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# **Increased use of intertidal resources benefits breeding success in a generalist gull species**

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Running head: Resource use and breeding success

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## ABSTRACT

Determining how resource use impacts on a species' demography is important, especially in habitats which are being altered by anthropogenic land-use change. If changes result in species consuming resources of reduced quality their demographic traits may be adversely affected. Generalist species are useful when investigating changes in resource availability as they can switch to alternatives if their preferred food becomes unavailable. For species that can forage on marine and terrestrial resources, it is often not known whether a switch from marine to terrestrial resources will have negative consequences. The herring gull, *Larus argentatus*, is one widespread generalist that opportunistically forages within marine and terrestrial habitats that are increasingly altered by humans. We determined marine and terrestrial resource use of gulls from eight colonies over two years across south-west Scotland and Northern Ireland using pellets and stable isotope analysis of chick feathers, which gave comparable results. Herring gulls in the study region used very little marine offshore resources but birds from colonies located in areas with sheltered coastlines, which provide abundant and diverse marine food from the intertidal zone, foraged more on marine intertidal resources. In contrast, colonies closer to built-up areas used more terrestrial resources. Herring gulls raised larger broods in colonies where they consumed a higher proportion of marine resource. Therefore, where generalist species, such as gulls, switch to an alternative resources that is available to them within their foraging range this may come at a cost of lower breeding success.

## INTRODUCTION

Organisms require adequate food resources for successful reproduction and survival therefore resource use is expected to affect population dynamics (White 2008). It is not only the abundance of food that is important, the type of food resources can also differ in their consequences for the consumers' demographic traits (Österblom et al. 2008, Sorensen et al. 2009, Weiser & Powell 2010). In generalists, which have a diverse diet with food sources that vary in quality, we often have difficulties identifying the critical resources that affect a consumer's reproduction or survival (Resano-Mayor et al. 2016).

Foraging theory predicts that consumers prefer prey that benefits their key demographic traits (Schoener 1971, Pyke et al. 1977). Foragers will therefore consume resources from what is available within their foraging range depending on the abundance and quality of these resources (Österblom et al. 2008, White 2008). If a food resource is abundant and of high quality, consumers will forage most efficiently by specialising on these most profitable prey items (specialists). The demographic traits of these specialists can therefore be sensitive to changes in the environment that affect their preferred prey and therefore their demographic traits will respond rapidly to changes in the availability of these prey species (Montevecchi 1993, Davoren & Montevecchi 2003, Vucetich & Peterson 2004, Millon & Bretagnolle 2008). Generalists, on the other hand, may buffer against changes in the profitability of one food source by switching to consume alternative food sources (Schoener 1971, Pyke et al. 1977). If alternative foods are similar in profitability, prey switching may mask potential effects of changes in the environment on consumer populations. The identification of critical resources that influence demographic traits of generalists is therefore more difficult, however this is important to understand generalists' population dynamics.

The profitability of a food resource will be determined by its abundance, the quality of the resource to meet the consumers' energetic and structural needs and the cost to obtain that resource (Stephens & Krebs 1986). Within a generalist's diet resources will differ in their quality, in terms of energy content and /or nutrients (Wanless et al. 2005, Österblom et al. 2006, Kadin et al. 2012). If the alternative food a consumer switches to returns less energy or fewer nutrients per foraging expenditure, either because of higher acquisition costs or poorer food quality, this can adversely affect the forager's demographic

traits (junk-food hypothesis: Alverson 1992, Grémillet et al. 2008, Österblom et al. 2008). The quality of resources a forager consumes can be related to demographic traits, particularly breeding success (Uttley et al. 1989, Pierotti & Annett 1990, van Heezik 1990, Suddaby & Ratcliffe 1997, Romano et al. 2006, Osterblom et al. 2008). However, other studies have found no evidence that changes in food quality affects reproductive output, with a high abundance of food possibly compensating for its lower quality (Jodice et al. 2006, Hjernquist & Hjernquist 2010). Environmental change may additionally affect the relative profitability of available resources, altering the consumers' resource use, which can impact on its population size depending on the quality of the alternative resources.

One group of widespread, opportunistic generalists that exploit a wide range of resources are the Laridae. They feed on a variety of foods from offshore, inshore and intertidal habitats, but also from agricultural fields, on refuse from built-up areas and fishery discards (Hunt & Hunt 1973, Götmark 1984). In evolutionary terms, the majority of gull species foraged mainly on fish and invertebrates from marine habitats, however, in certain species and populations gulls are increasingly exploiting anthropogenic resources from fishery discards in the marine environment to resources associated with farmland, landfill sites and other built-up areas in the terrestrial environment (Burger & Gochfeld 1983, Horton et al. 1983, Pons 1992, Belant et al. 1993, Smith & Carlile 1993, Brousseau *et al.* 1996, Weiser & Powell 2010, Yoda *et al.* 2012, Steigerwald *et al.* 2015). There is conflicting evidence on the consequences to gulls of consuming anthropogenic terrestrial food rather than marine resources. Higher proportions of marine invertebrates and fish have been associated with higher reproductive rates compared to birds mainly feeding on terrestrial human refuse (*Larus argentatus*: Pierotti & Annett 1991, and *L. occidentalis*: Annett & Pierotti 1999, respectively). Moreover, the long-term decline in *L. glaucescens* has been attributed to a dietary shift from marine to more terrestrial resources, mainly refuse (Hobson et al. 2015, Blight et al. 2015a). In contrast, a number of studies have found higher reproductive rates in gulls feeding on refuse compared to birds feeding on mixtures of mainly other alternative terrestrial foods, and occasionally also fish (*L. argentatus*: Hunt 1972, Pons 1992, Pons & Migot 1995, *L. hyperboreus*: Weiser & Powell 2010, *L. michahellis*: Steigerwald et al. 2015). An increase in *L. michahellis* numbers has been linked to the availability of anthropogenic food (Duhem et al. 2008). This suggests that the value of

particular food resources for breeding gulls depends on what food resources are available within the gulls' foraging range.

Here we investigate the environmental correlates of variation in resource use between colonies and its consequences on demographic traits in the herring gull *L. argentatus*. The gulls' resource use was established in multiple colonies across south-west Scotland and Northern Ireland over two breeding seasons using pellets and stable isotope analysis of chick feathers. We predict that (i) the gulls from each colony will exploit the resources most readily available within their foraging range; and (ii) that resource use will differentially affect breeding productivity and population growth rates. These results will clarify our understanding of the impact of marine and terrestrial resource consumption on the demography of a generalist seabird and whether this is an important driver of gull population trends.

## **METHODS**

The herring gull is a widespread colonial seabird, which is a generalist, opportunistic forager, traditionally foraging on marine resources (primarily in intertidal habitats), however they now increasingly forage on terrestrial and anthropogenic resources (e.g. Hunt 1972,, Götmark 1984, Pons 1992, Kubetzki & Garthe 2003). To investigate the relationship between the resources they use and their breeding success we studied eight colonies during 2013 and 2014 over a region covering approximately 200 by 250 km of south-west Scotland and Northern Ireland (Fig. 1). Within this region, we selected colonies along a gradient from low to high human population density; three in the Southern Hebrides, two in Northern Ireland and three in the Firth of Clyde. Resource use information was obtained from pellets from both years, providing 14 colony years, and chick feather samples, which were analysed for stable isotope ratios, from seven colonies in 2014 (Table 1). Different methods that infer information about diet can result in biases when estimating resource use (Barrett et al. 2007). Pellets can over-represent food items with hard parts, whilst under-representing easily digested items, and only provide a snapshot of the birds' diet (Barrett et al. 2007). However, several studies have shown that diet estimates from pellets are comparable with diet estimated from regurgitates, which under-estimate easily digested foods less than the pellets do (Spaans 1971, Annett & Pierotti 1989). Stable isotopes provide a more integrated

representation of resource use for a longer period of time over which the sampled tissue was formed, however they are less taxonomically resolved (Bond & Jones 2009, Phillips et al. 2014). Resource use therefore needs to be inferred from stable isotopes cautiously where a population consumes a variety of foods with similar stable isotope values, however in our case stable isotopes can distinguish between the two main resources (marine and terrestrial anthropogenic) that we are interested in for herring gulls. Combining both methods therefore provides complimentary information on resource use (Barrett et al. 2007).

#### **Pellets analysis**

Each colony was visited one to six times over the breeding season during the pre- and post-hatching period; between 17/05/2013-12/07/2013 and 02/05/2014-13/07/2014. At each visit complete, fresh pellets were collected from known herring gull territories during incubation (pre-hatching period) and during chick rearing (post-hatching period). The timing of breeding was similar across all colonies and the majority of clutches had hatched by 1st June, therefore this date was used to distinguish between pre- and post-hatching samples. Territories were identified from nest watches aimed to identify location of broods. Where the typical location of a brood could not be identified from watches or during incubation, we collected only pellets within or immediately adjacent to known and occupied herring gull nests. In the majority of cases one pellet was collected per territory and visit; when several pellets were collected from the same territory on the same visit they were combined into one pellet sample. As much as possible pellets were collected from different areas at subsequent visits to minimise disturbance of birds and repeated sampling of the same territories. We collected a total of 300 pellet samples from six colonies in 2013 and 481 from eight colonies in 2014 (Table 1).

Pellet samples were stored frozen until dissection and identification of food items in the laboratory, using a binocular microscope where necessary. Food items were identified to the lowest taxonomic level possible and then assigned to one of three broad foraging habitats; terrestrial, intertidal or offshore (Table 2). Terrestrial vegetation and anthropogenic items were included as indicators of terrestrial foraging habitat as these items are expected to have been consumed indirectly whilst foraging, for example, for terrestrial invertebrates or soft anthropogenic food items that might not otherwise be

represented in the pellets. For the analysis, we assigned all food items listed under 'Food type' and 'Indicator of foraging habitat' in Table 2 to the three broad foraging habitat. Each food item was scored based on whether it made up more or less than 25% of the pellet's bulk. Frequency of occurrence for each food item was then calculated as the number of pellet samples where that food item was scored as over 25% of the pellet's bulk divided by the total number of pellet samples (Duffy et al. 1986). Frequency of occurrence was determined separately for each colony, for each breeding season and whether collected during incubation (pre-hatching: 02/05 - 31/05) or chick rearing (post-hatching: 01/06 – 13/07). For 120 pellet samples (15% of total) two food items were scored as above 25% and therefore were included in the proportions of each of the relevant foraging habitats, and therefore the sum of frequency of occurrences can be greater than 100%.

#### **Stable isotope analysis**

Stable isotope values  $^{13}\text{C}/^{12}\text{C}$  ( $\delta^{13}\text{C}$ ) and  $^{15}\text{N}/^{14}\text{N}$  ( $\delta^{15}\text{N}$ ) of consumer tissue can be used to determine where along a gradient between terrestrial and marine habitats, and from what trophic level, respectively, resources are consumed (Hobson et al. 1994).

To represent consumer tissue, we took samples of feather material from known herring gull chicks in 2014. We collected down feathers from chicks less than 1 week old to reflect the resource use of females during egg formation, with nutrients passed into the egg being incorporated into the chicks' down, and feathers from chicks older than 1 week that had grown since hatching, which reflect the resources the adults bring back during chick rearing (Klaassen et al. 2004). In chicks older than 1 week we avoided the tips of feathers as these could still contain down material. We cut small amounts of feather material from several feathers on the back, head and underside of the body in order to obtain a representative sample for a longer period than would be obtained from a single feather sample. All sampled material from the same chick, and from the same brood where more than one chick was sampled, was homogenised; therefore all feathers from chicks from the same brood were collated as one sample. We collected 133 down samples from seven colonies, and 126 chick feather samples from six colonies (Table 1).

Prior to stable isotope analyses all feather material was washed in liquid detergent (Ecover™) diluted with deionised water (approximate 1:99 dilution), and then in a 2:1



mixture of chloroform:methanol (Cherel et al. 2005). Feathers were then dried at 50°C overnight.

In order to relate stable isotope ratios more specifically to the foraging habitats used by the herring gulls, we also collected samples of known prey items from within our study area (Table 3). We collected prey samples from chick regurgitates, with the exception of the named fish species, which were collected from the Firth of Clyde (off Arran). High lipid concentrations in prey samples may result in apparently depleted  $\delta^{13}\text{C}$  values (Post et al. 2007). We therefore split each sample into two roughly equal sub-samples. From one sub-sample we extracted lipids using a Soxhlet apparatus with a 2:1 chloroform:methanol mixture until the solvent ran clear indicating all lipids were extracted.  $\delta^{13}\text{C}$  values were taken from these lipid-extracted samples.  $\delta^{15}\text{N}$  values were taken from the non-lipid extracted samples as  $\delta^{15}\text{N}$  can be altered by the lipid extraction (Yurkowski et al. 2015). Dried feather and prey samples were homogenized and weighed (mass between 0.7-0.8mg) into tin capsules before being combusted and analysed by continuous-flow isotope ratio mass spectrometry (Costech Elemental Analyser, Milan Italy linked to a Thermo Finnigan Delta Plus XP Mass Spectrometer, Bremen Germany) at the NERC Life Sciences Mass Spectrometry Facility, East Kilbride. Stable isotope values  $\delta$  are expressed as parts per thousand (‰) relative to the international references PeeDee belemnite marine fossil limestone for carbon and atmospheric  $\text{N}_2$  for nitrogen. Measurement precision, calculated as the standard deviation of repeated analyses of an internal standard (tryptophan), was  $\pm 0.09$  ‰ for  $\delta^{13}\text{C}$  and  $\pm 0.12$  ‰ for  $\delta^{15}\text{N}$ .

We checked for spatial variation in baseline stable isotope values across our study region by comparing stable isotope values from down feathers from nests of common eiders *Somateria mollissima* that we collected from five colonies. Common eiders are year-round residential, specialised mussel feeders (Player 1971, Guillemette et al. 1992) with their tissue reflecting local stable isotope values at a low trophic level in the marine coastal environment, the main foraging habitat of herring gulls. Eider down feathers were processed and analysed as the gull feathers.  $\delta^{13}\text{C}$  did not vary between colonies ( $F_{5,15} = 0.34$ ,  $p = 0.88$ ), but for  $\delta^{15}\text{N}$  there were some between-colony differences ( $F_{5,15} = 4.78$ ,  $p = 0.008$ ) with only the contrast between the lowest (Oronsay) and highest values (Copeland and Lady Isle) being significant. Since the spatial variation in  $\delta^{15}\text{N}$  was due to a single site and other

work on this region showed no geographic variation (Jennings & Cogan 2015), we did not correct for spatial variation in baseline stable isotope values. To estimate the contribution of different resources to the gulls' assimilated diet in each colony we ran a Bayesian stable-isotope mixing model (MixSIAR GUI, Stock & Semmens 2013).  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for chick down and feathers were included in the analysis as consumer tissue. Among the prey samples the  $\delta^{13}\text{C}$  values only differed between terrestrial and the two marine food sources (intertidal and offshore) but not between intertidal and offshore (ANOVA:  $F_{2,5} = 38.21$ ,  $p < 0.001$ ; post-hoc Tukey HSD pair-wise comparisons between offshore and intertidal  $p = 0.93$ , both marine resources were significantly different from terrestrial items  $p < 0.003$ ). We therefore pooled offshore and intertidal food sources into one marine resource and considered only the two sources (marine and terrestrial) for the mixing model. Isotopic discrimination factors are not available for herring gull feathers therefore we used published values for ring-billed gull *L. delawarensis* feathers ( $0.2 \pm 1.3$  ‰ for carbon and  $3 \pm 0.2$  ‰ for nitrogen, Hobson & Clark 1992).

## **Environmental variables**

To determine whether between-colony variation in resource use was driven by variation in the local availability of resources we obtained data on environmental variables that potentially reflect the different resources herring gulls can utilise. Environmental variables were extracted for a foraging range of 50 km around each study colony corresponding to the average maximum foraging range of herring gulls (Spaans 1971, Götmark 1984, Camphuysen 1995, Tasker et al. 2000, Thaxter et al. 2012), and to a subsample of GPS-tagged herring gulls from four colonies in our study region where we observed maximum foraging trips of up to 44 km from the colony (NJO'H, unpublished data).

We used a range of proxies of resource availability reflecting herring gulls' broad range of foraging habitats. For the intertidal habitat, an important foraging area of the herring gull (Götmark 1984, Kubetzki & Garthe 2003), the abundance and diversity of invertebrates of rocky shores, the main shore habitat in the study region, is predicted by wave fetch (Burrows et al. 2008). In our study region, wave fetch is an important driver of changes in herring gull colony size (O'Hanlon 2016). Wave fetch is calculated based on the exposure of a coastline depending on its topography (Burrows et al. 2008). For each coastal

point on a 200 m grid the nearest distance to land along 16 equal angular sectors of 22.5° are measured and the sum of all wave fetch values from the 16 angular sectors within a 200 m grid cell are calculated ('fetchsum'). A low wave fetch value reflects a more sheltered intertidal habitat, with short distances to the nearest land mass, whilst high wave fetch values reflect an exposed coastline, with greater distances to the nearest land mass. Rocky shorelines with low wave fetch support a greater abundance and diversity of potential intertidal prey species (Burrows et al. 2012). For the analysis we averaged 'fetchsum' for all 200 m coastal grid cells within the gulls' 50 km foraging range around the breeding colony based on wave fetch data obtained from Burrows (2009) using ArcMap 10.1 (ArcMap ver.10. ESRI, USA).

As herring gulls can also forage in terrestrial habitats; in particular on landfill sites, in built-up areas and on farmland (e.g. Pons 1992, Belant et al. 1993), we also included the extent of built-up area and farmland, the nearest distance to built-up areas and farmland, and the number of landfill sites within each colony's foraging range, as proxies for the potential availability of terrestrial/anthropogenic food. We classified farmland as agricultural land and improved grassland, and classified built-up area as urban and sub-urban areas; the total area and nearest distances to colonies were calculated from Landsat 2007 (Morton et al. 2011) using ArcMap 10.1. The number of landfill sites within 50 km of each colony was obtained for Scotland from SEPA (2015) and for Northern Ireland from NIEA (Kelly, pers. comm.).

The main source of food from offshore habitat is likely from fisheries, although this food type was rarely consumed in our study. Unfortunately, for the UK there are no publically available data on discard tonnages (Gibson et al. 2015) and landing data are only available on a coarser spatial level than we use here. Instead as an index for variability in conditions in the offshore marine environment we obtained estimates of sea surface temperature (SST) and chlorophyll a concentrations. SST influences marine processes associated with thermoclines and upwellings which in turn will affect the distribution and abundance of potential prey species, whilst chlorophyll a concentration acts as a proxy for primary productivity at the base of the marine food web (Huot et al. 2007). SST (11µ night-time) and chlorophyll a concentration (mg/m<sup>3</sup>) composites were extracted from Aqua MODIS at 4 km resolution (<http://oceancolor.gsfc.nasa.gov/cgi/l3>) separately for May (pre-

hatching period) and June (post-hatching period) in each year. For the analysis, the mean values of SST and chlorophyll a concentration within 50 km of each colony were used. The between-site variability in SST was low (CV = 10.2%) with site-specific values ranging from 8.94 to 12.08°C, but was higher for chlorophyll a (CV = 62.6%) ranging from 2.39 to 13.31 mg/m<sup>3</sup>).

## **Demographic traits**

We investigated the relationships between resource use and brood size, as a short-term measure of annual breeding success. Our metric to determine breeding success of a colony was the average size of broods of chicks of at least three weeks old; chicks that reach that age are likely to successfully fledge (Bolton et al. 1991). The number and age of chicks, were obtained from nest watches in each colony (mean of 16±9 nests, range 4-33, n = 13 colony years as no data on brood size was available for Jura in 2014; see Table 4), and brood sizes were averaged per colony-year; hereafter referred to as mean brood size. Most chicks had hatched by the first of June across all colonies and years. To establish that chicks were at least three weeks old we took this date into consideration as well as noting the size and feather development of chicks that were of a known age based on published information on herring gull chick development (Kadlec et al. 1969). In each colony, multiple nest watches of three hours were carried out generally every 10-14 days throughout the chick rearing period between 01/06/2013-16/07/2013 and 03/06/2014-04/07/2014 (see Supplementary Table 1 for individual colony visit dates). Watches were made from specific vantage points allowing up to 24 focus nests to be observed simultaneously, whilst not causing disturbance to the birds, using an observation hide where necessary. Focus nests were selected that had an unobstructed view from the vantage point and that had been identified as herring gull nests from observing the attending adults. Watches from the same vantage point were repeated on different colony visits. Observed levels of predation and disturbance were low across all colonies, although we were only present in each colony for a small proportion of time across the breeding season to keep disturbance to a minimum.

Mean brood size only considered nests that still had at least one chick three or more weeks after hatching. It will therefore over-estimate actual breeding success as it does not include any nesting attempts that failed prior to this point. However, partial and total brood

failures are likely positively correlated and therefore brood sizes are larger in years with higher productivity. Indeed, from published information on large gulls (see Supplementary Table 2), we found that the brood size of successful nests was significantly positively correlated to overall productivity based on the number of successfully fledged chicks from all nests where eggs were laid ( $r = 0.60$ ,  $n = 17$ ,  $p = 0.012$ ). In addition, for a sub-sample of our colonies, where we could determine the total number of chicks of at least three weeks old from all occupied nest sites within a plot, we found a similar positive correlation between mean brood size of successful nests and productivity of all occupied nests ( $r = 0.70$ ,  $n = 7$ ).

### Statistical analysis

All statistical analyses were performed in R, Version 3.2.1 (R Development Core Team 2014). Diagnostic plots were checked to ensure all model assumptions were met. In all models colony size was natural logarithm transformed.

We compared the estimates of the proportion of marine resources from pellet data (sum of offshore and intertidal) with those from the stable isotope data. The proportion of pellets containing offshore and intertidal items, per colony and breeding stage, was included as the response variable with the proportion of marine resources obtained from the output of the Bayesian stable isotope mixing model and breeding stage as explanatory variables in linear mixed effect multivariate models (GLMM) in R's *lme4* package (Bates et al. 2014). Colony was included as a random effect to account for samples taken in both the early and late stage of the breeding season from each colony.

The proportions of resources in the diet based on pellets were related to colony site, year and breeding stage, with colony-by-year, and colony-by-breeding stage interactions, using a two-way analysis of variance (ANOVA); separate models for offshore, intertidal and terrestrial food resources. The two interactions were included to test whether between colony differences were consistent between breeding stages and years. To identify where differences occurred post-hoc multiple comparisons were carried out using the *glht* function in R's *multcomp* package (Hothorn, Bretz & Westfall 2008). We also calculated the consistency repeatability  $R_c$  of resource use within colonies between years and breeding

stages according to Biro & Stamps (2015) using the *rptR* package in R (Nakagawa & Schielzeth 2010).

To test whether proxies of local food availability influenced the gulls' resource use we carried out mixed effect multivariate models with the proportion of pellets containing each resource as the response variable and environmental variables reflecting local food availability as explanatory variables. Colony was included as a random effect to account for pellets being collected from the same colony in multiple years and during the incubation and chick-rearing stage. As the colonies sampled varied between 15 and 830 apparently occupied nests (AON) we also considered colony size as an explanatory variable to account for potential higher levels of competition and local resource depletion in larger colonies (Furness & Birkhead 1984, Birt et al. 1987, Lewis et al. 2001). However, colony size was not found to relate to the proportion of pellets containing offshore, intertidal or terrestrial items ( $p > 0.15$ ) and therefore was not considered further in the resource use models. Due to the number of environmental variables being too large for one model, and to allow us to investigate the three main resource types individually, we ran three separate models. The first reflecting conditions in the offshore marine environment (chlorophyll a concentration and SST); the second reflecting the intertidal environment (wave fetch); and the third including variables reflecting the availability of terrestrial resources (distance to and the extent of built-up area and farmland, and number of landfill sites). Due to potential multicollinearity of explanatory variables, pairwise correlations and variance inflation factor (VIF) values were checked and only variables with a  $VIF < 3$  were included in further analysis (Zuur et al. 2010). For the terrestrial model the number of landfill sites and the amount of built-up area within the foraging range both had VIF values greater than three and therefore both were excluded, as they were both correlated to the nearest distance to built-up areas and only the latter was used in this analysis. In each model we also included year and breeding stage, and second-order interaction between these and the environmental variables. Due to the majority of pellets containing terrestrial items, the coefficient of variation (CV) for the proportion of pellets containing terrestrial items was low ( $CV = 24.0\%$ ) meaning that there would be difficulty in relating the proportion of pellets containing terrestrial items to potential influencing terrestrial environmental variables. Therefore, instead, we used the

proportion of pellets containing marine (offshore and intertidal with CV = 82.1%) resources as the response variable in the terrestrial model.

To test for a relationship between resource use and breeding success we used a mixed effect multivariate model with brood size, as a measure of breeding success, as the response variable. Year and colony size were included as main effects, along with the proportion of pellets containing offshore, intertidal or terrestrial items; with a separate model run for each resource type. Colony was included as a random effect to account for the non-independence of broods from the same colony; we used 217 broods from 13 colony years. Resource use of pre- and post-hatching stages were pooled as they did not differ (see Results). To investigate the relationship with colony growth rate we ran separate linear models for each resource type, with the average proportion of offshore, intertidal or terrestrial sources in pellets across the two years and breeding stages for each colony as the explanatory variable. To calculate the effect sizes of marine resource use on the gulls' demography we calculated  $f$  values; with  $f$  values of 0.15 and 0.35 indicating a medium and large effect size, respectively (Cohen 1988).

Starting with the most complex model we used backwards-stepwise model selection to determine the minimal adequate model using Likelihood Ratio tests (Crawley 2007). Only statistically significant interactions are reported and main effects that are part of significant interaction terms were not tested as they could not be removed from the model in isolation. Significance thresholds were set at two-tailed  $p < 0.05$ . To estimate the variance explained by each model we calculated  $R^2_{\text{GLMM}}$  in the R package *MuMIn* (Barton 2012).  $R^2$  is the "marginal"  $R^2$  value ( $R^2_{\text{GLMM}(m)}$ ) which is the proportion of the variance in the response variable that is explained by the explanatory variables. The "conditional"  $R^2$  value ( $R^2_{\text{GLMM}(c)}$ ) is also calculated which is the proportion of the variance in the response variable explained by the explanatory and random variables (Johnson 2014).

## RESULTS

### Spatio-temporal variation in resource use during the breeding season

In 2014, when results from both methods were available for the same colonies, the pellet analysis and the MixSIAR model, using  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of down and chick feathers,

gave comparable results for the proportions of herring gull diet comprised by marine (GLMM:  $\chi^2_1 = 25.22$ ,  $p < 0.001$ ,  $R^2_{\text{GLMM(m)}} = 0.88$ , Fig. 2) and terrestrial resources ( $\chi^2 = 27.21$ ,  $p < 0.001$ ,  $R^2_{\text{GLMM(m)}} = 0.86$ ). Breeding stage did not influence the proportion of marine resources estimated from pellet data relative to the proportion of marine resources estimated from the Bayesian MixSIAR model, ( $\chi^2 = 2.77$ ,  $p = 0.10$ ). However the proportion of terrestrial resources estimated from the pellet data was higher during the post-hatching stage compared to the pre-breeding stage relative to the terrestrial estimates obtained from the Bayesian MixSIAR model (breeding stage:  $\chi^2 = 6.15$ ,  $p = 0.01$ ).

Based on the herring gull pellet samples, significant spatial variation in resource use occurred among colonies (Fig. 3) for the frequency of occurrence of offshore items ( $F_{5,15} = 7.53$ ,  $p < 0.001$ ,  $R^2 = 0.68$ ); intertidal items ( $F_{5,15} = 18.29$ ,  $p < 0.001$ ,  $R^2 = 0.85$ ) and terrestrial items ( $F_{5,15} = 3.19$ ,  $p = 0.028$ ,  $R^2 = 0.41$ ). There were no significant interactions between the three resource categories and year or breeding stage ( $p > 0.10$ ). Colonies differed in the proportion of offshore food items with birds from Pladda using significantly more offshore resources than all other colonies (post-hoc multiple comparisons:  $p < 0.002$ ). Intertidal food items were more common on Oronsay, Jura and Strangford than all other colonies (post-hoc multiple comparisons:  $p < 0.005$ ). However, in all colonies, except Jura, the most consumed resources come from terrestrial foraging habitats with Jura having significantly lower use of terrestrial resources than all other colonies (post-hoc multiple comparisons:  $p < 0.03$ ).

In 2014, based on the MixSIAR model, the utilisation of marine resources (pooling offshore and intertidal, see Methods) differed between gull colonies depending on the breeding stage (colony-by-breeding stage interaction:  $F_{12,246} = 31.51$ ,  $p < 0.001$ ,  $R^2 = 0.80$ , Fig. 4). The contribution of marine resources was higher in the post- than in the pre- hatching stage for two colonies, Oronsay and Pladda (post-hoc multiple comparisons:  $p < 0.001$ ).

The within-colony consistency repeatability ( $R_c$ ) of the proportion of marine (intertidal and offshore pooled) and terrestrial food types found in the pellets of the eight colonies sampled during both breeding stages of 2013 and 2014 was high for marine food types ( $R_c = 0.87$ , 95% CI: 0.54 – 0.96,  $p = 0.002$ ) but less so for terrestrial food types ( $R_c = 0.39$ , 95% CI: 0.00 – 0.76,  $p = 0.05$ ). As expected, there was a negative correlation between the proportion of marine and terrestrial items in the diet ( $r = -0.85$ ,  $p < 0.001$ ). As the estimated use of marine resources by herring gulls from the pellets is consistent across



years and was highly correlated with the stable isotope analysis we used the pellet data to reflect the gulls' resource use for the remaining analyses as it provided a larger sample size.

### **Influence of environmental variables on spatial variation in resource use**

The use of intertidal resources by herring gulls was higher in colonies with lower average wave fetch within their foraging range ( $\chi^2_1 = 8.55$ ,  $p = 0.004$ ,  $R^2_{\text{GLMM}(m)} = 0.58$ , Fig. 5A). There was no significant relationship between the use of offshore resources and the two proxies for conditions in the marine environment (Chlorophyll a:  $p = 0.316$ ; SST:  $p = 0.751$ ). Investigating the terrestrial environmental variables, the proportion of marine resources (offshore and intertidal) in pellets decreased the closer the colony was located to a built-up area ( $\chi^2_1 = 4.92$ ,  $p = 0.027$ ,  $R^2_{\text{GLMM}(m)} = 0.43$ , Fig. 5B). We found no significant relationship with the nearest distance to farmland ( $p = 0.56$ ) or with the amount of farmland within 50 km of the colony ( $p = 0.44$ ). Neither year nor breeding stage explained variation in resource use in any of the models ( $p > 0.10$ ).

### **Influence of spatial variation in resource use on demographic parameters**

The frequency of occurrence of intertidal items in pellets, colony size and year all influenced final brood size (FO of intertidal items:  $\chi^2_1 = 5.40$ ,  $p = 0.020$ ; Colony size  $\chi^2_1 = 4.73$ ,  $p = 0.030$ ; Year:  $\chi^2_1 = 5.97$ ,  $p = 0.015$ ;  $R^2_{\text{GLMM}(m)} = 0.57$ ). Mean brood size increased with increasing proportions of intertidal resources consumed in that colony (Fig. 6,  $f = 0.12$ ). Mean brood sizes were larger in 2014 ( $1.97 \pm \text{SD } 0.29$  chicks) than 2013 ( $1.71 \pm \text{SD } 0.24$  chicks), and increased with colony size. The proportion of offshore resources consumed had no influence on final brood size ( $p = 0.68$ ); nor did the proportion of terrestrial resources consumed ( $p = 0.69$ ).

## **DISCUSSION**

This study shows that spatial variation in resource use is associated with variation in one measure of herring gull demography; breeding success. Herring gull colonies differed in their predominant resource use and this was associated with differences in the availability of foraging habitats within the colony's foraging range. Colonies along sheltered coasts, with a low wave fetch, which harbour more abundant and diverse marine invertebrate

communities, used more intertidal resources whilst colonies closer to built-up areas consumed more terrestrial resources; compared to colonies at more exposed coasts and further away from built-up areas, respectively. Consuming a higher proportion of intertidal food resources was positively associated with the gulls' demography with colonies that used more intertidal resources during the breeding season showing higher seasonal breeding success. This highlights the importance of variation in resource use even for populations of an opportunistic generalist consumer.

Based on pellet data, the herring gulls within our study area fed on a wide variety of food items from different foraging habitats both within and between colonies. Breeding herring gulls predominantly foraged on terrestrial food sources, except for one colony (Jura). Terrestrial food items consumed were mainly grain and terrestrial invertebrates, or terrestrial feeding was indicated by the presence of vegetation and anthropogenic refuse such as plastic, foil and glass within the pellets. The marine items within the gulls' diets mostly comprised of intertidal invertebrates. Resources from offshore habitats were typically the least frequent food found in the pellets, and consisted of Nephrops and several benthic fish species, predominantly gadoids, which were most likely obtained from local fishery activities. This mix of resources is typical for breeding herring gulls (Harris 1965, Götmark 1984, Pons 1992, Kubetzki & Garthe 2003). However, diet data from pellets are likely biased towards prey with indigestible hard parts (Barrett et al. 2007, Karnovsky et al. 2012), with the majority of prey items from terrestrial and intertidal foraging habitat being characterised by such hard parts. Although fish may be softer, more digestible prey they still contain indigestible otoliths, and vertebrae that can indicate that fish had been consumed, however consumption of fish may therefore be under-represented in our pellet samples.

The stable isotope data provided a lower taxonomic resolution than the pellet data and, within our data, it was not possible to distinguish between the carbon and nitrogen isotope values of intertidal and offshore resources. In future analyses including additional isotopes, specifically sulphur, may allow intertidal and offshore resources to be distinguished (Connolly et al. 2004, Bond & Jones 2009, Ramos et al. 2009, Hobson et al. 2015). Nonetheless, the two methods gave highly comparable results, despite the different biases of each method. Similarities between results from pellet and stable isotope analysis of resource use have been observed in other studies (Ramos et al. 2009, 2012, Kim et al.

2010, Weiser & Powell 2010, Resano-Mayor et al. 2014 but see Steenweg et al. 2011). This suggests that although each pellet provides only a snap shot of resource use they can accurately be used to reflect the gulls' assimilated diets, at the colony level, over the period the sampled feathers were grown. The pellets did, however, under-estimate the contribution of marine food, compared to the assimilated diet based on stable isotopes. One explanation for this could be that we did not use the most relevant isotopic discrimination factor, as we had to use the values from a different species, and discrimination factors may vary between species. The choice of discrimination factor can impact on the outputs of mixing models (Bond and Diamond 2011). Nonetheless, although we could not clearly distinguish between offshore and intertidal prey, as we were primarily interested in whether gulls foraged in marine or terrestrial habitats our pellet analyses provided an adequate reflection of the broad resource use of breeding herring gulls across our study region.

Across the colonies, we found that resource use did not differ between years, although there is some suggestion that it may have differed between breeding stages, at least for some colonies. The frequency of occurrence of offshore, intertidal and terrestrial food items in pellets in each colony was similar between years. This was further confirmed by the high within-colony repeatability estimates for the proportion of marine resources used in the pellets. The resource use within a colony was generally consistent across breeding stages, however the stable isotope analyses suggested that the use of marine resources was higher during the post-hatching period in Pladda and Oronsay, compared to pre-hatching. A number of studies have found that parents can feed chicks a more nutritious diet during chick-rearing (Annett & Pierotti 1989, Golet et al. 2000, Romano et al. 2006, Steenweg et al. 2011, Kadin et al. 2012; but see Washburn et al. 2013), with marine food typically providing the higher protein and fat content (Supplementary Table 3), required by chicks to build muscle and fuel growth. . However, fish is the most likely food item to be missed from pellets being soft-bodied, although not in the stable isotope data, which might explain the higher bias towards terrestrial resources in the post-hatching period by the pellet data and why the pellet data did not show an effect of breeding stage on marine resource use. It is possible, however, that colonies differ in their capacity to increase the contribution of marine-derived resources with the exception of Oronsay, which

is close to a large intertidal area, and Pladda, which is near some local Nephrops trawling activity. A factor that complicates the interpretation of a difference in resource use between breeding stages is that breeding seabirds, including gulls, may provision their chicks with different food than they consume themselves (Spaans 1971, Nogales et al. 1995, Wilson et al. 2004, Steenweg et al. 2011). In our case, pre-hatching pellets come from adults only, whilst post-hatching pellets are likely to have come from adults and chicks. In addition, the stable isotope values of down feathers will mainly reflect the resource use by the female whereas chick feathers will reflect resource use of both parents. Obtaining separate stable isotope data from each parent and the chick is unlikely to resolve the issue if the diet differences are not reflected in differences in stable isotope values. It should also be considered that any differences in resource use between breeding stages may be driven by seasonal differences in food availability.

Between-colony feeding specialisation may occur due to greater efficiency of specific foraging strategies; be attributed to variation in the availability of preferred food (Whitfield et al. 2009); or be due to social cues with birds within the same colony able to observe and learn where to forage based on their conspecifics' habitat selection (information centre hypothesis: Ward & Zahavi 1979, Andersson et al. 1981, Evans 1982). Within this study, our results suggest that the spatial variation in the contribution of resources to the herring gulls' diet, and therefore the type of foraging habitat they predominantly used, is related to the habitat most readily available within their foraging range.

We found no relationship between the frequency of offshore resources in the gulls' diet and SST or Chlorophyll a, our proxies for marine productivity. This may be due to these proxies not accurately reflecting the potential availability of these resources to the gulls. However, in this study, it does not appear that the herring gulls foraged extensively on fish or other discard items within the region, namely Nephrops (Stratoudakis et al. 2001), given the low proportion of pellets containing offshore items (Fig. 3; offshore, making up over 25% of the pellet, was only found in 9.22% of pellets (average per colony:  $6.86\% \pm 7.25$ , range 0-21.5). The only colony where the proportion of offshore food items in the pellets reached over 14% was Pladda, due to the occurrence of Nephrops fisheries within the foraging range of this colony. From GPS tracking data of several individuals from four of the Scottish study colonies we know that birds spend very little time foraging offshore or near

ports, where they could have picked up offshore food from fishery discards (N. O'Hanlon unpubl. data).

We found that herring gulls used more intertidal resources when nesting in areas of low wave fetch i.e. sheltered coasts that support a greater abundance and diversity of potential intertidal prey species (Burrows et al. 2012). Although shorelines may also vary in characteristics other than wave fetch, wave fetch explains a statistically significant part of the use of intertidal resources by breeding herring gulls. There may be additional variation in intertidal habitat across the study region that had not been captured by wave fetch and could explain further variation in intertidal resource use between colonies.

Herring gull colonies that used a higher proportion of intertidal resources had a larger broods of chicks of at least 3 weeks of age. The profitability of a particular food resource will be influenced by the abundance and quality of the food; the rate at which it can be collected and the cost of capturing, handling and transporting it back to the nest. All of these characteristics may affect the survival of chicks. The quantity and quality of food provisionings can determine whether a chick receives adequate nutrition or will fail due to starvation. The time the parents spent away from the nest and forage can also affect offspring survival through the risk of con-specific predation when chicks are unattended (Hunt & McLoon 1975). Our data cannot distinguish between the different potential causes of mortality.

It is interesting that we found a positive association between intertidal resource use and breeding success in herring gulls, in agreement with other studies on gulls (Pierotti & Annett 1990, Annett & Pierotti 1999). Ronconi et al. (2014) also found that intertidal invertebrates made up an important part of breeding herring gull diet, with individuals foraging at a higher trophic level having better body condition. This suggests that intertidal invertebrates are an important prey for breeding herring gulls, either because they are a reliable and abundant food source and/or provide a high quality food for the growing chick. Herring gulls foraging on intertidal resources may benefit from highly predictable tidal cycles, however neither the energy density nor composition of macro nutrients of intertidal invertebrates are more favourable than alternative food resources (Supplementary Table 3). Although, some other micro-nutrients may differ between food resources, which could make intertidal invertebrates particular suitable for breeding gulls, for example calcium,

which is important for chick growth (Annett and Pierotti 1989; Noordhuis and Spaans 1992) and which is particularly low in grain, the main terrestrial food item (65.30% of pellets containing >25% of grain). More soft-bodied marine food, such as fish, is likely to be under-reported in pellets and was indistinguishable from intertidal resources in our stable isotope data. As fish prey are typically larger and richer in energy and nutrients (Supplementary Table 3) than intertidal invertebrates their contribution to the gulls' assimilated diet might be disproportionately higher. However, we found no relationship between the proportion of offshore resources in pellets and breeding success; potentially due to this resource not being particularly available within the region. Therefore, within this study it appears that intertidal resources are more important to the gulls than offshore marine resource i.e. obtained from fishery activities. Several colonies did rely heavily on terrestrial food, in particular if they were located close to built-up areas, potentially because they were attracted by these resources, or due to intertidal resources being scarcer within the vicinity of these colonies. It is worth noting that colonies located nearer to built-up areas also had a less favourable wave fetch (Pearson's correlation:  $r = -0.79$ ,  $n = 24$ ,  $p < 0.001$ ); further indicating that the gulls were foraging on the resources most accessible to them. However, the most frequently consumed terrestrial food items was grain, which is relatively low in energy and lipids in comparison to other terrestrial items and to intertidal prey.

We do not have specific foraging rates or processing costs for the resources within this study. The feeding rates of herring gulls on landfill sites have been observed to be lower than if foraging on intertidal prey (Sibly & McCleery 1983). However, herring gulls foraged at least as successfully on earthworms as on the most profitable intertidal invertebrate (Sibly & McCleery 1983), suggesting that earthworms from farmland could be another valuable resource although they will be under-estimated in the pellet data (Coulson & Coulson 2008). Unfortunately there is no information on the herring gulls' foraging rate on grain. It may also be that the trips of gulls foraging in terrestrial habitat, and particularly in built-up areas were longer and more expensive, or took longer due to lower feeding rates in terrestrial habitats compared to intertidal habitats. Although terrestrial resources are generally thought to be more predictable (Burger & Gochfeld 1983, Horton et al. 1983, Yoda et al. 2012), certain anthropogenic resources such as landfill may be currently less predictable than they previously were due to management actions to discourage foraging by

opportunistic species such as gulls (Baxter and Allan 2006; Cook et al. 2008). We have also include distance to nearest farmland and built-up area and found that distance to built-up area plays a role, possibly suggesting that long trips to built-up areas may not worth the effort. Nearest distance to farmland, however, did not play a role, suggesting that gulls are less selective how far they travel to this foraging habitat. Therefore, reduced feeding rates and longer or further foraging trips could result in lower provisioning rates and / or lower nest attentiveness, which can increase the chicks' vulnerability to attacks or predation by other gulls (Hunt & McLoon 1975). Within the scope of this study we were unable to obtain information on foraging rates and trip characteristics, and further exploring these foraging characteristics will help to better understand the value of the different foarging habitats to herring gulls.

We also found that final brood size was higher in our larger study colonies, potentially suggesting that density dependent processes were occurring. British herring gulls also showed negative density dependent population growth rates over the last three decades of the last century (Nager & O'Hanlon 2016). Density-dependent resource depletion or competition for local resources or larger groups being more susceptible to conspecific nest predation or disease can result in reduced productivity in larger colonies (Hunt et al. 1986). However, it may also be that within this study, the larger colonies were located in areas of preferred foraging habitat (Oro et al. 1996).

In conclusion, we found that inter-colony differences in the resource use of herring gulls were associated with the availability of resources within a colony's foraging range and this had consequences for demographic traits associated with annual productivity. Within this study it appears that diet differentiation between gull colonies is due to spatial variation in the availability of the gulls' preferred marine food, specifically in this case intertidal items, and if this is not available, they resort to terrestrial food, mostly anthropogenic. This result may also help in understanding the recent declines observed in herring gull numbers (Mitchell et al. 2004, Eaton et al. 2015).

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**Table 1.** Number of pellet and feather samples collected from eight herring gull colonies during the 2013 and 2014 breeding seasons for resource use analyses. All feather samples were collected during the 2014 breeding season.

Colony	Pellet samples				Pellet Total	Feather samples		
	2013		2014			Chicks		
	Pre-hatching	Post-hatching	Pre-hatching	Post-hatching		Down	Feathers	Total
Copeland <sup>1</sup>	1	20	27	79	127	22	25	47
Islay	21	66	36	4	127	11	0	11
Jura	16	7	25	0	48	0	0	0
Lady Isle	0	0	31	39	70	28	28	56
Oronsay	13	49	0	30	92	33	15	48
Pladda	40	62	81	30	213	24	31	55
Portpatrick	0	0	43	6	49	2	14	16
Strangford <sup>2</sup>	0	5	24	26	55	13	13	26
Total	91	209	265	216	781	133	126	259

<sup>1</sup> All samples collected from Lighthouse Island however, colony size is for the three Copeland Islands combined due to their close proximity. <sup>2</sup> Pellet samples at Strangford were collected from two different sites (Round Island in 2013, Green Island in 2014) that are within 7 km of each other and treated as a single colony.



**Table 2.** Food items or items that indicate the foraging habitat , identified from herring gull pellets collected during the 2013 and 2014 breeding season from eight colonies and broad foraging habitat they were assigned to. Frequency of occurrence (FO%) of items making up at least 25% of a pellet sample across all 781 pellet samples. Individual pellet samples may contain multiple food items.

Foraging habitat	Food type	FO (%)	Indicator of foraging habitat	FO (%)
Terrestrial	Grain	65.30	Terrestrial vegetation (exc. grain)	16.26
	Invertebrates	41.35	Anthropogenic items:	
	Mammal bone/fur	2.31	Plastic	3.20
	Bird bone/feathers	1.66	Paper	1.54
			Glass	0.90
			Man-made fibre	0.90
			Metal/tin foil	0.51
			Unknown anthropogenic	0.26
Intertidal	Crab species	16.01		
	Marine shells	1.79		
	<i>Mytilus edulis</i>	1.66		
	Marine snails	0.51		
	Starfish	0.13		
Offshore	Fish species <sup>a</sup>	6.40		
	<i>Nephrops norvegicus</i>	2.82		

<sup>a</sup> Fish species (identified from otoliths found in pellets) included Poor cod *Trisopterus minutus*, Whiting *Merlangius merlangus*, unidentified gadoids (due to very worn otoliths) and a wrasse spp.

**Table 3.** Stable isotope values of marine and terrestrial food sources obtained during the 2014 breeding season to use as reference values in the stable isotope mixing models.

Food Item	Category	Samples	$\delta^{13}\text{C} \pm \text{SD}$	$\delta^{15}\text{N} \pm \text{SD}$
Grain	Terrestrial	1	-28.62	9.38
Invertebrates	Terrestrial	5	-27.73 $\pm$ 0.34	7.08 $\pm$ 1.81
Rodent species	Terrestrial	1	-29.41	8.64
Refuse	Terrestrial	2	-23.93 $\pm$ 2.52	5.13 $\pm$ 3.66
Crab species	Intertidal	15	-16.17 $\pm$ 1.52	11.20 $\pm$ 2.09
Coelopidae larvae	Intertidal	1	-20.04	8.05
Marine fish <sup>1</sup>	Offshore	11	-17.62 $\pm$ 0.65	14.46 $\pm$ 0.83
<i>(Blenidae spp.</i>		2	-17.88 $\pm$ 0.14	13.79 $\pm$ 0.88)
<i>(Pollachius pollachius</i>		1	-17.57	16.00)
<i>(Trisopterus minutus</i>		5	-17.99 $\pm$ 0.26	13.63 $\pm$ 0.23)
<i>(Gaidropsarus spp.</i>		1	-15.96	14.03)
(Unidentified spp. <sup>2</sup>		2	-17.29 $\pm$ 0.37	15.13 $\pm$ 0.13)
Nephrops norvegicus	Offshore	6	-17.41 $\pm$ 0.36	13.08 $\pm$ 2.08

<sup>1</sup> Actual fish species listed below in parenthesis. <sup>2</sup> Unidentified fish from chick regurgitates.

**Table 4.** Demographic information for target herring gull colonies during 2013 and 2014. For all colony counts the same standardised count methods were used (Walsh et al. 1995, Mitchell et al. 2004).

Colony	Colony Size <sup>c</sup>	Growth Rate <sup>d</sup>	Year	Final brood size	Number of nests <sup>e</sup>	
Copeland <sup>a</sup>	683	0.55	2013	1.5	8	(0.01)
	(2012)		2014	2.27	15	(0.02)
Islay	25	0.00	2013	1.43	7	(0.28)
	(2013)		2014	1.75	4	(0.16)
Jura	15	-0.70	2013	1.83	6	(0.40)
	(2013)		2014	-	-	-
Lady Isle	830	-0.45	2013	-	-	-
	(2012)		2014	2.13	15	(0.02)
Oronsay	95	-0.30	2013	1.65	20	(0.21)
	(2013)		2014	1.75	24	(0.25)
Pladda	150	-0.40	2013	1.78	23	(0.13)
	(2013)		2014	1.77	13	(0.09)
Portpatrick	175	-0.20	2013	1.64	11	(0.06)
	(2013)		2014	1.71	31	(0.18)
Strangford <sup>b</sup>	190	0.69	2013	2.14	18	(0.10)
	(2013)		2014	2.39	33	(0.17)

<sup>a</sup> Colony size is that of three Copeland islands together due to their close proximity. <sup>b</sup> Colony size is the average of Green Island (115) and Round Island (265). Final brood size is the average across both islands. <sup>c</sup> Colony size from the most recent colony count (year of count in parenthesis) and is given as Apparently Occupied Nests (AON). <sup>d</sup> Colony growth rate between Seabird 2000 (Mitchell et al. 2004) and the most recent count. <sup>e</sup> Number of nests final chick brood size was estimated from; with the proportion of total nests with known final chick brood sizes from the total apparently occupied nests (AON) of each colony in parenthesis.





## Figure legends

**Figure 1.** Study region and location of the eight herring gull breeding colonies across south-western Scotland and Northern Ireland. 1 Islay, 2 Oronsay, 3 Jura, 4 Lady Isle, 5 Pladda, 6 Portpatrick, 7 Copeland Islands, 8 Strangford Lough (Green and Round Island). Grey shading shows built-up (urban and sub-urban) areas from Landcover 2007.

**Figure 2.** Relationship between the proportion of use of marine (intertidal and offshore, Table 2) sources by herring gulls in 2014 estimated as frequency of occurrence (FO) from pellets (vertical axis) and the proportion of marine sources based on stable isotope analysis of feather samples (horizontal axis; median and 95% Bayesian credible intervals given by MixSIAR, see Methods). Each point represents a colony, and closed symbols show the pre-hatching period (pellets collected during the incubation period and stable isotopes of down feathers) and open symbols show the post-hatching period (pellets collected during chick rearing and stable isotopes of chick feathers). Solid line indicates the trend line with 95% confidence intervals (dashed lines) predicted from a Mixed Effect Model.

**Figure 3.** Frequency of occurrence of pellets containing offshore (black), intertidal (dark grey) and terrestrial (light grey) items, pooled for years and breeding stages as no differences between years or breeding stages were found. Number of pellet samples above bars. Colonies are ordered from left to right in increasing frequency of occurrence of marine (offshore and intertidal combined) food items.

**Figure 4.** Estimated proportion of herring gull diet comprised by marine sources (offshore and intertidal resources combined) based on stable isotope analysis of feather samples during the pre- (grey) and post-hatching period (white) over the 2014 breeding season, estimated by MixSIAR, see Methods. Boxplots show median (horizontal line), inter-quartile ranges (box), and minimum and maximum values (whiskers). Colonies ordered from the highest proportion of marine sources.

**Figure 5.** Relationship between the frequency of occurrence of intertidal items in pellets collected from each colony during the 2013 (open circles) and 2014 (filled circles) breeding season and (A) the average wave fetch within the breeding colony's foraging range and (B) the distance to the nearest built-up area. Solid line indicates the trend line with 95% confidence intervals (dashed lines) predicted from a Mixed Effect Model.

**Figure 6.** Colonies that had a higher frequency of occurrence of pellets containing intertidal items during the pre-laying period had larger average mean ( $\pm$ SD) brood sizes in 2013 (open black filled grey circles) and 2014 (filled grey circles) (see Table 6 for the full statistics). Pellet and final brood size information was available for six colonies (with no pellet data available for Lady Isle and Portpatrick) in 2013 and seven colonies (with no brood size data available for Jura) in 2014. Solid lines indicates the trend line with 95% confidence intervals (dashed lines) predicted from a Mixed Effect Model.

Fig. 1.

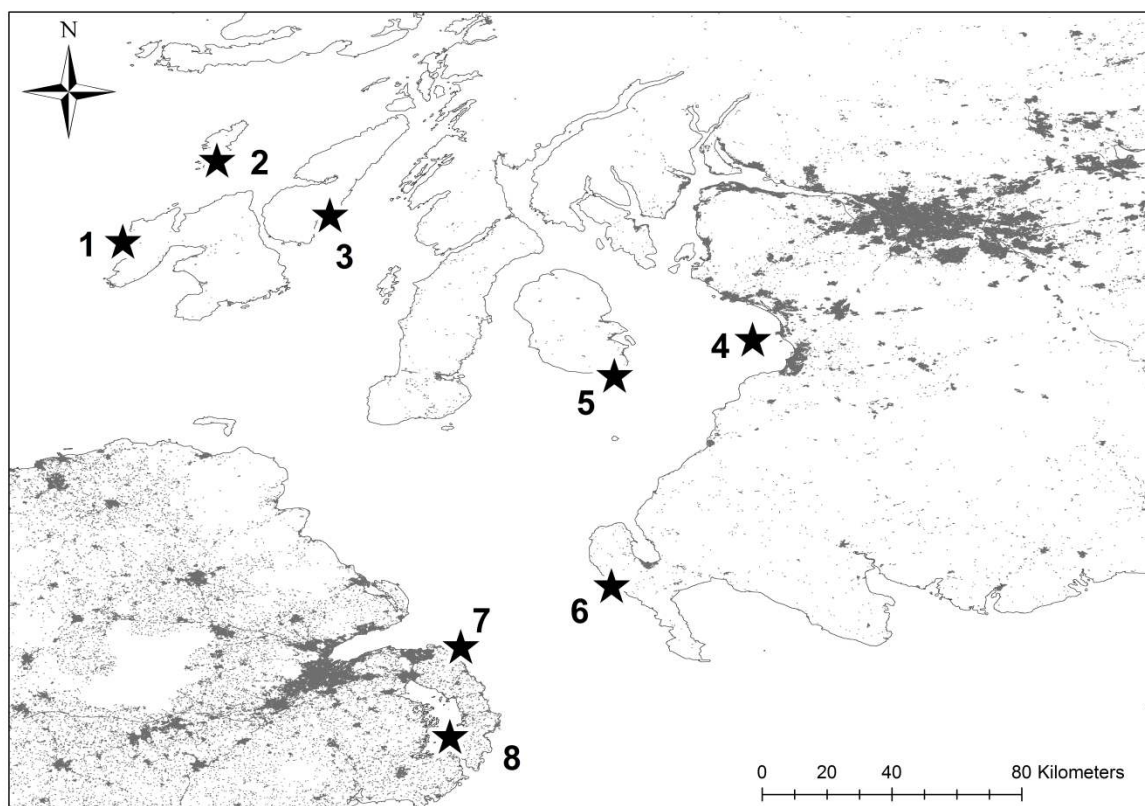




Fig. 2.

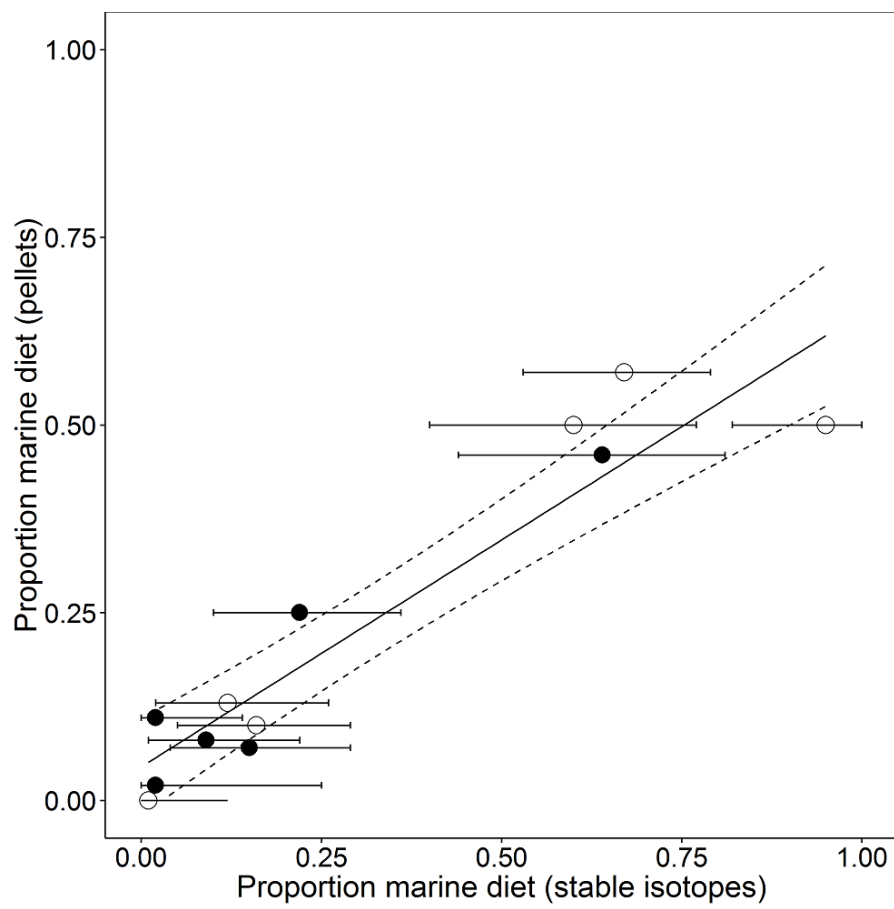


Fig. 3.

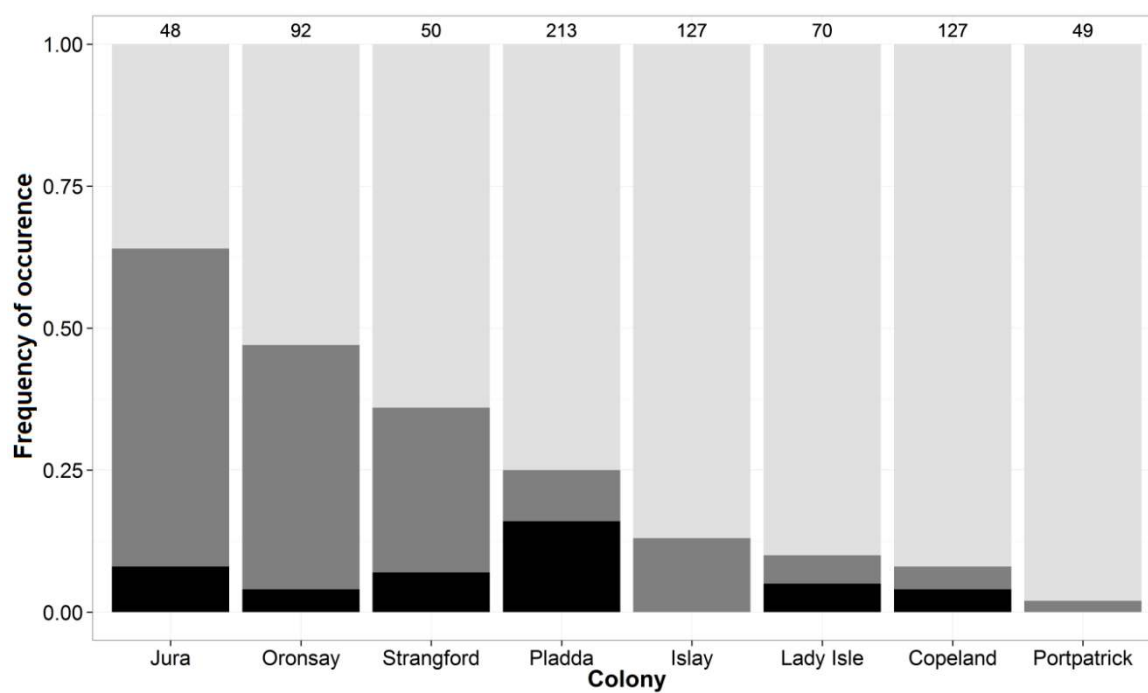


Fig. 4.

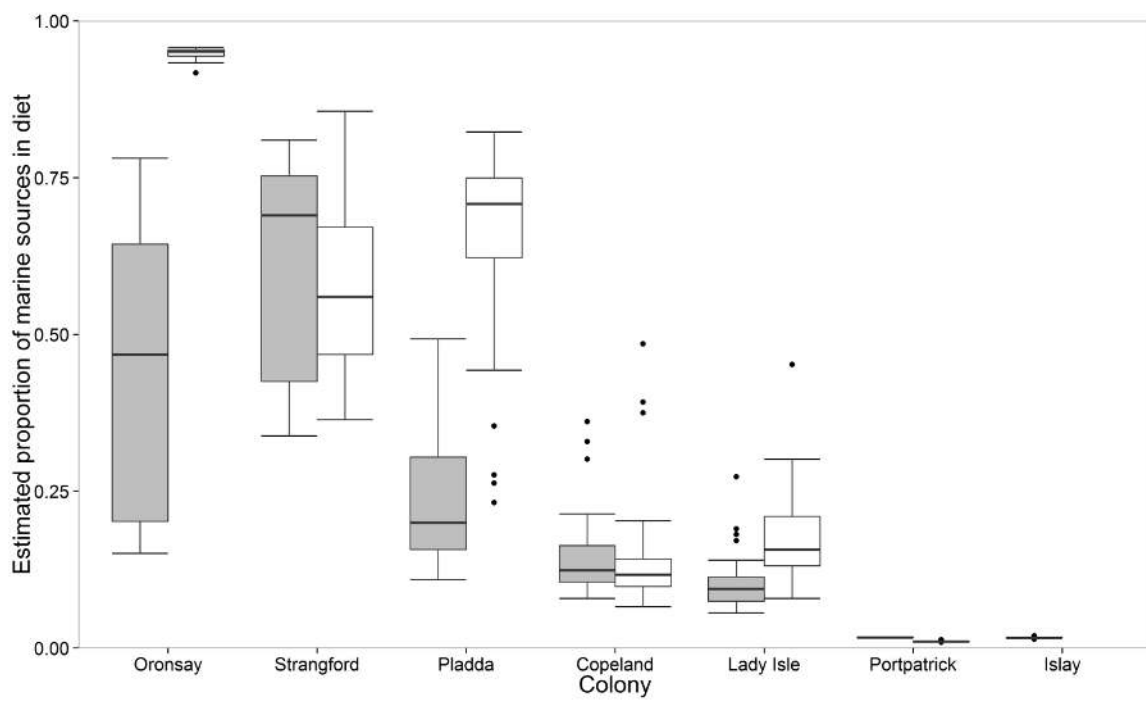
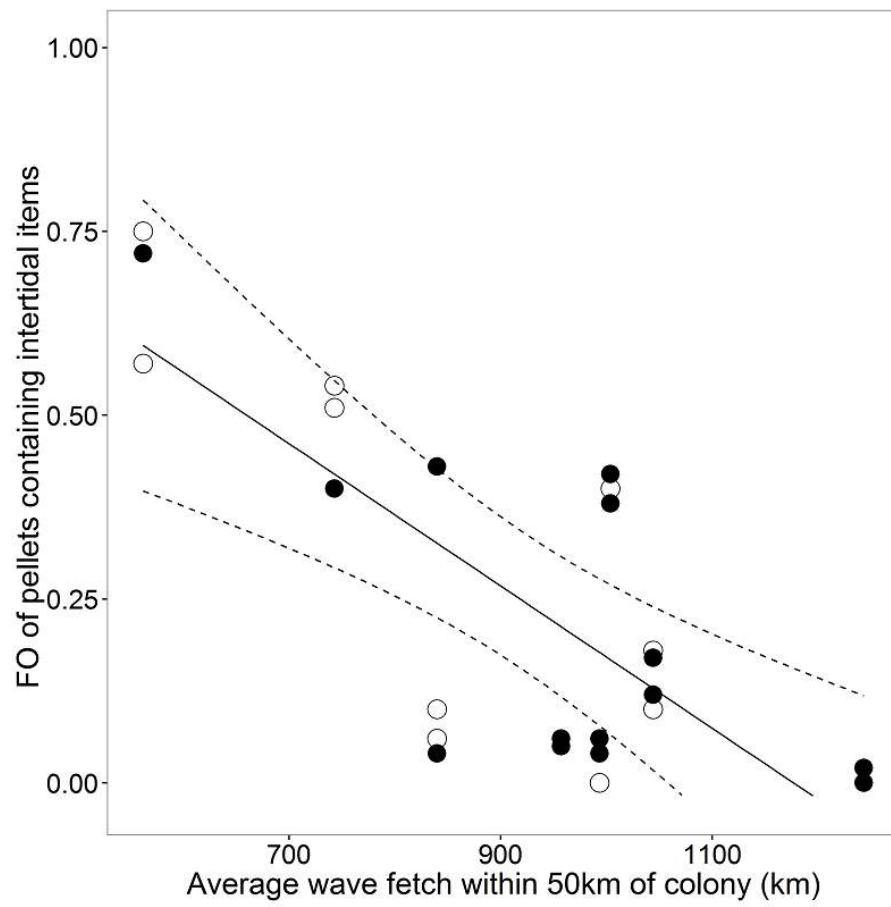


Fig. 5

A



B

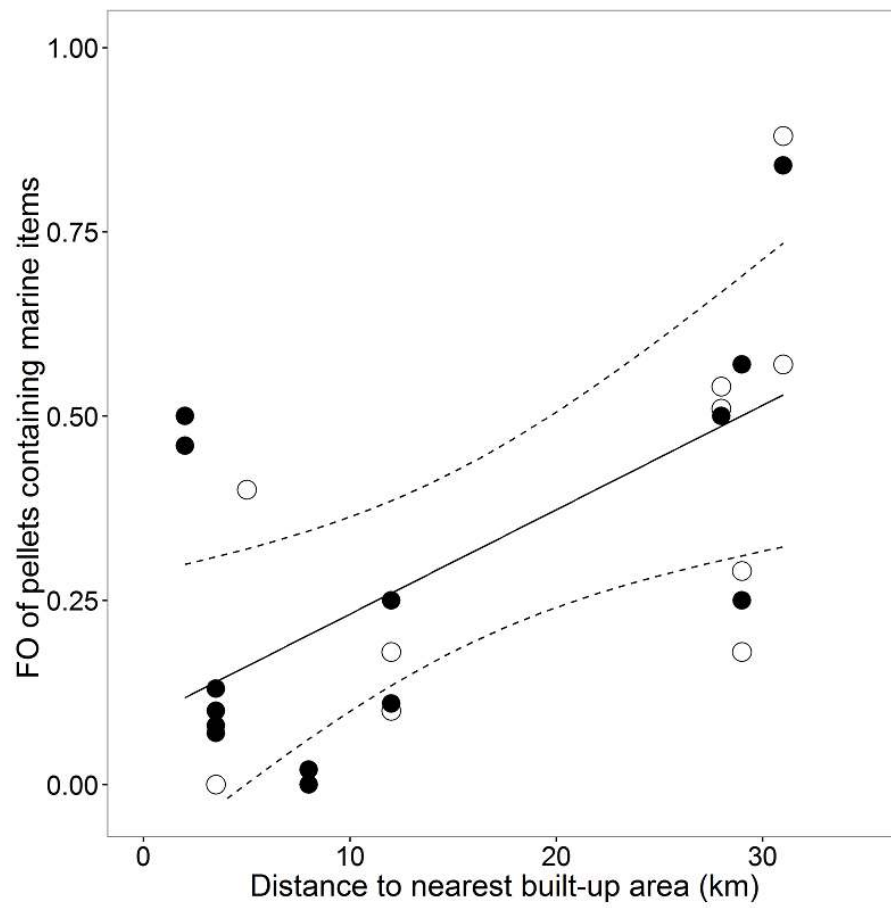
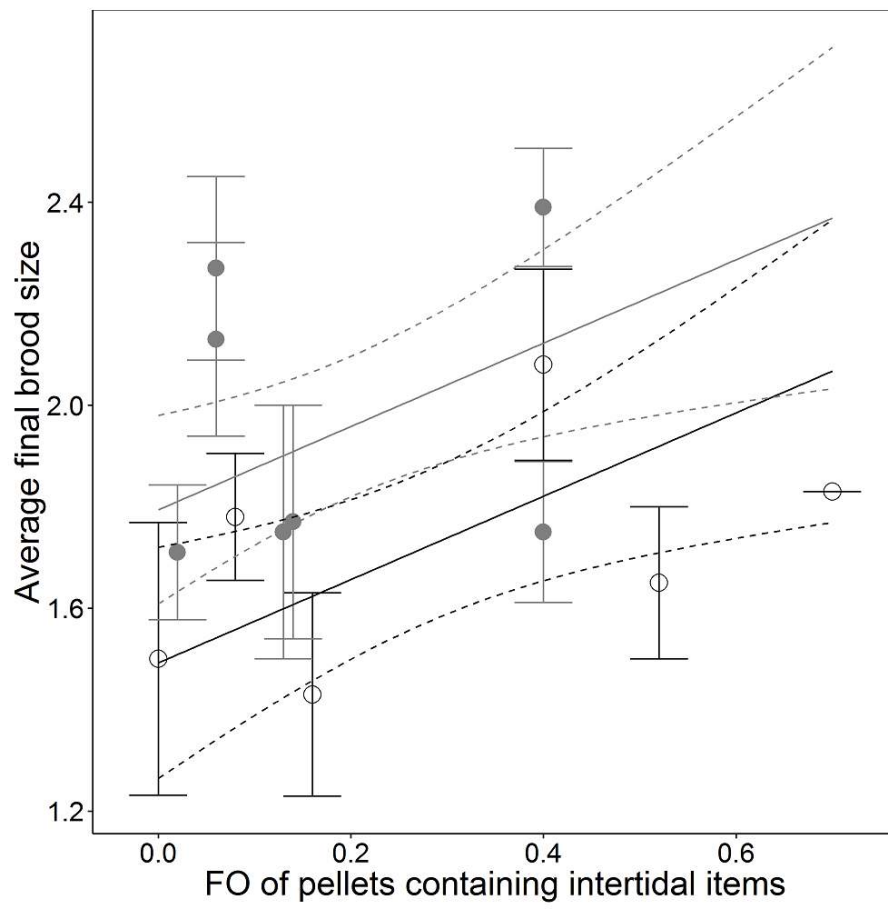


Fig. 6.



## Supplementary Material

Prior to stable isotope analyses all feather material was washed in liquid detergent (Ecover™) diluted with deionised water (approximate 1:99 dilution), and then in a 2:1 mixture of chloroform:methanol (Cherel et al. 2005). Feathers were then dried at 50°C overnight. For the prey samples, high lipid concentrations may result in apparently depleted  $\delta^{13}\text{C}$  values (Post et al. 2007). We therefore split each sample into two roughly equal sub-samples. From one sub-sample we extracted lipids using a Soxhlet apparatus with a 2:1 chloroform:methanol mixture until the solvent ran clear indicating all lipids were extracted.  $\delta^{13}\text{C}$  values were taken from these lipid-extracted samples.  $\delta^{15}\text{N}$  values were taken from the non-lipid extracted samples as  $\delta^{15}\text{N}$  can be altered by the lipid extraction (Yurkowski et al. 2015).

We checked for spatial variation in baseline stable isotope values across our study region by comparing stable isotope values from down feathers from nests of common eiders *Somateria mollissima* that we collected from five colonies. Common eiders are year-round residential, specialised mussel feeders (Player 1971, Guillemette et al. 1992) with their tissue reflecting local stable isotope values at a low trophic level in the marine coastal environment, the main foraging habitat of herring gulls. Eider down feathers were processed and analysed as the gull feathers.  $\delta^{13}\text{C}$  did not vary between colonies ( $F_{5,15} = 0.34$ ,  $p = 0.88$ ), but for  $\delta^{15}\text{N}$  there were some between-colony differences ( $F_{5,15} = 4.78$ ,  $p = 0.008$ ) with only the contrast between the lowest (Oronsay) and highest values (Copeland and Lady Isle) being significant. Since the spatial variation in  $\delta^{15}\text{N}$  was due to a single site and other work on this region showed no geographic variation (Jennings & Cogan 2015), we did not correct for spatial variation in baseline stable isotope values.

**Table S1A.** Dates of colony visits during the 2013 breeding season.

<b>Copeland</b>	<b>Islay</b>	<b>Jura</b>	<b>Lady Isle</b>	<b>Oronsay</b>	<b>Pladda</b>	<b>Portpatrick</b>	<b>Strangford</b>
16/05/2013	12/05/2013	28/05/2013	07/05/2013	16/05/2013	04/05/2013	09/05/2013	06/05/2013
19/05/2013	13/05/2013	29/05/2013		17/05/2013	21/05/2013	23/05/2013	22/05/2013
01/06/2013	14/05/2013	09/07/2013		18/05/2013	31/05/2013	02/06/2013	03/06/2013
02/06/2013	15/05/2013			19/05/2013	01/06/2013	03/06/2013	18/06/2013
08/06/2013	26/05/2013			10/06/2013	17/06/2013	04/06/2013	
09/06/2013	27/05/2013			11/06/2013	18/06/2013	05/06/2013	
15/06/2013	28/05/2013			12/06/2013	19/06/2013	15/06/2013	
16/06/2013	30/05/2013			13/06/2013	01/07/2013	16/06/2013	
29/06/2013	31/05/2013			14/06/2013	02/07/2013	04/07/2013	
	06/06/2013			23/06/2013	03/07/2013	05/07/2013	
	07/06/2013			24/06/2013	04/07/2013	06/07/2013	
	08/06/2013			25/06/2013	17/07/2013	15/07/2013	
	09/06/2013			26/06/2013	18/07/2013	16/07/2013	
	13/06/2013			27/06/2013	19/07/2013		
	17/06/2013			10/07/2013	22/07/2013		
	20/06/2013			11/07/2013			
	21/06/2013			12/07/2013			
	22/06/2013			13/07/2013			
	07/07/2013			14/07/2013			
	08/07/2013						

**Table S1B.** Dates of colony visits during the 2014 breeding season.

<b>Copeland</b>	<b>Islay</b>	<b>Jura</b>	<b>Lady Isle</b>	<b>Oronsay</b>	<b>Pladda</b>	<b>Portpatrick</b>	<b>Strangford</b>
10/05/2014	05/05/2014	19/05/2014	13/05/2014	03/06/2014	02/05/2014	01/05/2014	14/05/2014
11/05/2014	10/05/2014		24/05/2014	04/06/2014	17/05/2014	05/05/2014	09/06/2014
23/05/2014	18/05/2014		30/05/2014	05/06/2014	27/05/2014	15/05/2014	11/06/2014
09/06/2014	26/05/2014		11/06/2014	06/06/2014	31/05/2014	08/06/2014	12/06/2014
14/06/2014	27/05/2014		18/06/2014	07/06/2014	01/06/2014	09/06/2014	25/06/2014
15/06/2014	28/05/2014		26/06/2014	15/06/2014	06/06/2014	10/06/2014	26/06/2014
28/06/2014	29/05/2014		15/07/2014	16/06/2014	07/06/2014	20/06/2014	
29/06/2014	03/06/2014			17/06/2014	15/06/2014	21/06/2014	
02/07/2014	04/06/2014			18/06/2014	20/06/2014	22/06/2014	
	06/06/2014			01/07/2014	28/06/2014	23/06/2014	
	08/06/2014			02/07/2014	29/06/2014		
	11/06/2014			03/07/2014	10/07/2014		
	16/06/2014			04/07/2014			
	17/06/2014			13/07/2014			
	18/06/2014						
	19/06/2014						
	20/06/2014						
	23/06/2014						
	25/06/2014						
	27/06/2014						
	28/06/2014						
	29/06/2014						
	30/06/2014						
	03/07/2014						
	07/07/2014						



**Table S2.** Breeding success based on all active nests (including total nest failure) and average brood size of nests where the chicks reached at least three weeks of age

Total number of nests	Brood size from all nests	Brood size from successfully hatched nests	Year	Location	Reference
249	1.29	1.46	1963	Sandy Point South, New England	Kadlec & Drury 1968
121	1.47	1.65	1963	Sandy Point North, New England	Kadlec & Drury 1968
44	1.09	1.5	1963	Coatue, New England	Kadlec & Drury 1968
275	1.02	1.52	1963	Block Island, New England	Kadlec & Drury 1968
258	0.93	0.98	1965	Block Island, New England	Kadlec & Drury 1968
266	1.42	1.47	1966	Block Island, New England	Kadlec & Drury 1968
36	0.75	1.5	1970	Skokholm, Wales	Davis 1974
366	0.6	1.9	1970	Skokholm, Wales	Davis 1975
224	0.63	1.7	1972	Skokholm, Wales	Davis 1975
223	1.25	1.55	1976	Great Island, Newfoundland	Pierotti 1982
297	1.63	1.98	1977	Great Island, Newfoundland	Pierotti & Annett 1991
332	1.83	2.09	1978	Great Island, Newfoundland	Pierotti & Annett 1991
335	1.3	1.74	1983-1988	Trerebon, France	Pons 1992
63	0.51	1.33	1989	Trerebon, France	Pons 1992
26	0.5	1.86	1992	Terschelling, Netherlands	Bukacinska et al 1996
41	2.37	2.69	1997	Walney, England	Nager unpub. data
84	1.43	1.65	1998	Walney, England	Nager unpub. data

**Table S3.** Nutritional information on food items consumed by herring gulls within this study (taken from the literature). \*energy density estimated from pDM: James et al. 2012.

Food type	Mass (g)	Energy density kJ/g wet weight	Protein (%)	Lipid (%)	Water (%)	Reference
<b>Terrestrial</b>						
Grain	0.07	0.24	11.80	0.00	87.10	Heuzé et al. 2016
Terrestrial invertebrates						
earthworm	0.20	2.96	10.50	1.60	83.60	Finke 2002
cricket	0.47	5.87	20.50	6.80	69.20	Finke 2002
Mammal (adult house mouse)	-	7.18	18.20	7.70	67.30	Dierenfeld et al. 2002
Bird (chicken, one day old)	-	6.21	16.60	5.70	74.40	Dierenfeld et al. 2002
Refuse						
chicken	-	1.22	21.39	3.08	75.46	USDA 2016
beef	-	5.59	10.91	26.13	55.31	USDA 2016
pork	-	1.26	20.65	17.55	74.97	USDA 2016
chips	-	6.87	3.49	14.04	43.19	USDA 2016
raw potato	-	0.67	2.05	0.09	79.25	USDA 2016
bacon	-	2.29	28.31	2.78	62.50	USDA 2016
sausages	-	3.57	13.60	14.3	60.50	USDA 2016
white bread	-	6.01	10.66	2.15	39.60	USDA 2016
<b>Intertidal</b>						
Crab, <i>Carcinus maenas</i>	-	0.16*	12.30	0.20	68.00	Fulton & Fairchild 2013
<i>Mytilus edulis</i>	1.00	0.30	11.90	2.20	-	Ciancio et al. 2007
<i>Littorina littorina</i>	0.25	0.33	-	-	-	Chambers & Milne 1979
<b>Marine offshore</b>						
Cod	131.00	4.20	16.10	2.60	78.50	Lawson et al. 1998
Nephrops	-	3.68	14.30	1.30	74.20	Björnsson 2004

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