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

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22 Stable isotope

23 **ABSTRACT**

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

## 43 INTRODUCTION

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

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

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

74 traits (junk-food hypothesis: Alverson 1992, Grémillet et al. 2008, Österblom et al. 2008).  
75 The quality of resources a forager consumes can be related to demographic traits,  
76 particularly breeding success (Uttley et al. 1989, Pierotti & Annett 1990, van Heezik 1990,  
77 Suddaby & Ratcliffe 1997, Romano et al. 2006, Osterblom et al. 2008). However, other  
78 studies have found no evidence that changes in food quality affects reproductive output,  
79 with a high abundance of food possibly compensating for its lower quality (Jodice et al.  
80 2006, Hjernquist & Hjernquist 2010). Environmental change may additionally affect the  
81 relative profitability of available resources, altering the consumers' resource use, which can  
82 impact on its population size depending on the quality of the alternative resources.

83         One group of widespread, opportunistic generalists that exploit a wide range of  
84 resources are the Laridae. They feed on a variety of foods from offshore, inshore and  
85 intertidal habitats, but also from agricultural fields, on refuse from built-up areas and fishery  
86 discards (Hunt & Hunt 1973, Götmark 1984). In evolutionary terms, the majority of gull  
87 species foraged mainly on fish and invertebrates from marine habitats, however, in certain  
88 species and populations gulls are increasingly exploiting anthropogenic resources from  
89 fishery discards in the marine environment to resources associated with farmland, landfill  
90 sites and other built-up areas in the terrestrial environment (Burger & Gochfeld 1983,  
91 Horton et al. 1983, Pons 1992, Belant et al. 1993, Smith & Carlile 1993, Brousseau *et al.*  
92 1996, Weiser & Powell 2010, Yoda *et al.* 2012, Steigerwald *et al.* 2015). There is conflicting  
93 evidence on the consequences to gulls of consuming anthropogenic terrestrial food rather  
94 than marine resources. Higher proportions of marine invertebrates and fish have been  
95 associated with higher reproductive rates compared to birds mainly feeding on terrestrial  
96 human refuse (*Larus argentatus*: Pierotti & Annett 1991, and *L. occidentalis*: Annett &  
97 Pierotti 1999, respectively). Moreover, the long-term decline in *L. glaucescens* has been  
98 attributed to a dietary shift from marine to more terrestrial resources, mainly refuse  
99 (Hobson et al. 2015, Blight et al. 2015a). In contrast, a number of studies have found higher  
100 reproductive rates in gulls feeding on refuse compared to birds feeding on mixtures of  
101 mainly other alternative terrestrial foods, and occasionally also fish (*L. argentatus*: Hunt  
102 1972, Pons 1992, Pons & Migot 1995, *L. hyperboreus*: Weiser & Powell 2010, *L. michahellis*:  
103 Steigerwald et al. 2015). An increase in *L. michahellis* numbers has been linked to the  
104 availability of anthropogenic food (Duhem et al. 2008). This suggests that the value of

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

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

117

## 118 **METHODS**

119 The herring gull is a widespread colonial seabird, which is a generalist, opportunistic forager,  
120 traditionally foraging on marine resources (primarily in intertidal habitats), however they  
121 now increasingly forage on terrestrial and anthropogenic resources (e.g. Hunt 1972,,  
122 Götmark 1984, Pons 1992, Kubetzki & Garthe 2003). To investigate the relationship  
123 between the resources they use and their breeding success we studied eight colonies during  
124 2013 and 2014 over a region covering approximately 200 by 250 km of south-west Scotland  
125 and Northern Ireland (Fig. 1). Within this region, we selected colonies along a gradient from  
126 low to high human population density; three in the Southern Hebrides, two in Northern  
127 Ireland and three in the Firth of Clyde. Resource use information was obtained from pellets  
128 from both years, providing 14 colony years, and chick feather samples, which were analysed  
129 for stable isotope ratios, from seven colonies in 2014 (Table 1). Different methods that infer  
130 information about diet can result in biases when estimating resource use (Barrett et al.  
131 2007). Pellets can over-represent food items with hard parts, whilst under-representing  
132 easily digested items, and only provide a snapshot of the birds' diet (Barrett et al. 2007).  
133 However, several studies have shown that diet estimates from pellets are comparable with  
134 diet estimated from regurgitates, which under-estimate easily digested foods less than the  
135 pellets do (Spaans 1971, Annett & Pierotti 1989). Stable isotopes provide a more integrated

136 representation of resource use for a longer period of time over which the sampled tissue  
137 was formed, however they are less taxonomically resolved (Bond & Jones 2009, Phillips et  
138 al. 2014). Resource use therefore needs to be inferred from stable isotopes cautiously  
139 where a population consumes a variety of foods with similar stable isotope values, however  
140 in our case stable isotopes can distinguish between the two main resources (marine and  
141 terrestrial anthropogenic) that we are interested in for herring gulls. Combining both  
142 methods therefore provides complimentary information on resource use (Barrett et al.  
143 2007).

144  
145 **Pellets analysis**

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

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

168 represented in the pellets. For the analysis, we assigned all food items listed under 'Food  
169 type' and 'Indicator of foraging habitat' in Table 2 to the three broad foraging habitat. Each  
170 food item was scored based on whether it made up more or less than 25% of the pellet's  
171 bulk. Frequency of occurrence for each food item was then calculated as the number of  
172 pellet samples where that food item was scored as over 25% of the pellet's bulk divided by  
173 the total number of pellet samples (Duffy et al. 1986). Frequency of occurrence was  
174 determined separately for each colony, for each breeding season and whether collected  
175 during incubation (pre-hatching: 02/05 - 31/05) or chick rearing (post-hatching: 01/06 –  
176 13/07). For 120 pellet samples (15% of total) two food items were scored as above 25% and  
177 therefore were included in the proportions of each of the relevant foraging habitats, and  
178 therefore the sum of frequency of occurrences can be greater than 100%.

179

### 180 **Stable isotope analysis**

181 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  
182 determine where along a gradient between terrestrial and marine habitats, and from what  
183 trophic level, respectively, resources are consumed (Hobson et al. 1994).

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

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



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

201 In order to relate stable isotope ratios more specifically to the foraging habitats used  
202 by the herring gulls, we also collected samples of known prey items from within our study  
203 area (Table 3). We collected prey samples from chick regurgitates, with the exception of the  
204 named fish species, which were collected from the Firth of Clyde (off Arran). High lipid  
205 concentrations in prey samples may result in apparently depleted  $\delta^{13}\text{C}$  values (Post et al.  
206 2007). We therefore split each sample into two roughly equal sub-samples. From one sub-  
207 sample we extracted lipids using a Soxhlet apparatus with a 2:1 chloroform:methanol  
208 mixture until the solvent ran clear indicating all lipids were extracted.  $\delta^{13}\text{C}$  values were  
209 taken from these lipid-extracted samples.  $\delta^{15}\text{N}$  values were taken from the non-lipid  
210 extracted samples as  $\delta^{15}\text{N}$  can be altered by the lipid extraction (Yurkowski et al. 2015).  
211 Dried feather and prey samples were homogenized and weighed (mass between 0.7-0.8mg)  
212 into tin capsules before being combusted and analysed by continuous-flow isotope ratio  
213 mass spectrometry (Costech Elemental Analyser, Milan Italy linked to a Thermo Finnigan  
214 Delta Plus XP Mass Spectrometer, Bremen Germany) at the NERC Life Sciences Mass  
215 Spectrometry Facility, East Kilbride. Stable isotope values  $\delta$  are expressed as parts per  
216 thousand (‰) relative to the international references PeeDee belemnite marine fossil  
217 limestone for carbon and atmospheric  $\text{N}_2$  for nitrogen. Measurement precision, calculated  
218 as the standard deviation of repeated analyses of an internal standard (tryptophan), was  
219  $\pm 0.09$  ‰ for  $\delta^{13}\text{C}$  and  $\pm 0.12$  ‰ for  $\delta^{15}\text{N}$ .

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

230 work on this region showed no geographic variation (Jennings & Cogan 2015), we did not  
231 correct for spatial variation in baseline stable isotope values. To estimate the contribution  
232 of different resources to the gulls' assimilated diet in each colony we ran a Bayesian stable-  
233 isotope mixing model (MixSIAR GUI, Stock & Semmens 2013).  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for chick  
234 down and feathers were included in the analysis as consumer tissue. Among the prey  
235 samples the  $\delta^{13}\text{C}$  values only differed between terrestrial and the two marine food sources  
236 (intertidal and offshore) but not between intertidal and offshore (ANOVA:  $F_{2,5} = 38.21$ ,  $p <$   
237  $0.001$ ; post-hoc Tukey HSD pair-wise comparisons between offshore and intertidal  $p = 0.93$ ,  
238 both marine resources were significantly different from terrestrial items  $p < 0.003$ ). We  
239 therefore pooled offshore and intertidal food sources into one marine resource and  
240 considered only the two sources (marine and terrestrial) for the mixing model. Isotopic  
241 discrimination factors are not available for herring gull feathers therefore we used published  
242 values for ring-billed gull *L. delawarensis* feathers ( $0.2 \pm 1.3$  ‰ for carbon and  $3 \pm 0.2$  ‰ for  
243 nitrogen, Hobson & Clark 1992).

244

#### 245 **Environmental variables**

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

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

261 point on a 200 m grid the nearest distance to land along 16 equal angular sectors of 22.5°  
262 are measured and the sum of all wave fetch values from the 16 angular sectors within a 200  
263 m grid cell are calculated ('fetchsum'). A low wave fetch value reflects a more sheltered  
264 intertidal habitat, with short distances to the nearest land mass, whilst high wave fetch  
265 values reflect an exposed coastline, with greater distances to the nearest land mass. Rocky  
266 shorelines with low wave fetch support a greater abundance and diversity of potential  
267 intertidal prey species (Burrows et al. 2012). For the analysis we averaged 'fetchsum' for all  
268 200 m coastal grid cells within the gulls' 50 km foraging range around the breeding colony  
269 based on wave fetch data obtained from Burrows (2009) using ArcMap 10.1 (ArcMap ver.10.  
270 ESRI, USA).

271 As herring gulls can also forage in terrestrial habitats; in particular on landfill sites, in  
272 built-up areas and on farmland (e.g. Pons 1992, Belant et al. 1993), we also included the  
273 extent of built-up area and farmland, the nearest distance to built-up areas and farmland,  
274 and the number of landfill sites within each colony's foraging range, as proxies for the  
275 potential availability of terrestrial/anthropogenic food. We classified farmland as  
276 agricultural land and improved grassland, and classified built-up area as urban and sub-  
277 urban areas; the total area and nearest distances to colonies were calculated from Landsat  
278 2007 (Morton et al. 2011) using ArcMap 10.1. The number of landfill sites within 50 km of  
279 each colony was obtained for Scotland from SEPA (2015) and for Northern Ireland from  
280 NIEA (Kelly, pers. comm.).

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

292 hatching period) and June (post-hatching period) in each year. For the analysis, the mean  
293 values of SST and chlorophyll a concentration within 50 km of each colony were used. The  
294 between-site variability in SST was low (CV = 10.2%) with site-specific values ranging from  
295 8.94 to 12.08°C, but was higher for chlorophyll a (CV = 62.6%) ranging from 2.39 to 13.31  
296 mg/m<sup>3</sup>).

297

## 298 **Demographic traits**

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

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

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

332

### 333 **Statistical analysis**

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

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

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

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

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

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

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

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

408

## 409 **RESULTS**

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

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

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

421 Based on the herring gull pellet samples, significant spatial variation in resource use  
422 occurred among colonies (Fig. 3) for the frequency of occurrence of offshore items ( $F_{5,15} =$   
423  $7.53$ ,  $p < 0.001$ ,  $R^2 = 0.68$ ); intertidal items ( $F_{5,15} = 18.29$ ,  $p < 0.001$ ,  $R^2 = 0.85$ ) and terrestrial  
424 items ( $F_{5,15} = 3.19$ ,  $p = 0.028$ ,  $R^2 = 0.41$ ). There were no significant interactions between the  
425 three resource categories and year or breeding stage ( $p > 0.10$ ). Colonies differed in the  
426 proportion of offshore food items with birds from Pladda using significantly more offshore  
427 resources than all other colonies (post-hoc multiple comparisons:  $p < 0.002$ ). Intertidal food  
428 items were more common on Oronsay, Jura and Strangford than all other colonies (post-hoc  
429 multiple comparisons:  $p < 0.005$ ). However, in all colonies, except Jura, the most consumed  
430 resources come from terrestrial foraging habitats with Jura having significantly lower use of  
431 terrestrial resources than all other colonies (post-hoc multiple comparisons:  $p < 0.03$ ).

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

437 The within-colony consistency repeatability ( $R_c$ ) of the proportion of marine  
438 (intertidal and offshore pooled) and terrestrial food types found in the pellets of the eight  
439 colonies sampled during both breeding stages of 2013 and 2014 was high for marine food  
440 types ( $R_c = 0.87$ , 95% CI:  $0.54 - 0.96$ ,  $p = 0.002$ ) but less so for terrestrial food types ( $R_c =$   
441  $0.39$ , 95% CI:  $0.00 - 0.76$ ,  $p = 0.05$ ). As expected, there was a negative correlation between  
442 the proportion of marine and terrestrial items in the diet ( $r = -0.85$ ,  $p < 0.001$ ). As the  
443 estimated use of marine resources by herring gulls from the pellets is consistent across



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

446

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

448 The use of intertidal resources by herring gulls was higher in colonies with lower average  
449 wave fetch within their foraging range ( $\chi^2_1 = 8.55$ ,  $p = 0.004$ ,  $R^2_{\text{GLMM}(m)} = 0.58$ , Fig. 5A).

450 There was no significant relationship between the use of offshore resources and the two  
451 proxies for conditions in the marine environment (Chlorophyll a:  $p = 0.316$ ; SST:  $p = 0.751$ ).

452 Investigating the terrestrial environmental variables, the proportion of marine resources  
453 (offshore and intertidal) in pellets decreased the closer the colony was located to a built-up  
454 area ( $\chi^2_1 = 4.92$ ,  $p = 0.027$ ,  $R^2_{\text{GLMM}(m)} = 0.43$ , Fig. 5B). We found no significant relationship  
455 with the nearest distance to farmland ( $p = 0.56$ ) or with the amount of farmland within 50  
456 km of the colony ( $p = 0.44$ ). Neither year nor breeding stage explained variation in resource  
457 use in any of the models ( $p > 0.10$ ).

458

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

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

468

#### 469 **DISCUSSION**

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

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

482         Based on pellet data, the herring gulls within our study area fed on a wide variety of  
483 food items from different foraging habitats both within and between colonies. Breeding  
484 herring gulls predominantly foraged on terrestrial food sources, except for one colony  
485 (Jura). Terrestrial food items consumed were mainly grain and terrestrial invertebrates, or  
486 terrestrial feeding was indicated by the presence of vegetation and anthropogenic refuse  
487 such as plastic, foil and glass within the pellets. The marine items within the gulls' diets  
488 mostly comprised of intertidal invertebrates. Resources from offshore habitats were  
489 typically the least frequent food found in the pellets, and consisted of Nephrops and several  
490 benthic fish species, predominantly gadoids, which were most likely obtained from local  
491 fishery activities. This mix of resources is typical for breeding herring gulls (Harris 1965,  
492 Götmark 1984, Pons 1992, Kubetzki & Garthe 2003). However, diet data from pellets are  
493 likely biased towards prey with indigestible hard parts (Barrett et al. 2007, Karnovsky et al.  
494 2012), with the majority of prey items from terrestrial and intertidal foraging habitat being  
495 characterised by such hard parts. Although fish may be softer, more digestible prey they still  
496 contain indigestible otoliths, and vertebrae that can indicate that fish had been consumed,  
497 however consumption of fish may therefore be under-represented in our pellet samples.

498         The stable isotope data provided a lower taxonomic resolution than the pellet data  
499 and, within our data, it was not possible to distinguish between the carbon and nitrogen  
500 isotope values of intertidal and offshore resources. In future analyses including additional  
501 isotopes, specifically sulphur, may allow intertidal and offshore resources to be  
502 distinguished (Connolly et al. 2004, Bond & Jones 2009, Ramos et al. 2009, Hobson et al.  
503 2015). Nonetheless, the two methods gave highly comparable results, despite the different  
504 biases of each method. Similarities between results from pellet and stable isotope analysis  
505 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

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

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

557         We found no relationship between the frequency of offshore resources in the gulls'  
558 diet and SST or Chlorophyll a, our proxies for marine productivity. This may be due to these  
559 proxies not accurately reflecting the potential availability of these resources to the gulls.  
560 However, in this study, it does not appear that the herring gulls foraged extensively on fish  
561 or other discard items within the region, namely Nephrops (Stratoudakis et al. 2001), given  
562 the low proportion of pellets containing offshore items (Fig. 3; offshore, making up over  
563 25% of the pellet, was only found in 9.22% of pellets (average per colony:  $6.86\% \pm 7.25$ ,  
564 range 0-21.5). The only colony where the proportion of offshore food items in the pellets  
565 reached over 14% was Pladda, due to the occurrence of Nephrops fisheries within the  
566 foraging range of this colony. From GPS tracking data of several individuals from four of the  
567 Scottish study colonies we know that birds spend very little time foraging offshore or near

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

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

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

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

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

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

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

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

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

657

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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.

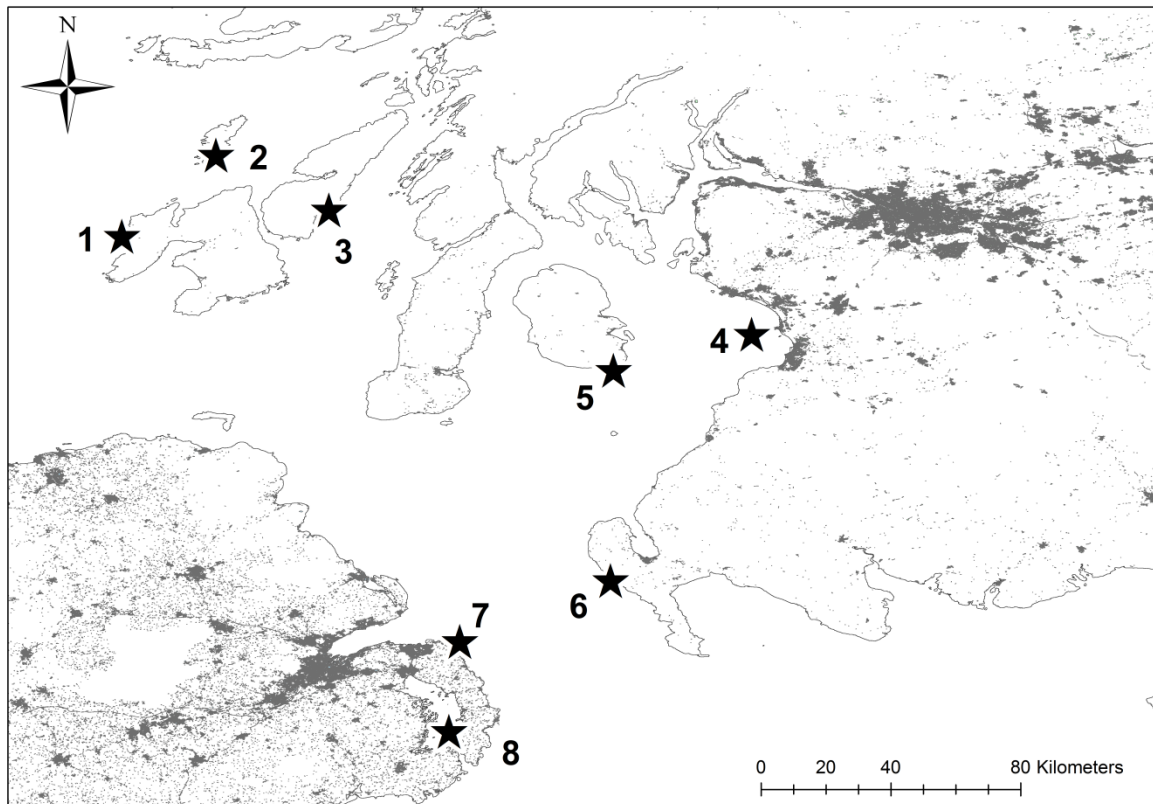




Fig. 2.

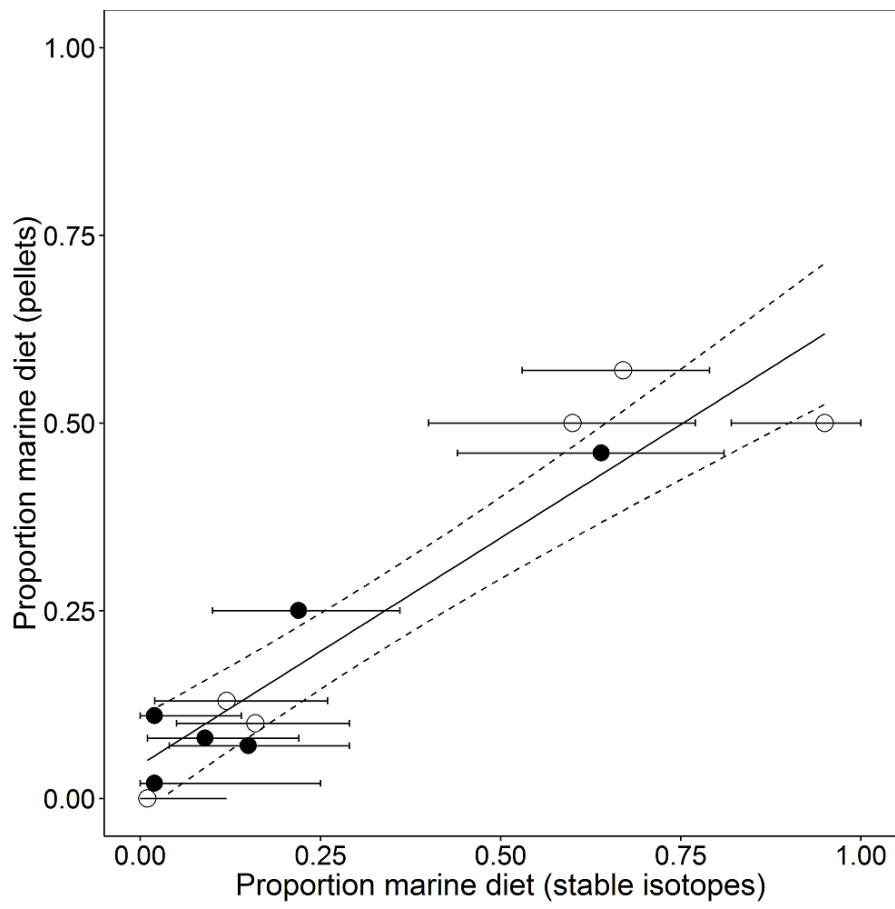


Fig. 3.

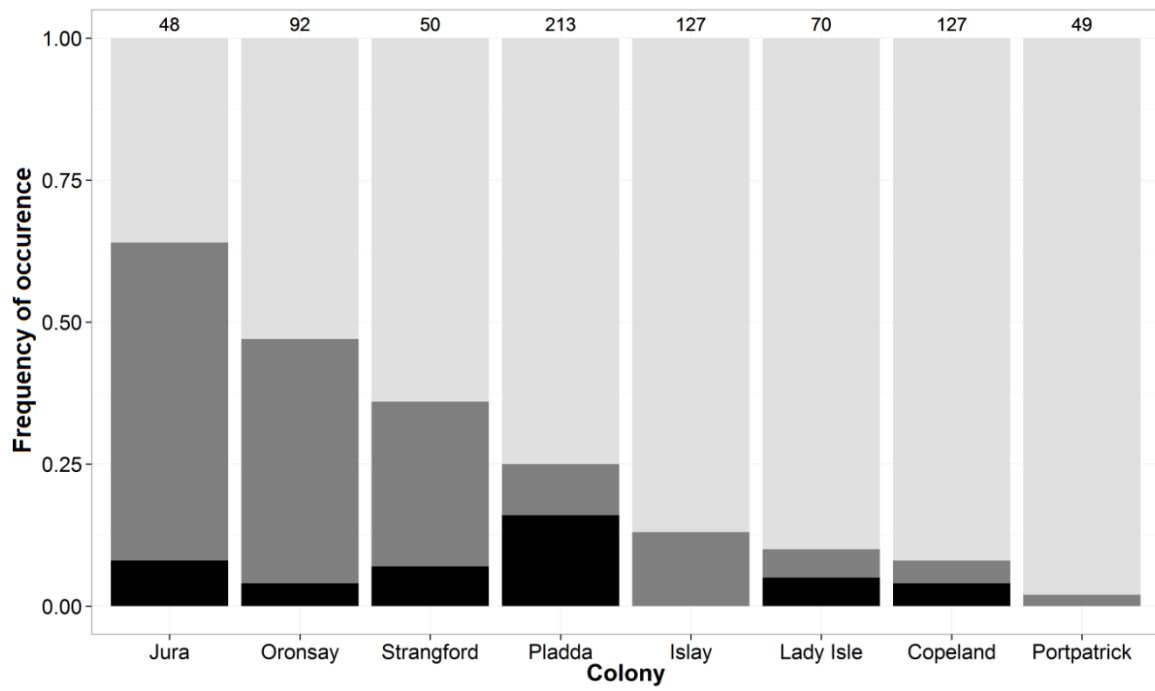


Fig. 4.

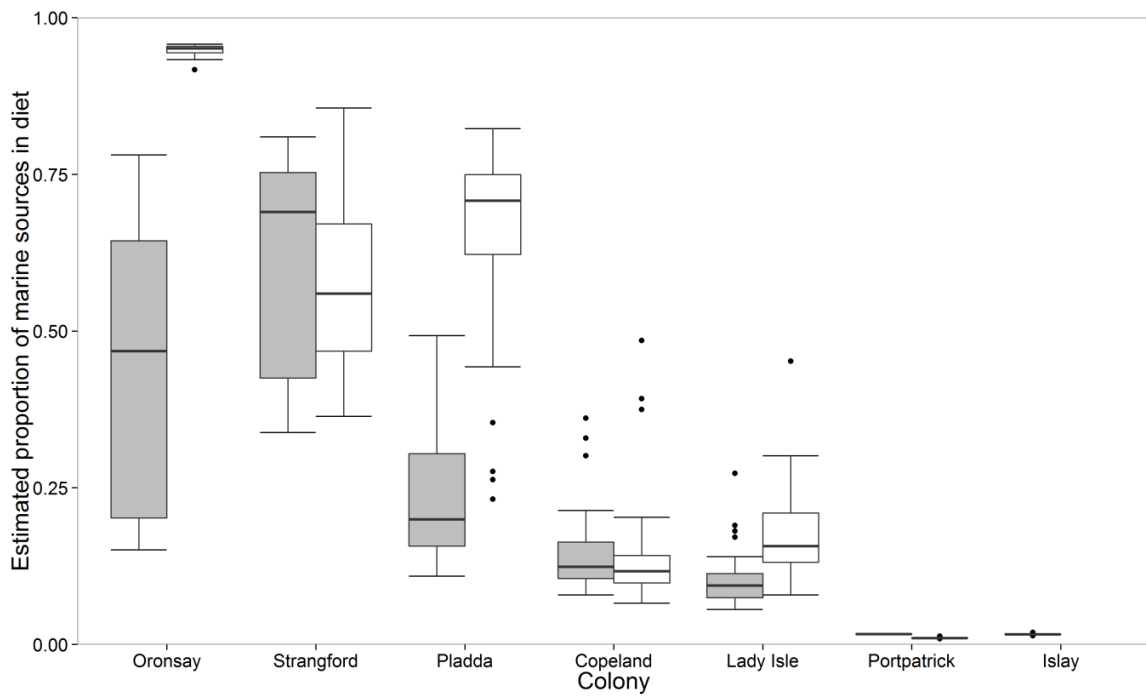
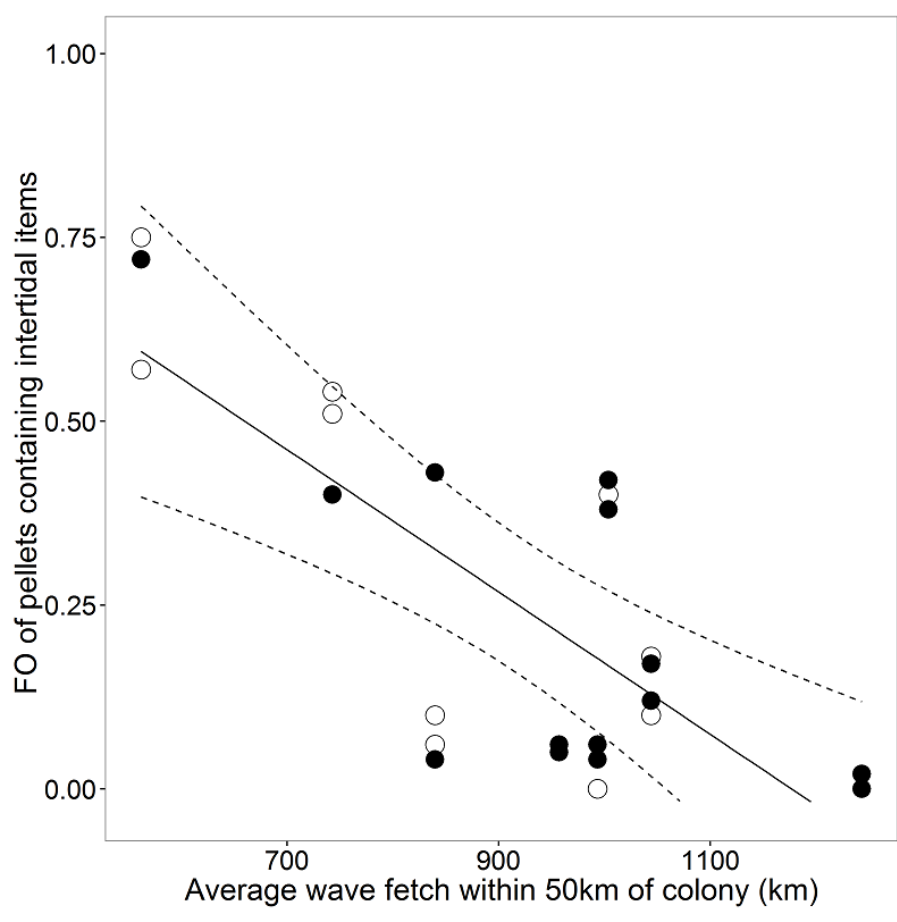


Fig. 5

A



B

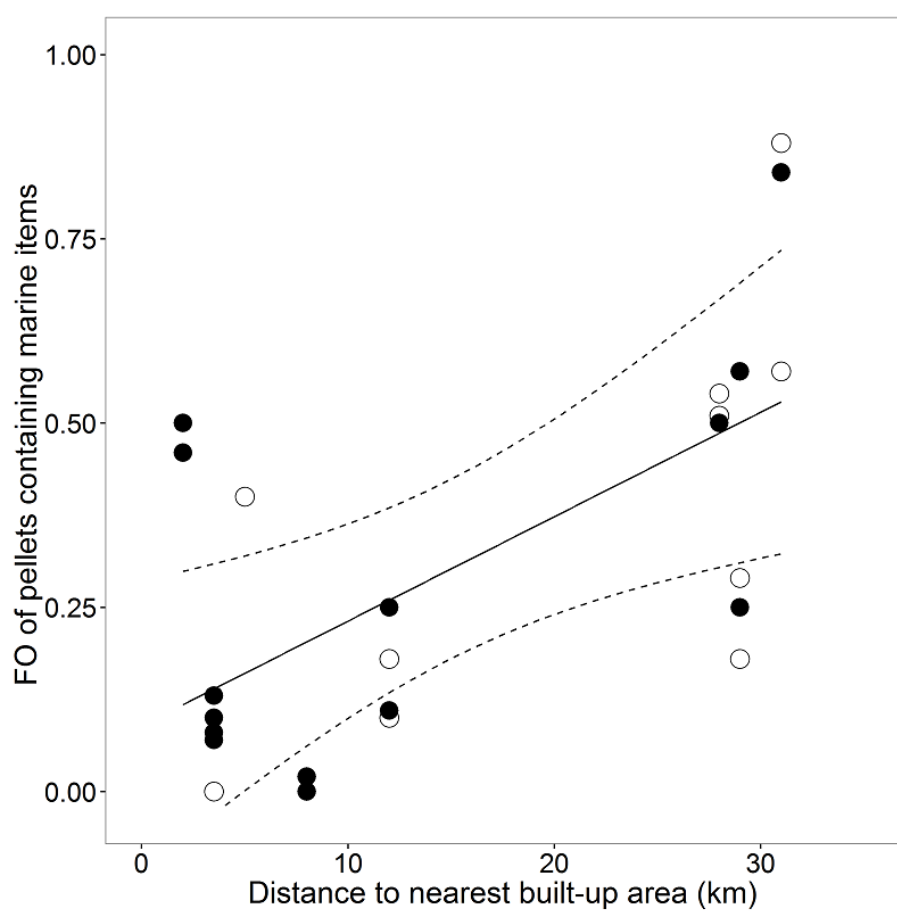
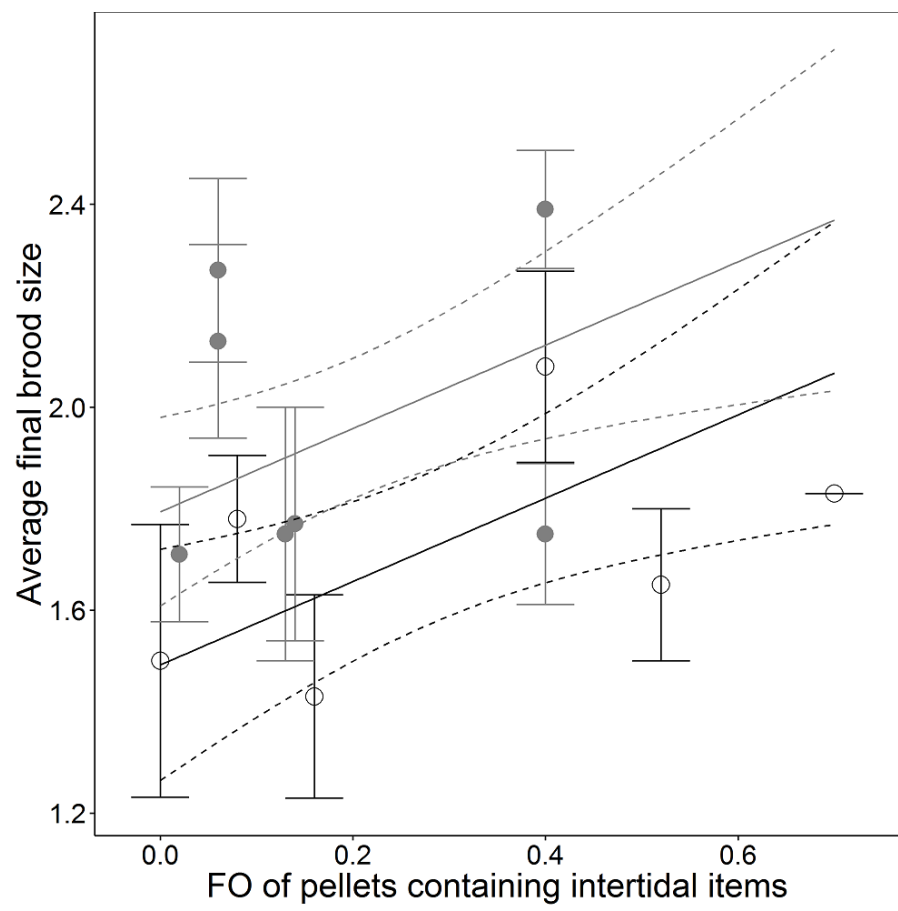


Fig. 6.



## 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.

<b>Food type</b>	<b>Mass (g)</b>	<b>Energy density kJ/g wet weight</b>	<b>Protein (%)</b>	<b>Lipid (%)</b>	<b>Water (%)</b>	<b>Reference</b>
<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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