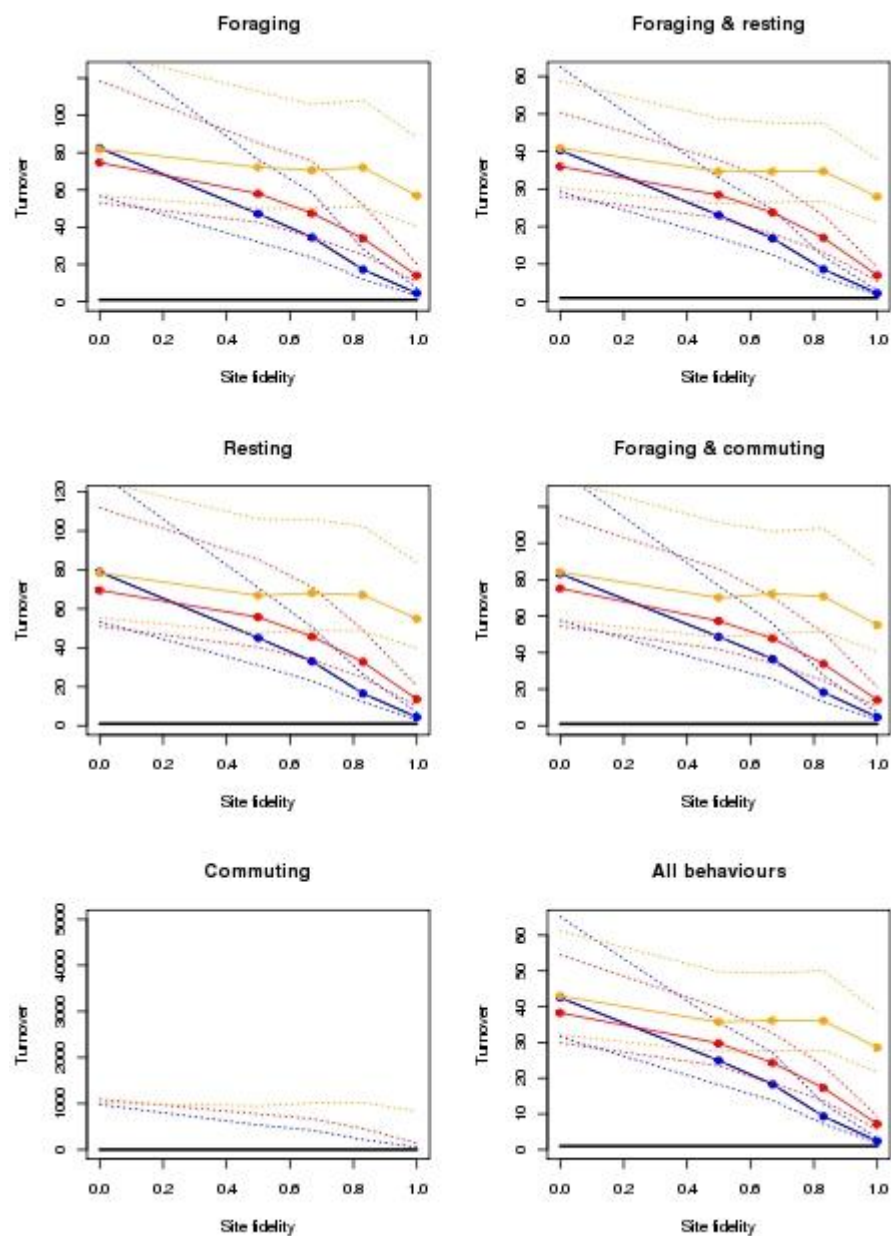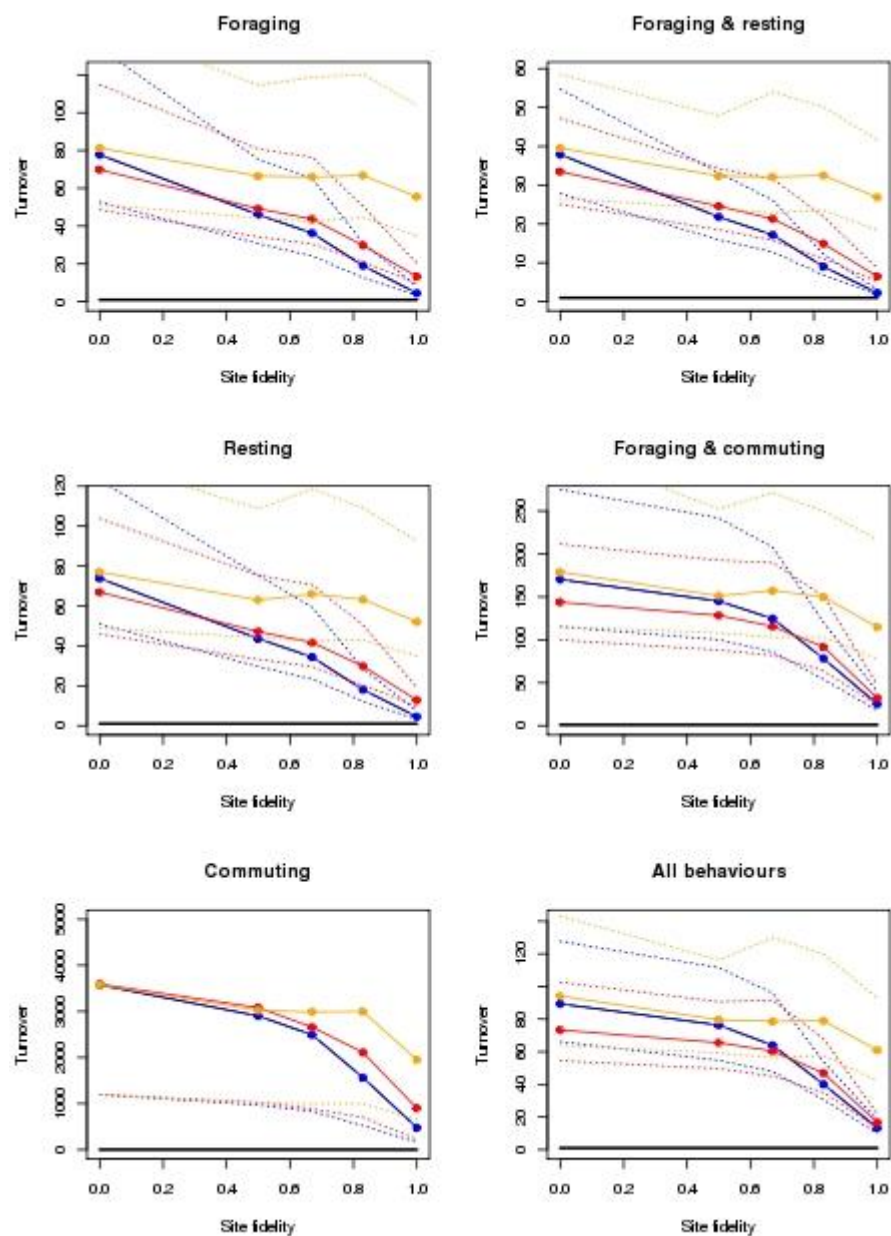
Figure 4.1.2: Plot of fidelity against turnover for kittiwake in relation to the NnG footprint. Colours denote the spatial scale at which site fidelity is assumed to operate (0.5 x 1 km: blue; 10 x 10 km: red; 50 x 50 km: orange). 95% confidence intervals are shown as dotted lines.
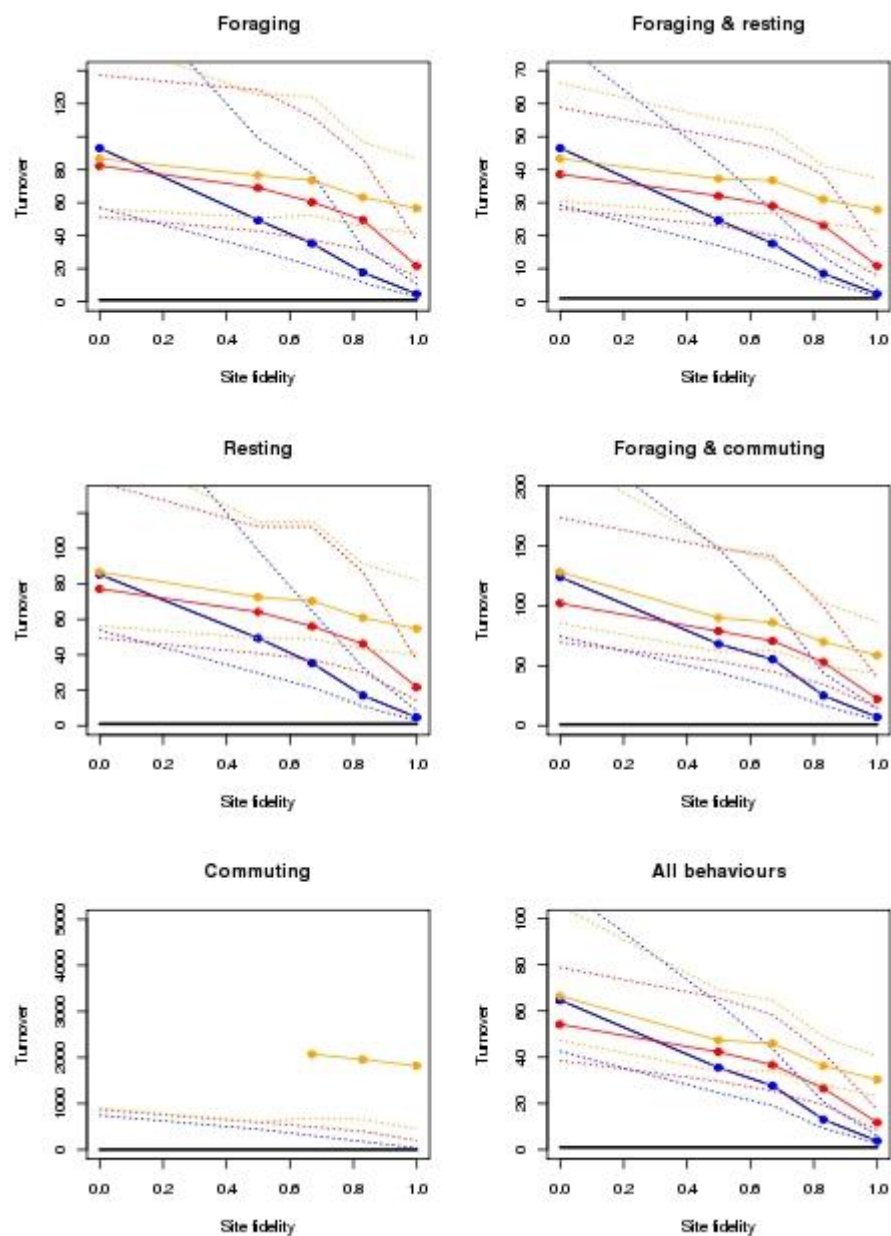
Figure 4.1.3: Plot of fidelity against turnover for kittiwake in relation to the Alpha footprint. Colours denote the spatial scale at which site fidelity is assumed to operate (0.5 x 1 km: blue; 10 x 10 km: red; 50 x 50 km: orange). 95% confidence intervals are shown as dotted lines.

Figure 4.1.4: Plot of fidelity against turnover for kittiwake in relation to the Bravo footprint. Colours denote the spatial scale at which site fidelity is assumed to operate (0.5 x 1 km: blue; 10 x 10 km: red; 50 x 50 km: orange). 95% confidence intervals are shown as dotted lines.
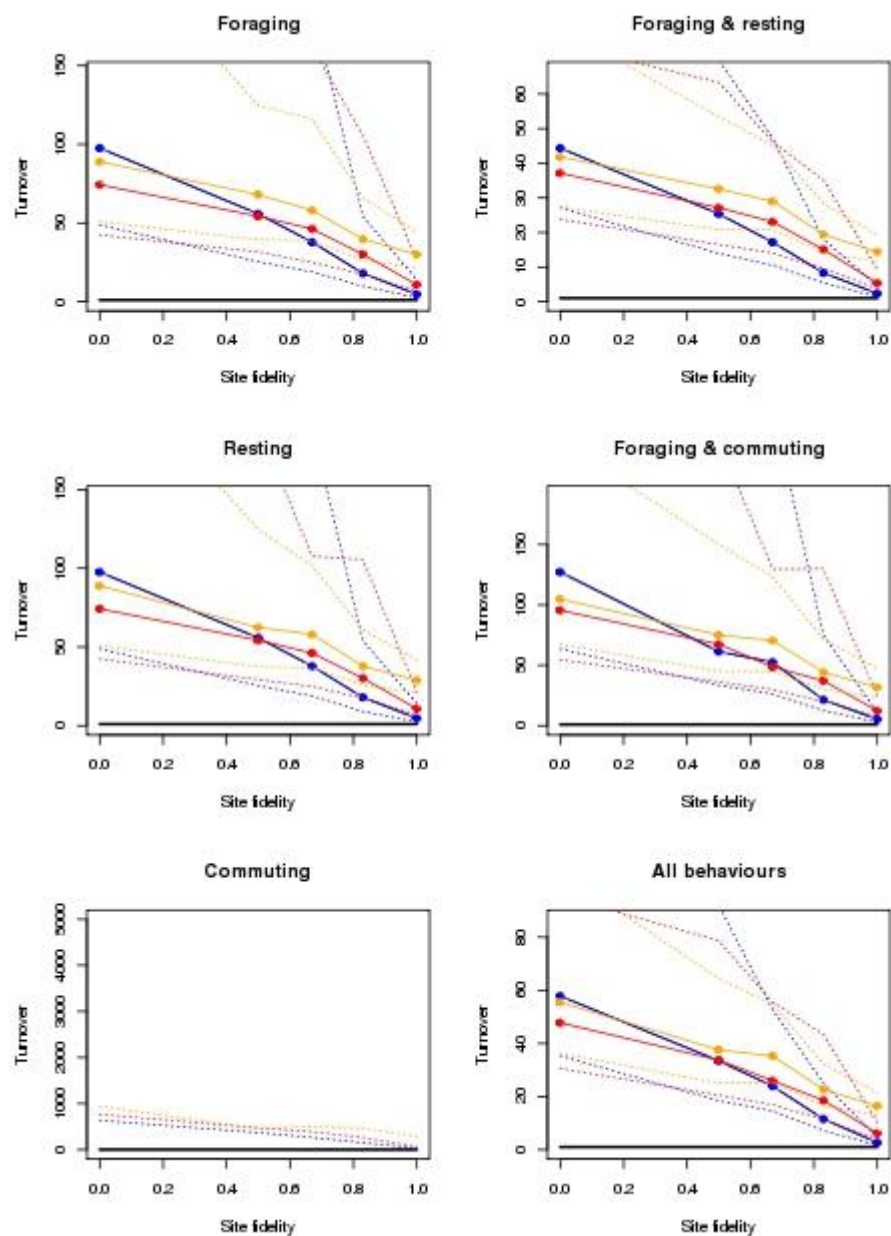
Figure 4.1.5: Plot of fidelity against turnover for kittiwake in relation to the combined Alpha-Bravo footprint. Colours denote the spatial scale at which site fidelity is assumed to operate (0.5 x 1 km: blue; 10 x 10 km: red; 50 x 50 km: orange). 95% confidence intervals are shown as dotted lines.
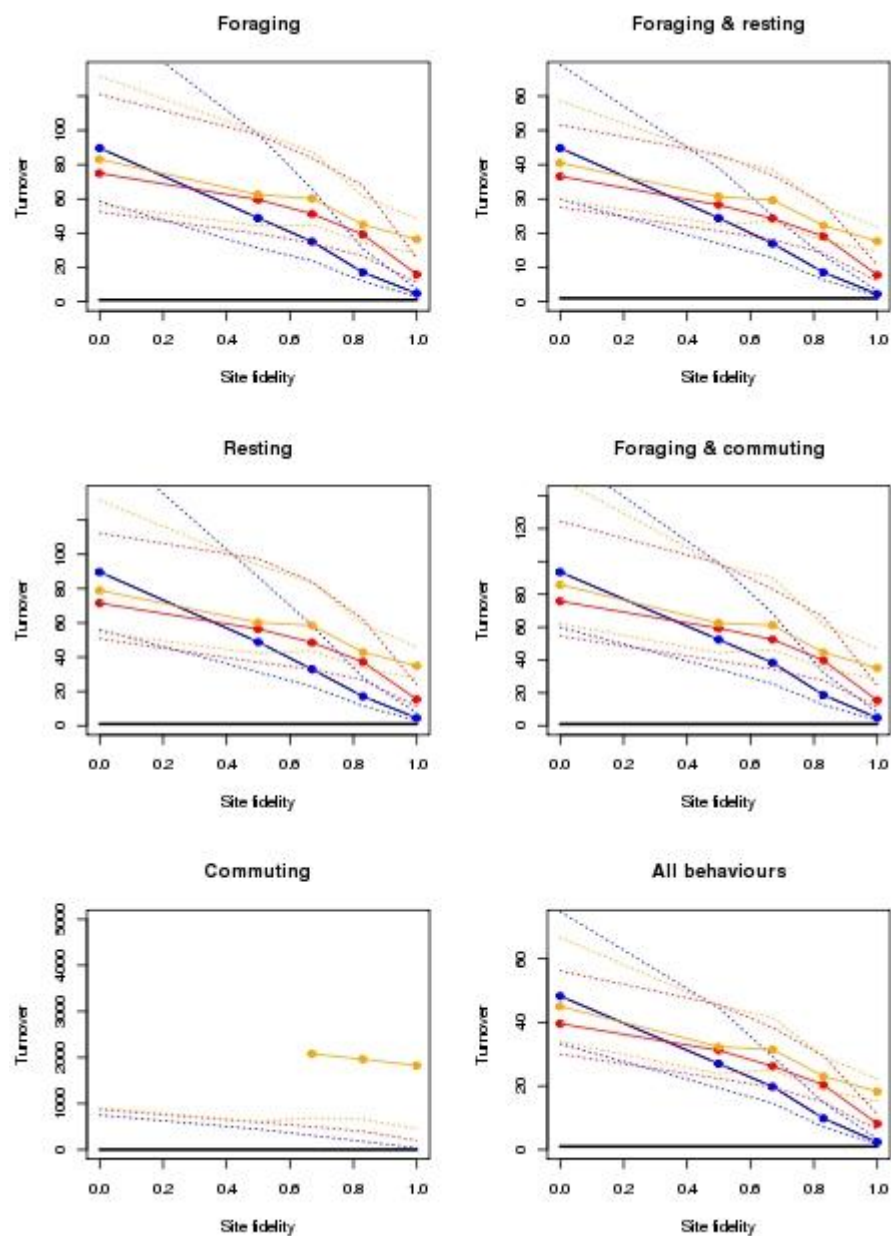
Figure 4.1.6: Plot of fidelity against turnover for guillemot in relation to the Inchcape footprint. Colours denote the spatial scale at which site fidelity is assumed to operate (0.5 x 1 km: blue; 10 x 10 km: red; 50 x 50 km: orange). 95% confidence intervals are shown as dotted lines.

Figure 4.1.7: Plot of fidelity against turnover for guillemot in relation to the NnG footprint. Colours denote the spatial scale at which site fidelity is assumed to operate (0.5 x 1 km: blue; 10 x 10 km: red; 50 x 50 km: orange). 95% confidence intervals are shown as dotted lines.
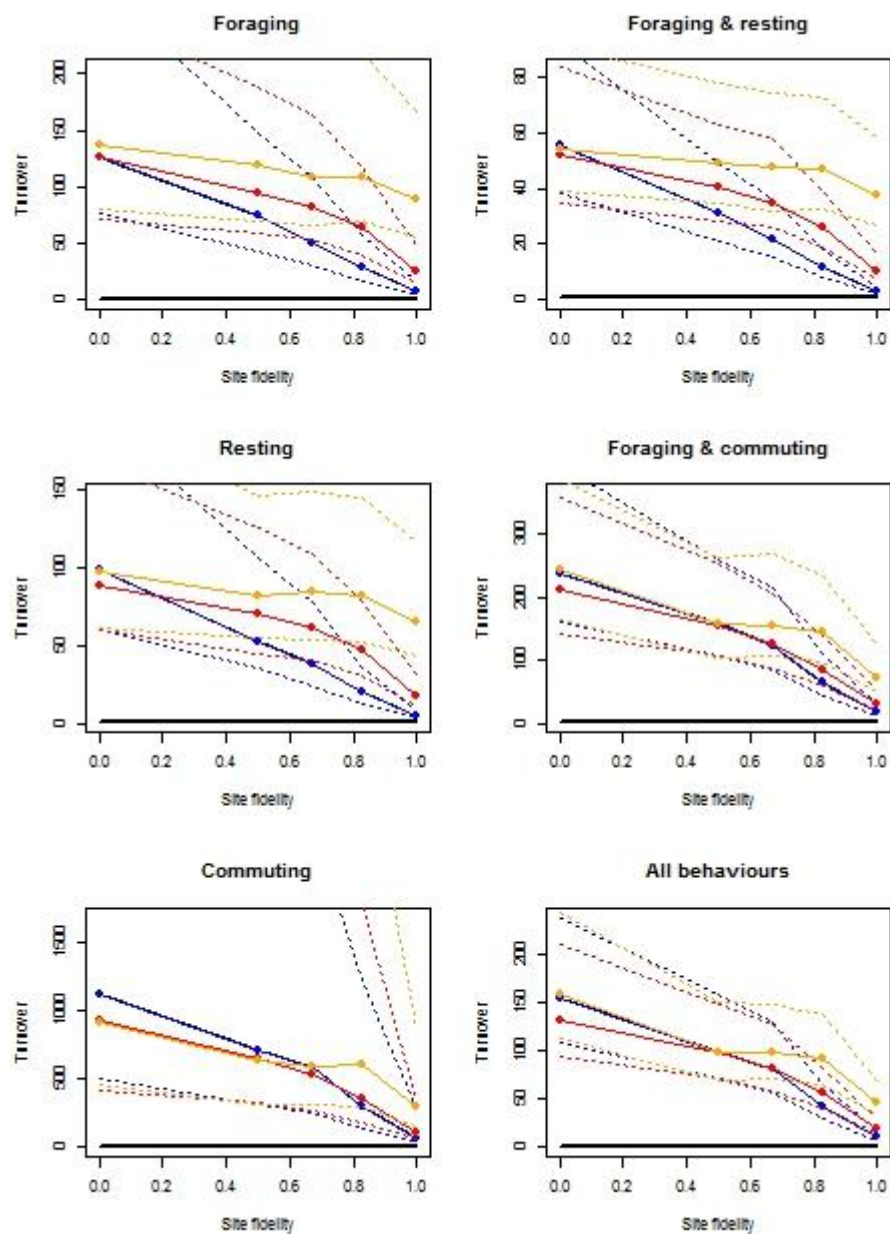
Figure 4.1.8: Plot of fidelity against turnover for guillemot in relation to the Alpha footprint. Colours denote the spatial scale at which site fidelity is assumed to operate (0.5 x 1 km: blue; 10 x 10 km: red; 50 x 50 km: orange). 95% confidence intervals are shown as dotted lines.
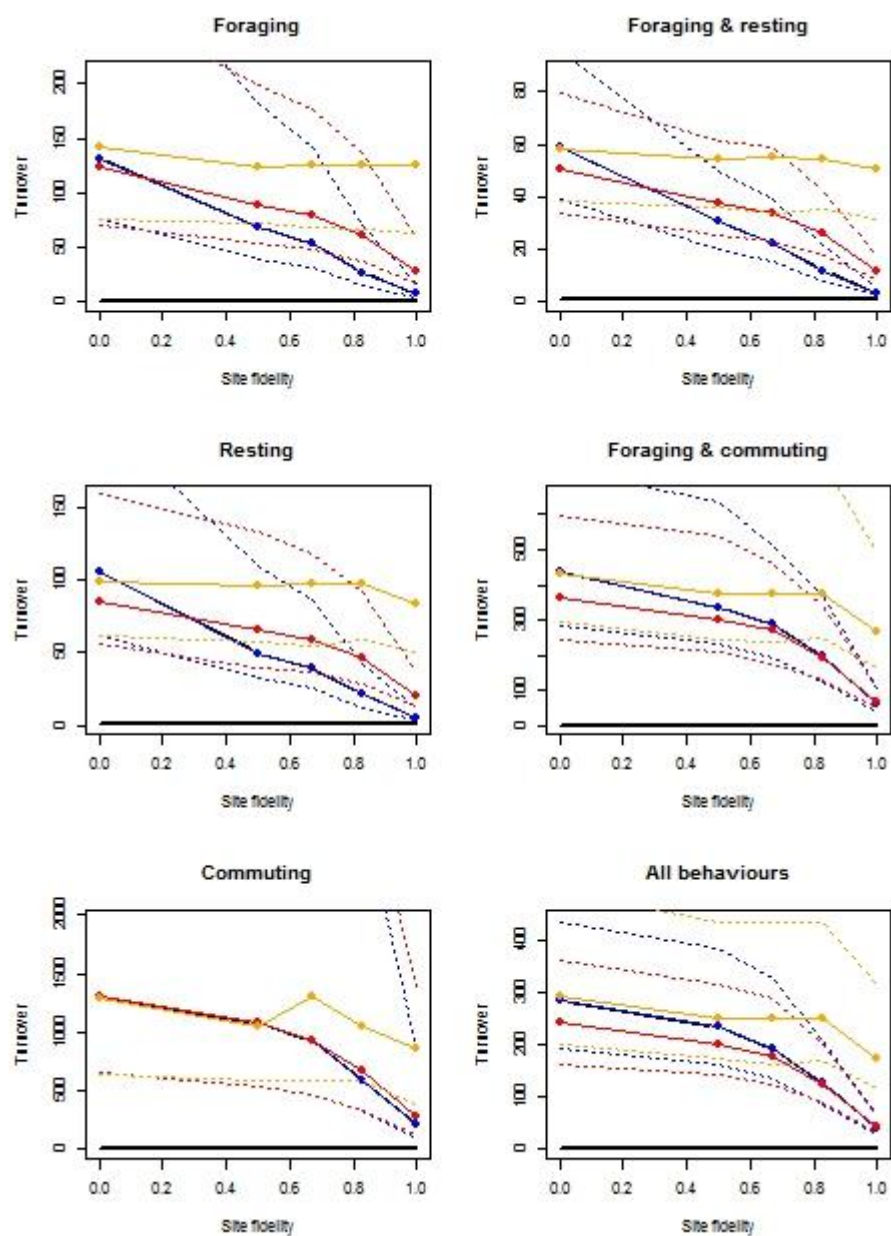
Figure 4.1.9: Plot of fidelity against turnover for guillemot in relation to the Bravo footprint. Colours denote the spatial scale at which site fidelity is assumed to operate (0.5 x 1 km: blue; 10 x 10 km: red; 50 x 50 km: orange). 95% confidence intervals are shown as dotted lines.

Figure 4.1.10: Plot of fidelity against turnover for guillemot in relation to the combined Alpha-Bravo footprint. Colours denote the spatial scale at which site fidelity is assumed to operate (0.5 x 1 km: blue; 10 x 10 km: red; 50 x 50 km: orange). 95% confidence intervals are shown as dotted lines.
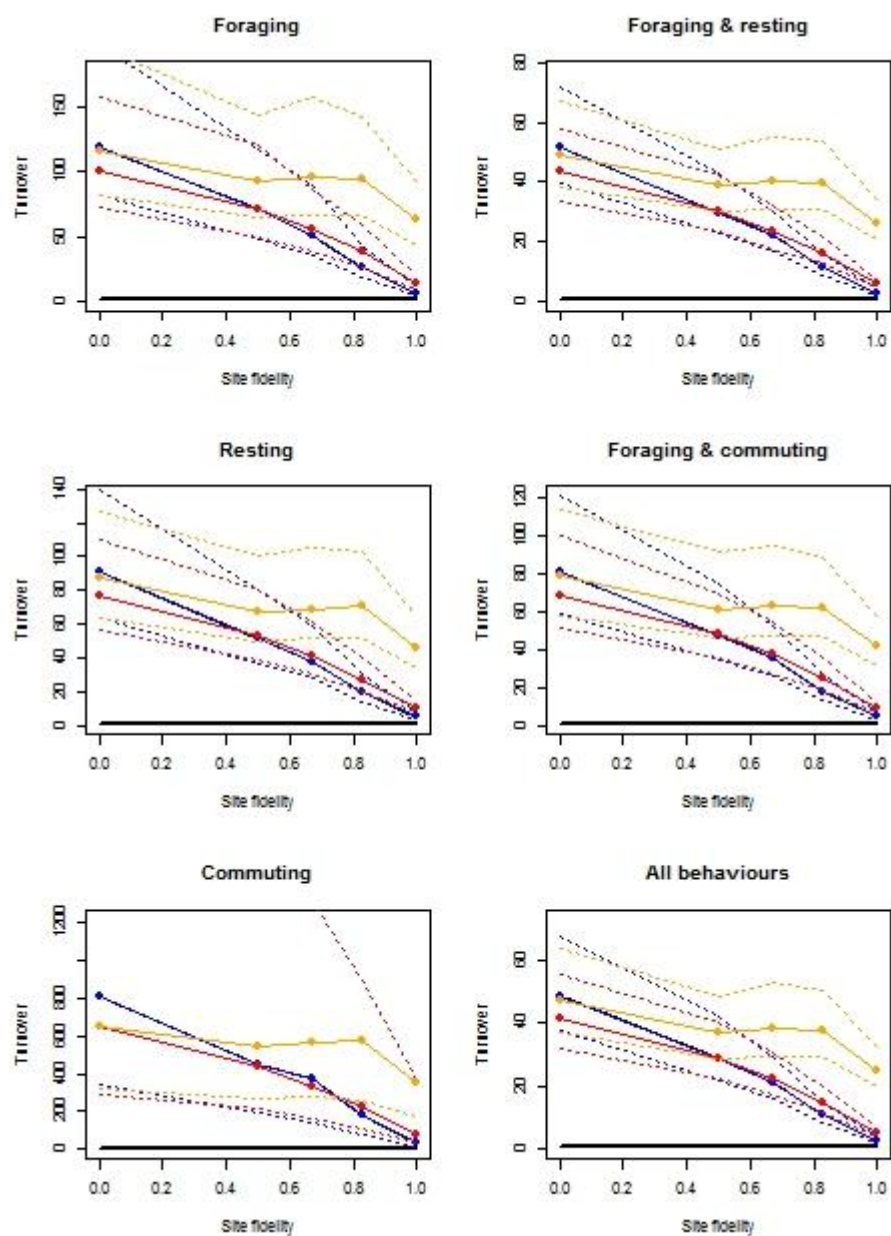
Figure 4.1.11: Plot of fidelity against turnover for razorbill in relation to the Inchcape footprint. Colours denote the spatial scale at which site fidelity is assumed to operate (0.5 x 1 km: blue; 10 x 10 km: red; 50 x 50 km: orange). 95% confidence intervals are shown as dotted lines.
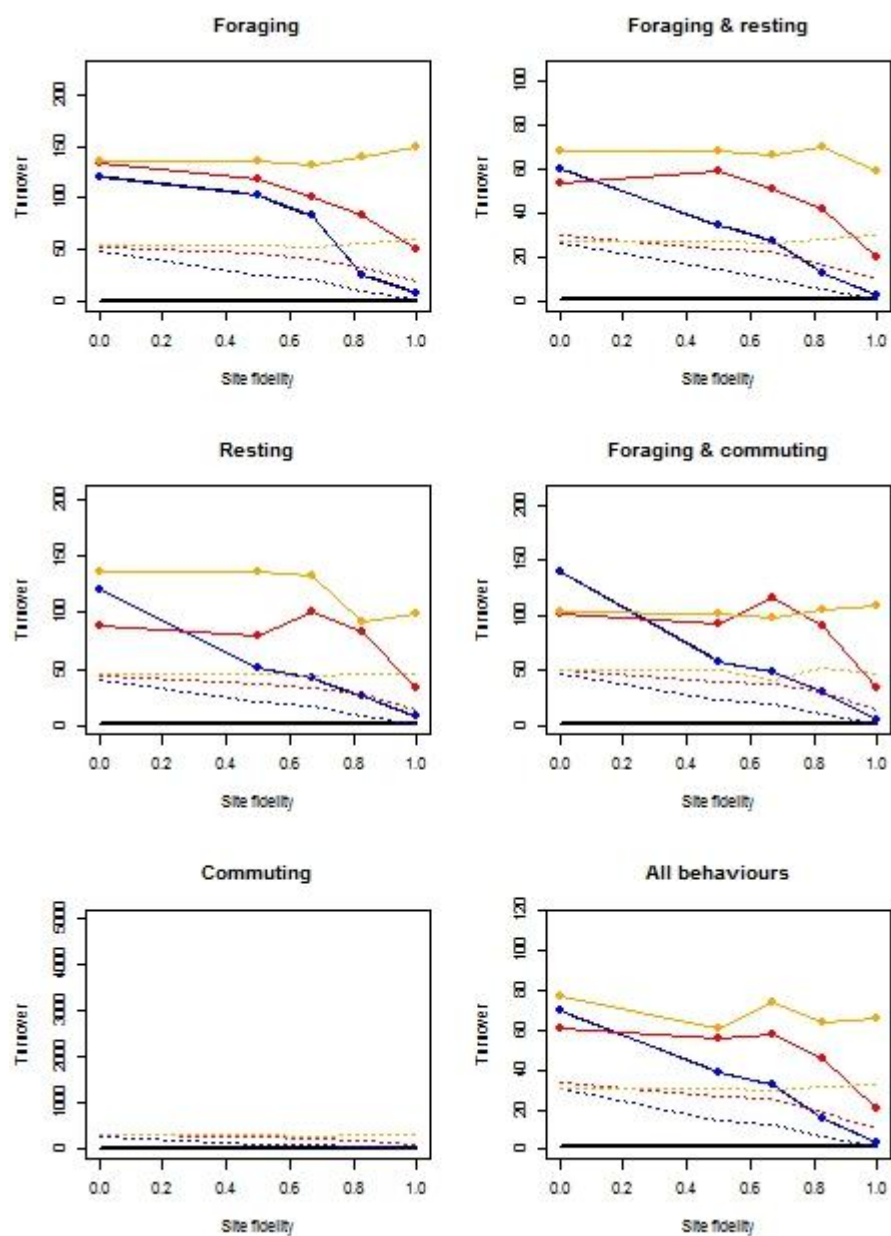
31

Figure 4.1.12: Plot of fidelity against turnover for razorbill in relation to the NnG footprint. Colours denote the spatial scale at which site fidelity is assumed to operate (0.5 x 1 km: blue; 10 x 10 km: red; 50 x 50 km: orange). 95% confidence intervals are shown as dotted lines.
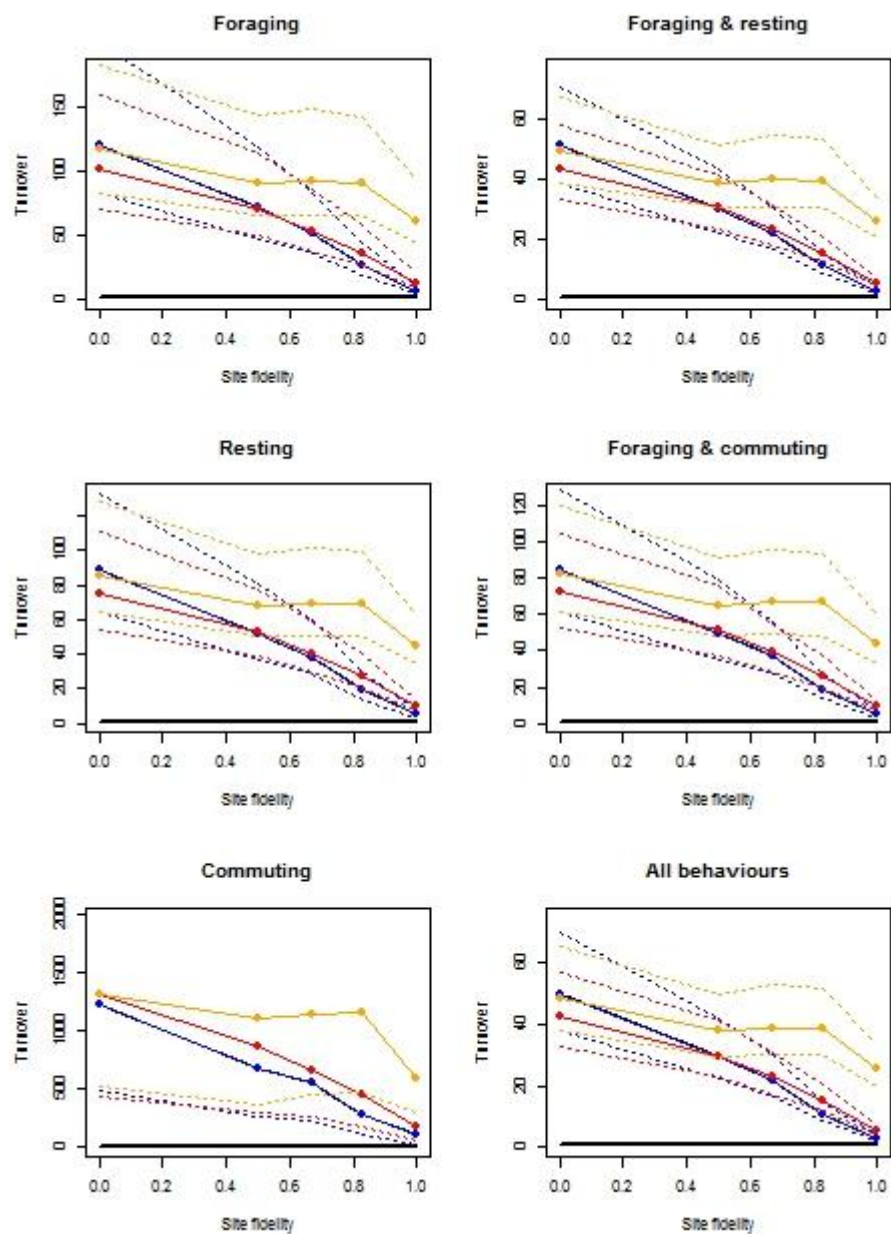
Figure 4.1.13: Plot of fidelity against turnover for razorbill in relation to the Alpha footprint. Colours denote the spatial scale at which site fidelity is assumed to operate (0.5 x 1 km: blue; 10 x 10 km: red; 50 x 50 km: orange). 95% confidence intervals are shown as dotted lines.

Figure 4.1.14: Plot of fidelity against turnover for razorbill in relation to the Bravo footprint. Colours denote the spatial scale at which site fidelity is assumed to operate (0.5 x 1 km: blue; 10 x 10 km: red; 50 x 50 km: orange). 95% confidence intervals are shown as dotted lines.
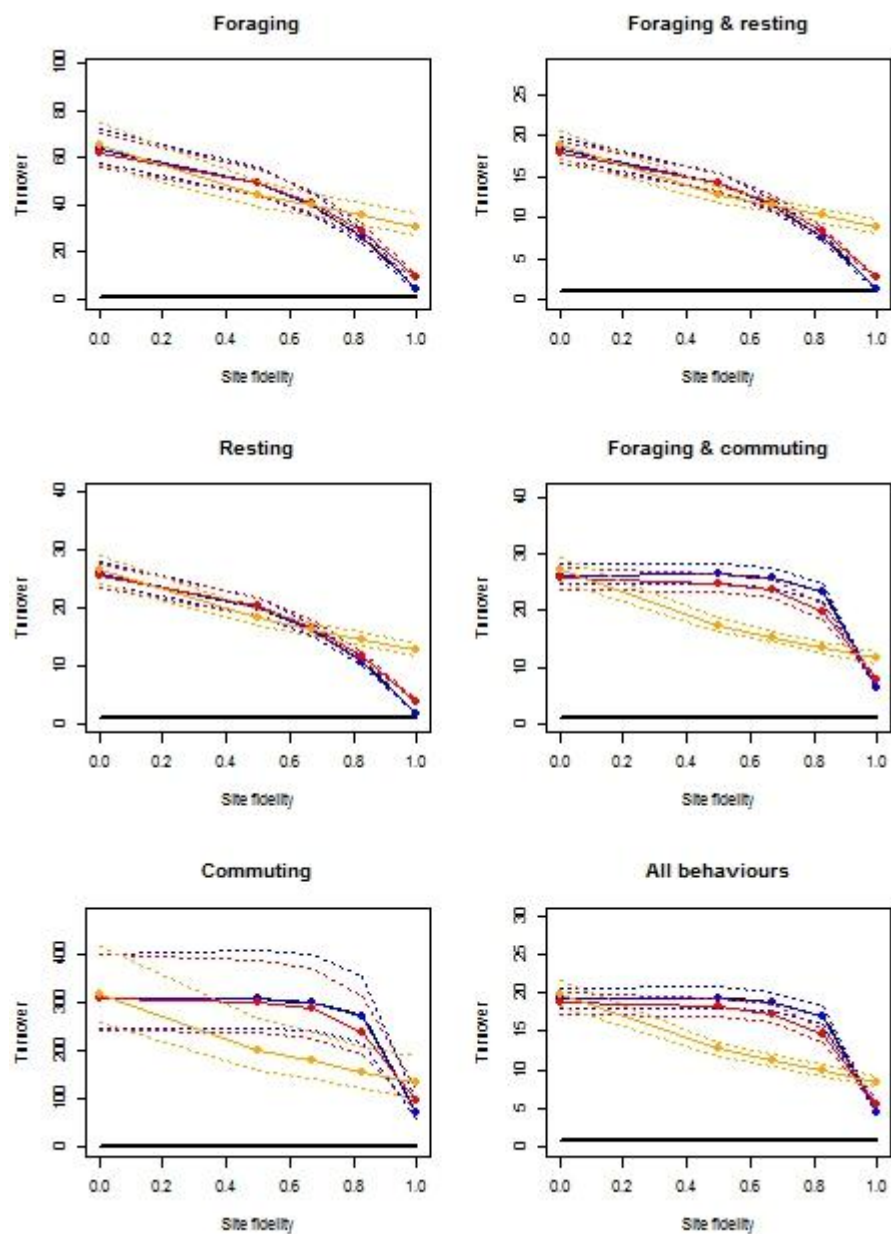
Figure 4.1.15: Plot of fidelity against turnover for razorbill in relation to the combined Alpha-Bravo footprint. Colours denote the spatial scale at which site fidelity is assumed to operate (0.5 x 1 km: blue; 10 x 10 km: red; 50 x 50 km: orange). 95% confidence intervals are shown as dotted lines.
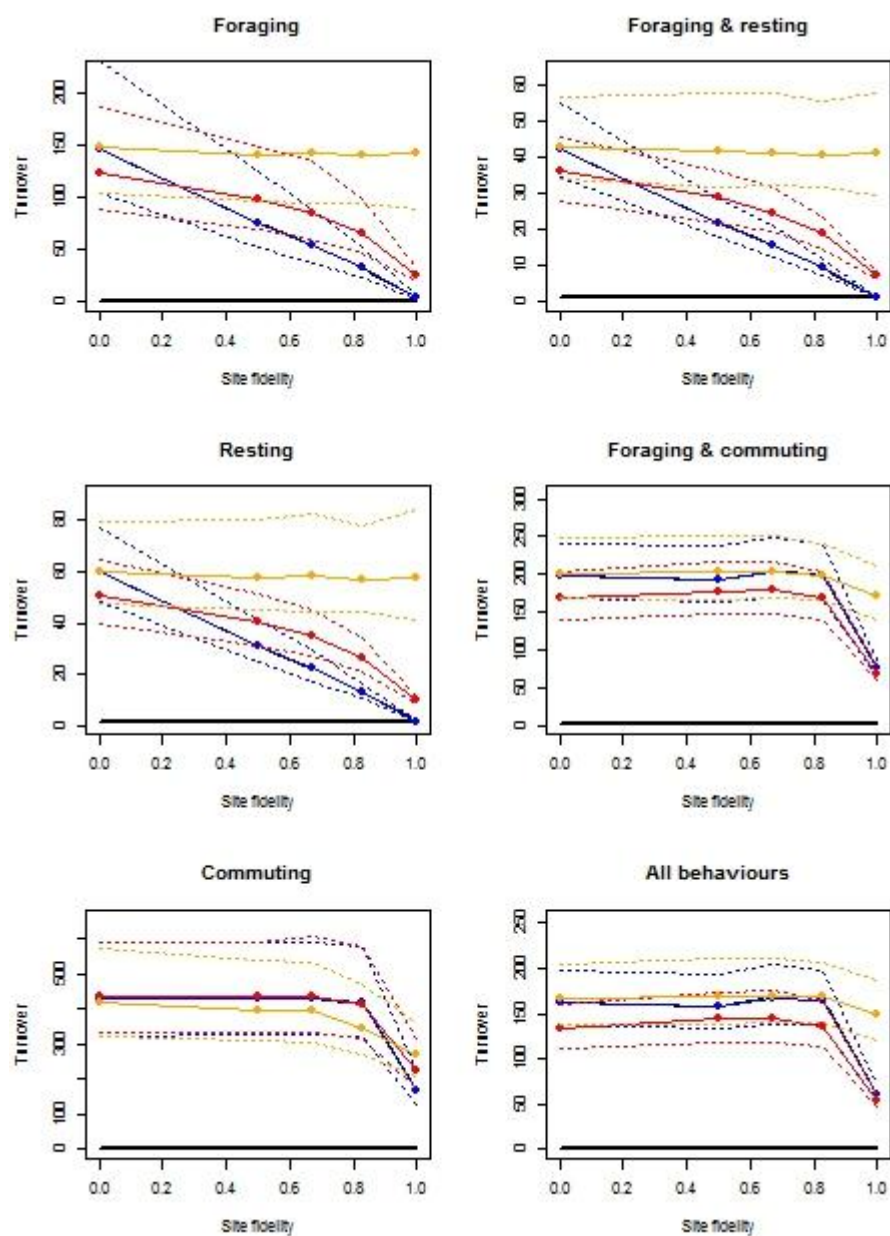
Figure 4.1.16: Plot of fidelity against turnover for puffin in relation to the Inchcape footprint. Colours denote the spatial scale at which site fidelity is assumed to operate (0.5 x 1 km: blue; 10 x 10 km: red; 50 x 50 km: orange). 95% confidence intervals are shown as dotted lines.

Figure 4.1.17: Plot of fidelity against turnover for puffin in relation to the NnG footprint. Colours denote the spatial scale at which site fidelity is assumed to operate (0.5 x 1 km: blue; 10 x 10 km: red; 50 x 50 km: orange). 95% confidence intervals are shown as dotted lines.
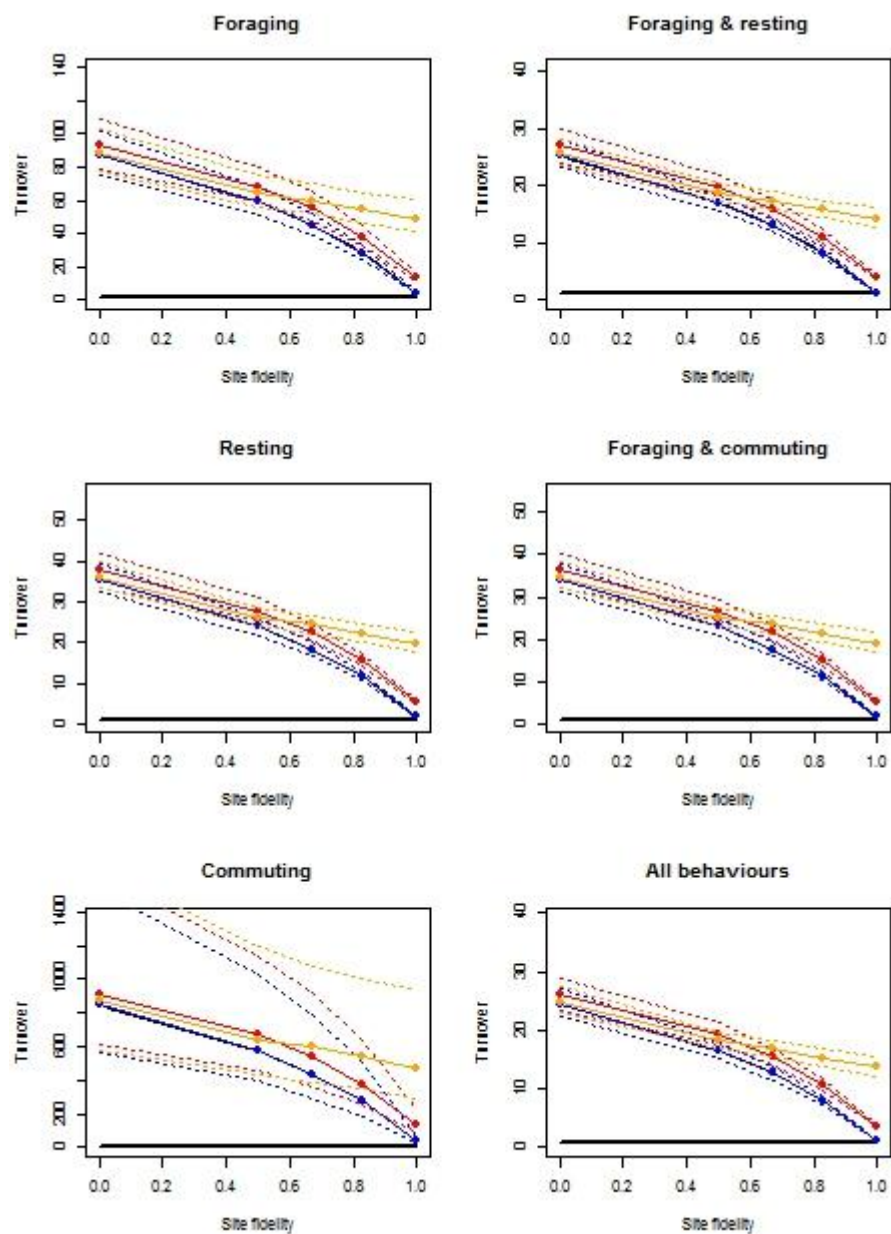
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Figure 4.1.18: Plot of fidelity against turnover for puffin in relation to the Alpha footprint. Colours denote the spatial scale at which site fidelity is assumed to operate (0.5 x 1 km: blue; 10 x 10 km: red; 50 x 50 km: orange). 95% confidence intervals are shown as dotted lines.
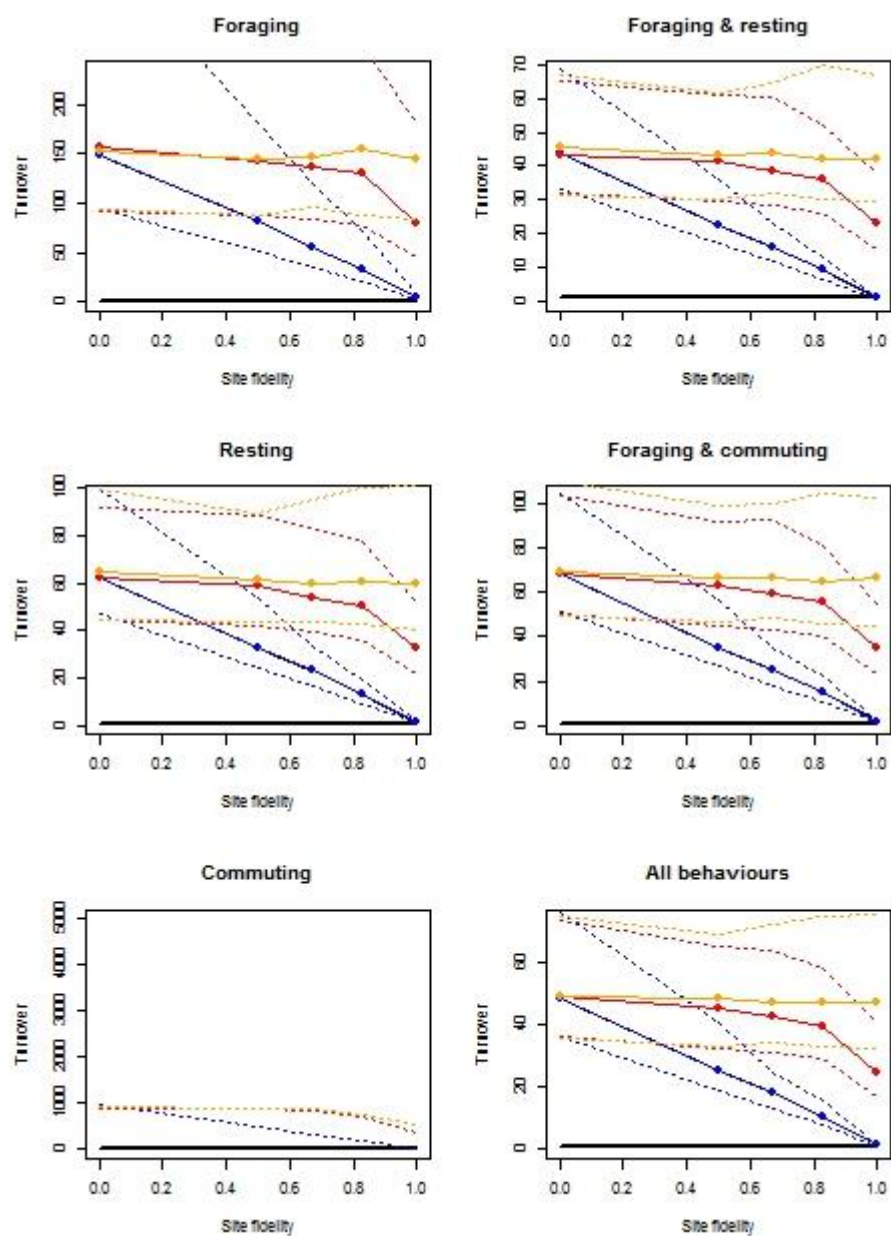
Figure 4.1.19: Plot of fidelity against turnover for puffin in relation to the Bravo footprint. Colours denote the spatial scale at which site fidelity is assumed to operate (0.5 x 1 km: blue; 10 x 10 km: red; 50 x 50 km: orange). 95% confidence intervals are shown as dotted lines.

Figure 4.1.20: Plot of fidelity against turnover for puffin in relation to the combined Alpha-Bravo footprint. Colours denote the spatial scale at which site fidelity is assumed to operate (0.5 x 1 km: blue; 10 x 10 km: red; 50 x 50 km: orange). 95% confidence intervals are shown as dotted lines.
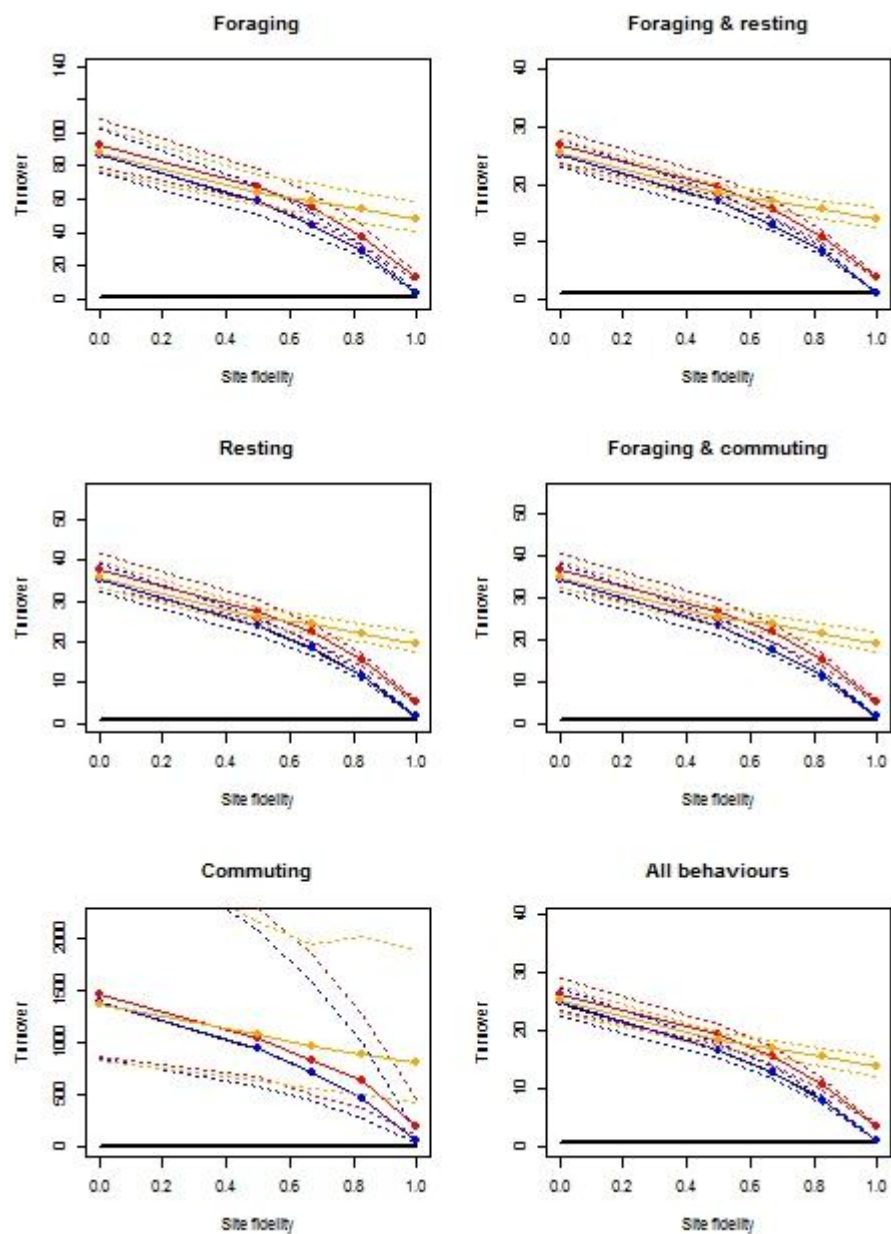
4.2.   The Influence of Footprint Size on Turnover

The above exercise was repeated, but using four 'artificial' wind farm footprints (10 km^2, 40 km^2, 100 km^2 and 200 km^2) that were each centred on the geographical centre of the five recently consented wind farm footprints.

For computational reasons this analysis was only run for one behaviour (foraging), one level of fidelity (0.5) and one spatial scale of fidelity (5 km x 5 km). The results are complicated and relatively noisy, but generally show a tendency for turnover to decrease as the footprint area increases.

Similarly, as the footprint area increases and snapshot surveys are conducted over a larger spatial extent, the estimate of turnover decreases (Figures below). Again, this is simply because as the areal extent of the survey increases it will capture a greater number of birds, so the proportion of the total population observed in the survey window increases. Differences in this relationship between the different wind farm footprints are simply due to differences in the estimated density of birds over the region or to the distance to colony.
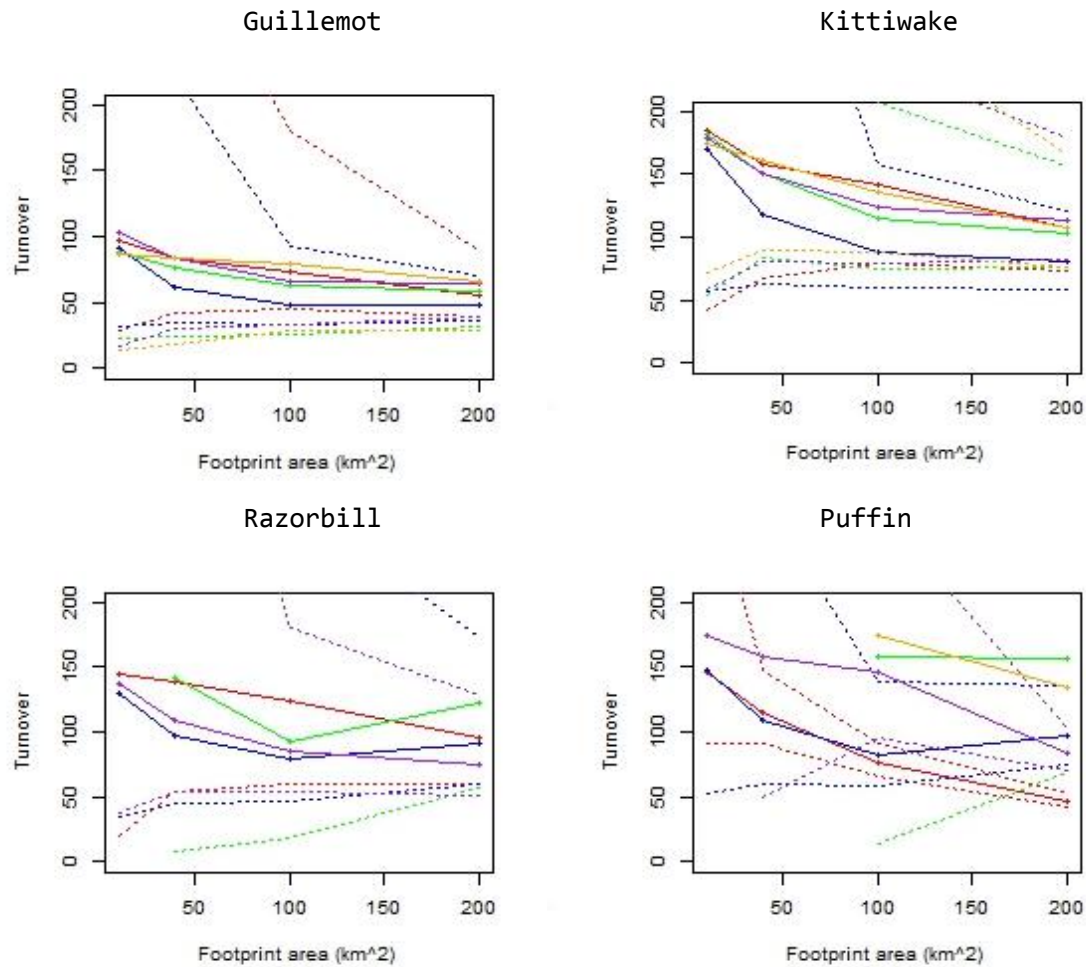
Figure. 4.2.1: Graph of the scale of the wind farm footprint area against turnover for each of the four species, foraging within each of the recently consented wind farm footprints (represented by successively larger 'artificial' footprints). The five colours represent Inch Cape (red), Neart na Gaoithe (blue), Round 3 Alpha and Bravo combined (green), Round 3 Alpha (purple), and Round 3 Bravo (orange). 95% confidence intervals are shown as dotted lines.95% confidence intervals are also shown (dotted) for each relationship.

5. Discussion

5.1. Summary of Results

We have found evidence for four key general patterns in relation to turnover, which hold across a range of species and footprints:

(1)   turnover decreases as site fidelity increases;

(2)   turnover decreases as the spatial scale of site fidelity becomes finer;

(3)   turnover is typically much higher for "commuting" behaviour than for "foraging" or "resting at sea" behaviours;

(4)   variation in turnover between surveys (as represented by the 95% confidence intervals shown in Section 4) is general very substantial. Variation appears to be much lower for puffin than for the remaining three species, but it is unclear if this is a real effect or a statistical artefact that results from the sparseness of available GPS data on puffin.

These four key broad trends are in line with the patterns that we would have expected to find, but there are also more subtle differences between individual species and footprints.

In general, kittiwake and razorbill had higher levels of turnover than did guillemots or puffins. This is true for both foraging and resting at sea. For all wind farm footprints, kittiwake and razorbill had estimates of turnover between approximately 100 and 150 with a site fidelity level of zero, in comparison to guillemot and puffin that had estimates between approximately 60 and 100. The differences in turnover levels among species may in part be due to differences in their foraging ranges and behavioural activity patterns.

Kittiwakes have larger foraging ranges compared to the other three species meaning a lower proportion of their total population is likely to be present in any given survey location within their foraging range, resulting in higher estimates of turnover compared to species with a smaller foraging range. The remaining three species have similar foraging ranges but differ in their time activity budgets.

Puffins spend less time at the colony than the other species because they are a burrow nesting species, which may in part explain the lower estimates for turnover in

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this species. Birds spending a greater proportion of their overall time budget attending a nest at the colony will have higher turnover estimates because they will be less likely to be observed at sea during a particular snapshot survey.

Finally, the higher overall estimate of turnover for razorbills compared to guillemots is likely due to differences in the proportion of time each species spends in commuting flight and foraging. The empirical time activity budgets used in this project (from Thaxter *et al.* 2013) show that razorbills spend relatively more time flying (approximately two hours flight per day) than do guillemots (approximately one hour flight per day). Razorbills also spend comparatively less time foraging (approximately four hours foraging per day) than do guillemots (approximately five hours foraging per day). These combined activity patterns mean that, for any snapshot survey, razorbills are more likely to be engaged in flight than are guillemots. Birds in flight will be less likely to be observed in a particular time window for a specific survey area because they only spend a short amount of time passing through each grid cell. Therefore, birds tending to spend a greater proportion of their time commuting are less likely to be observed within a particular snapshot survey and so resulting estimates of turnover will be greater.

Within a species, there was variation in estimates of turnover between wind farm footprints. Guillemots displayed the lowest variation in turnover estimates between the different footprints, with estimates of turnover for all wind farm footprints ranging between 70 and 90 when site fidelity was zero, for both foraging and resting at sea. Razorbills also exhibited relatively low variation in turnover estimates between wind farm footprints. When site fidelity was zero, estimates of turnover for foraging razorbills ranged between approximately 110 and 140 for all wind farm footprints, and estimates of turnover for razorbills resting at sea ranged from 80 to 120. Kittiwakes displayed a similar pattern in relation to variation amongst wind farm footprints as seen for razorbills, although overall turnover estimates for kittiwake were slightly higher than those estimated for razorbills, for both foraging and resting at sea. These differences in estimates of turnover between windfarms for each species are likely due to a combination of the relative foraging densities within each wind farm footprint (determining the likelihood of birds being present during a snapshot survey), and the relative location of the wind farm footprint in relation to all the colonies (determining in part the density of foraging birds, but also the number of birds commuting over the area to and from each colony).

Puffins had the lowest overall estimates of turnover for both foraging and resting at sea of the four species, but they did have noticeably higher estimates of turnover for foraging birds at the NnG and Bravo wind farm footprints in comparison to the other

wind farm footprints. This may be due to the more patchy foraging distribution of puffins in relation to the other three species, although this patchiness may be an arbitrary artefact of the small sample size in the GPS tracking dataset for this species.

5.2. Assumptions

The results that we have obtained depend on a number of key assumptions, which are discussed below.

5.2.1. Definitions

Most importantly, the results presented in this document are entirely contingent upon the definitions of turnover and site fidelity that we have used. The definition of turnover refers to the number of birds using a particular area (e.g. a wind farm footprint) during the entire breeding season, relative to the number of birds using it during an idealised snapshot census survey in which the entire population is recorded at a specific point in time. The idealised snapshot census assumes that all birds in the survey area in the survey time window are observed – we make this assumption not because it is true in practice (real survey data do not provide a snapshot census), but because it allows us to disentangle the effects of turnover from those of other features of survey data (non-detection, spatial sampling).

We define site fidelity relative to birds making an independent selection of sites on different days, not relative to a completely random selection of sites. In our simulations, all birds - regardless of site fidelity, have a tendency to return to areas of high bird density (estimated from the GPS tracking data for each species). This means that some birds will select the same foraging site multiple times during the breeding season even in the absence of site fidelity. Therefore, in this project, a site fidelity value of zero does not necessarily mean birds never return to the same foraging site over the breeding season. It is important to bear this in mind when looking at the results.

5.2.2. Scenarios

The results are also explicitly contingent upon the levels and spatial scales of site fidelity that have been assumed. As such, we have presented results under a range of different scenarios for these values to show how estimates of turnover change when the level of site fidelity is increased, or when the spatial scale over which site fidelity is assumed to operate increases. Estimating 'true' site fidelity values, or

spatial scales of fidelity, is beyond scope of this work, but could be possible for some species where GPS deployments have been of sufficient duration to obtain multiple trips per individual. Of the species considered here, this is likely to be possible in the auk species, where a proportion of deployments are of sufficient duration, though may be more challenging in kittiwakes where deployments are typically shorter and, in the majority of cases, only one to two foraging trips are recorded per bird. We have implemented site fidelity using a particular methodology (Appendix A), and while we believe this to be a reasonable approximation of the way in which foraging seabirds display site fidelity, the lack of precise empirical data for these processes means simulation output cannot be validated against observed patterns for these species.

5.2.3. Data Quality

The methodology assumes that the estimated bird density maps that we are using (and which were constructed through statistical modelling of GPS tracking data) provide an accurate representation of the spatial distribution of foraging birds. Our results suggest that bird density is not a key factor influencing turnover, evidenced by obtaining similar turnover estimates for the different wind farm footprints even though they have substantially different bird densities. As such the results presented here may be fairly robust to the failure of this assumption.

The method also assumes the empirical activity budgets we have used are an accurate representation of the behaviour of each species. These budgets were derived from a subset of the population from each colony from a small number of years or, in one case (puffins), a single year, corresponding to an assumption that activity budgets from this subset of the population represent those for the whole population. Turnover estimates are directly related to the percentage of time spent on each activity, so if time budgets are systematically wrong this will affect the turnover estimates for each behaviour.

5.2.4. Other Assumptions

The methodology that we have used to derive turnover values also depends upon a number of other specific assumptions:

1.   Our method assumes there is complete site fidelity within a day. In contrast, if individual birds went to different foraging locations within the same day the estimate of turnover would be different. If foraging locations selected by an individual are far apart (for instance some are in the footprint and some are

not) we might expect this effect to be more important than if they are close together, but in general it is difficult to know how important this assumption is likely to be. In addition, this assumption constrains the estimates of turnover to behave in a certain way in relation to the time activity budget. It forces the estimates of turnover to change in a particular direction (to decrease) as the time birds spend performing activities at sea increases. This is because by assuming birds only forage in one location per day the numerator of the turnover equation (number of birds that perform behaviour B within area A at any point during the entire breeding season) is constrained to not change in relation to the proportion of the four behavioural categories in the time activity budget, whereas the denominator (Mean across time-points of the number of birds that perform behaviour B visiting area A at each time-point t) will necessarily get larger as birds spend more time performing activities out at sea. As a consequence, estimates of turnover have to decrease as birds spend proportionately more time commuting, foraging or resting out at sea. The same directional relationship between time spent at sea and turnover would result from a simulation where birds selected multiple foraging locations each day (the more time birds spend away from the colony the more likely they are to be counted in an at-sea survey), but it is likely it would be less strong than that resulting from the formulation used in this project.

2. The method also assumes site fidelity is defined in terms of grid cells (used to estimate bird densities), not points or foraging patches. The results may be somewhat sensitive to the precise resolution and alignment of the grid used, but we expect that this effect is likely to be small.

3. Our implementation of site fidelity does not depend on foraging success, meaning that whether or not a bird is successful at a foraging location has no influence on their subsequent fidelity to that location. We suspect that this is not a critical assumption because we calculate turnover as a population-level quantity that will tend to average out individual-level effects.

4. The method also assumes that the order at which foraging sites are returned to is random (i.e. they are just as likely to return to the same foraging location on the following day as compared to any other day in the breeding season. We do not believe this assumption will have a significant effect on estimates of turnover because such effects are likely to be averaged out in the calculation of turnover at the population level.

5. Finally, we assume that birds fly in a straight line from the colony to the foraging locations.

5.3. Conclusions

The turnover values that we have presented could, in principle, provide a basis for scaling the abundance estimates of breeding individuals obtained during bird surveys of a particular area (such as a wind farm footprint) up to estimates of the number of breeding birds that are using that area during the entire breeding season. There are three key reasons why considerable caution needs to be taken in trying to do this, however:

1. The results that we have presented are contingent upon particular scenarios regarding the level and spatial scale of site fidelity. They provide a guide to assess how the level of turnover changes with site fidelity behaviours and patterns, and with the spatial scale of wind farm footprints, but they cannot provide specific estimates of turnover until further data on both the level and spatial scale of site fidelity of these species become available.

2. The literature review we conducted highlighted the considerable variability in seabird foraging ranges and foraging trip characteristics both within and between species, and within and between years. These parameters, in any one population and in any one year, will be influenced by food availability and distribution as well as stage of the breeding cycle. In addition, foraging behaviour in some species can be affected directly by human activities (gannets, for example, are known to follow fishing boats and feed on discards). Similarly, activity budgets and foraging site fidelity are likely to be affected by factors such as environmental conditions, predictability of prey distribution and population density-dependence, and can, therefore, vary among colonies and years. The variation in all these parameters may translate into among-population and inter-annual differences in turnover of individuals at sea that must be considered when assessing the potential impacts of offshore renewable energy developments on breeding seabirds.

3. The turnover values that we show here represent the value that a "snapshot" census of the complete population of birds within the footprint at a particular instant in time would need to be scaled up by in order to gain an estimate for the total population of birds that use the footprint at any point during the breeding season. In reality, current methods for surveying seabirds cannot achieve a complete census of all birds within an area the size of most wind

farm footprints. At-sea surveys will, therefore, generally be a sample, rather than a complete census, and will typically take place over a longer time period rather than at an instantaneous snapshot. In order to scale actual survey data (e.g. at-sea surveys) up to the total population it is, therefore, also necessary to use statistical adjustments to account for factors other than turnover: non-detection, for example, and the spatial up-scaling involved in translating transect counts (or other sample counts) up to an estimate of the total population within the area (Thomas *et al.* 2010). In addition, at sea survey estimates cannot distinguish between breeding and non-breeding individuals, nor assign birds to specific colonies. An additional step is required to adjust the at sea estimate by the proportion of non-breeding birds and to assign remaining birds to the appropriate colony or population of interest.

This project provides estimates of turnover for four species in the Forth-Tay region. However, the turnover estimates are contingent upon assumptions regarding the level and spatial scale of site fidelity. Empirically estimating site fidelity from tracking data was beyond the scope of the work within this project. Furthermore, available tracking data are generally from short-term deployments that would likely constrain our ability to reliably estimate these site fidelity parameters. In future work it may be possible to estimate these parameters for guillemots and razorbills, where birds may carry a logger for several days. However, deployment durations are very short for kittiwakes (12-36 hours, typically), and puffins are limited by the small sample size of GPS data sets. Analysis of appropriate existing data and detailed tracking studies involving long-term deployments would be required to better understand how foraging site fidelity operates in each species, and how it may be influenced by environmental conditions and seasonality. This more detailed understanding would allow for a more realistic capture of site fidelity processes within models, thereby facilitating a more accurate depiction of how turnover varies between species and survey methods.

This project has nonetheless provided an important first step in quantifying turnover in relation to wind farm footprints, and in understanding the ecological factors that influence turnover. It provides a basis for identifying knowledge gaps that will benefit from further data collection, and the results contribute to informing assessments of the potential impacts of development projects. The project, therefore, has significant strategic relevance for site characterisation and monitoring in Scotland and beyond. Turnover is clearly only one factor that will need to be considered when assessing the risks to seabird populations from offshore developments. A related task will involve quantifying the fate of birds that lie within the development footprint, and it is important to note that these two questions cannot meaningfully be considered in

isolation because they are fundamentally linked: higher levels of turnover imply that larger number of birds are using an area during the breeding season, but also imply that the impact of a development on any individual bird is likely to be lower (because the bird is present in the area for less time than if turnover were low). There will be a potentially complicated trade-off between these two processes, and further work is needed in order to understand the precise nature of this trade-off – i.e. to understand whether higher levels of turnover lead, all else being equal, to higher or lower estimates of development-related mortality.

Acknowledgements

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Appendix A

Algorithm for Simulating Foraging Locations

Without Site Fidelity

In the absence of site fidelity the foraging locations on each of the d days are simulated by splitting the study area into a fine resolution regular grid (0.5 x 0.5 degrees) that contains n grid cells. The expected foraging density f_i within each grid square i is estimated from GPS data, and for each bird j the foraging locations g_{jk} on days $k = 1,...,d$ are then simulated independently from a multinomial distribution with size one and probabilities $(f_1,...,f_n)$, so that

$$g_{jk} \sim \text{Multinomial}(1, (f_1,...,f_n))$$

This is exactly the same approach as that used in Searle *et al.*, 2014.

With Site Fidelity

We now assume that fidelity operates at the spatial scale of a grid which is coarser than the fine grid (and which is based on aggregating cells of the fine grid, so that the fine grid is nested within the coarse), and that the level of fidelity is given by a parameter ϕ that lies between zero (fidelity is the same as that obtained under independence) and one (perfect fidelity). For each bird j we modify the original independently-generated locations g_{jk} so that they have site fidelity, in the following way:

(1)   Find the coarse grid cells $c_{j1},...,c_{jd}$ that are associated with $g_{j1},...,g_{jd}$;

(2)   Find the number of these coarse grid cells that are unique – let this be $u(j)$;

(3)   Calculate the number of coarse grid cells that would be visited if fidelity were equal to ϕ to be;
$v(j) = \text{round}\{1 + (1 - \phi)\,(u(j) - 1)\}$;

(4)   Randomly select $v(j)$ from the set of $u(j)$ unique coarse grid cells;

(5)   Re-assign each day to lie within one of this set of coarse grid cells. Each coarse grid cell is allocated at least one day; the remaining days are allocated by simulating from a multinomial distribution in which the probability of being

allocated to coarse grid cell 'x' on a particular day is proportional to the frequency with which days were allocated to 'x' in the original simulations.

(6)   Then use the bird density p_i to simulate the grid cell for each bird on each day, conditional on the coarse grid cell that they are contained in on that day.

One potential problem at step (5) is that the random selection may lead to less than $v(j)$ unique coarse grid cells. We, therefore, begin by assigning each of the unique coarse grid cells randomly to one day each, guaranteeing that this does not happen; the coarse grid cells for the remaining $d - v(j)$ days are then allocated in proportion to their frequencies in the original selections made by each bird (before site fidelity is imposed).

Appendix B

Alternative Model-Based Approach to Simulation of Individual Time Budgets

B1.   Methodology

The main method that we use for estimating the proportion of time on each day that is spent undertaking each of the four activities (flying, foraging, resting at sea, time at the colony) is based on empirical activity data (we call this the "empirical approach").

An alternative approach is based on using the daily activity budgets that are simulated by the foraging model of Searle *et al.* (2014). This model assumes that individuals act in concordance with optimal foraging theory, and implies that the foraging behaviour of individual seabirds was driven by prey availability, travel costs, provisioning requirements for offspring, and behaviour of con-specifics. We called this methodology for determining time activity budgets the "model-based approach", because the foraging model directly simulates the proportion of time that each bird spends undertaking each of the four main activities on each day. This is done separately for each bird on each day. The key potential advantage of this approach is that the modelled time budget for individual birds, on individual days are linked directly to the foraging locations that they are assumed to visit. This "matching" should ensure that time budgets for individuals are directly linked to their choice of foraging location – something that we are unable to do with the empirical approach, because the time budget data and foraging location data relate to different sets of birds.

In order to assess the viability of this approach we compare the overall (mean) time budgets that are obtained from the foraging model (run without site fidelity, since this was the version of the model that was originally sense-checked in Searle *et al.*, 2014, and hence is the version that we may expect to be most closely matched to observational data) against those that are obtained from empirical data. The model-based data refer to the entire 24 hour period, whereas the empirical data can relate either to the full 24 hour period or to the more restricted period (05:00 – 20:00 hours) that is typically used for surveying.

B2   Results

Table B1

Daily time budgets for each species, based on empirical data and on the output from the optimal foraging model of Searle *et al.* (2014).

		Empirical for 24 hour period	Empirical for 05:00-20:00 study period	Model-based For 24 hour period
Kittiwake	Foraging	12.3	15.8	62.1
	Resting	19.3	16.4	4.2
	Commuting	17.3	19.7	7.5
Razorbill	Foraging	13.5	14.6	54.9
	Resting	27.1	19.7	4.2
	Commuting	7.3	10.0	3.2
Guillemot	Foraging	22.1	21.7	44.6
	Resting	29.0	22.6	4.2
	Commuting	3.3	3.5	3.8
Puffin	Foraging	22.4	25.0	34.4
	Resting	67.7	61.4	4.2
	Commuting	7.8	10.3	10.3

Comparisons of model-based and empirical mean activity budgets are shown in Table B1. The results of comparing the empirical and model-based results for the full 24 hour period suggest that, for all four species, the model-based results tend to substantially over-estimate the amount of time spent foraging and underestimate the amount of time spent resting. For kittiwake and razorbill the model-based results also substantially underestimate the amount of time spent commuting, but for puffin and guillemot this is somewhat overestimated.

The differences between the empirical results for the 05:00 - 20:00 hours survey window and those for the full 24 hour period are generally much smaller than the differences between the model-based and empirical results, suggesting that the poor performance of the model-based approach is not primarily driven by the fact that it fails to capture diurnal variations in activity.

B3.   Implications

The results of this comparison suggest that the model-based approach provides a poor estimate of typical time activity budgets. We, therefore, did not pursue the model-based approach further within this study.

It should be noted that the simulation model developed by Searle *et al.* (2014) was not validated against empirical time budgets for each species and was not intended to provide good estimates for these budgets, so the poor performance of this model in constructing empirical activity budgets is not necessarily surprising. In particular, the finding that simulation model of Searle *et al.* (2014) tends to underestimate the time birds spend resting at sea arises directly from the fact that the simulation model was parameterised to favour attendance at nests over time spent resting at sea. This characteristic was deliberately introduced to the simulation model to capture observed patterns of attendance at nests, and to ensure that simulated output matched observed patterns in chick production and chick mass gain over the breeding season (directly related to adult attendance at nests). Importantly, the greater confidence in the 'empirical' method for estimating turnover should not be taken as a reflection on the validity of the estimates for the effects of displacement from the simulation model presented in Searle *et al.* (2014); rather, it is simply an artefact of the parameterisation of the simulation model to match empirical patterns in adult mass change, adult survival, chick mass change, and chick production, the key variables of interest in estimating population consequences of displacement from wind farms.

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