

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

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**ABSTRACT:** Determining how resource use affects a species' demography is important, especially in habitats that 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 demographic consequences. The herring gull *Larus argentatus* is a 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 8 colonies over 2 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; however, birds from colonies located in areas with sheltered coastlines, which provide abundant and diverse marine food from the intertidal zone, foraged more on 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 intertidal resources. Therefore, when generalist species switch to alternative resources available to them within their foraging range, this may come at a cost of lower breeding success.

**KEY WORDS:** Anthropogenic impact · Coastal · Marine · Herring gull · *Larus argentatus* · Pellets · Stable isotopes

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## INTRODUCTION

Because organisms require adequate food resources for successful reproduction and survival, 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 that have a diverse diet with food sources that vary in quality, it is often difficult to identify 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 more efficiently by specialising on these more profitable prey items. 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 particularly relate to breeding success (Uttley et al. 1989, Pierotti & Annett 1990, van Heezik 1990, Suddaby & Ratcliffe 1997, Romano et al. 2006, Österblom et al. 2008). However, other studies have found no evidence that changes in food quality affects reproductive output, with a high abundance of food potentially compensating for its lower quality (Jodice et al. 2006, Hjærnquist & Hjærnquist 2010). Environmental change may additionally affect the relative profitability of available resources, altering the consumer's resource use, which can affect its demography 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 agri-

cultural 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, land-fill 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; *L. occidentalis*: Annett & Pierotti 1999). The long-term decline in *L. glaucescens* has been attributed to a dietary shift from marine to more terrestrial resources, mainly refuse (Blight et al. 2015, Hobson et al. 2015). 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). Furthermore, 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 investigated the environmental correlates of variation in resource use between colonies and its consequences on reproductive success in the herring gull *L. argentatus*. The gulls' resource use was established in multiple colonies across south-west Scotland and Northern Ireland over 2 breeding seasons using pellets and stable isotope analysis of chick feathers. We predicted that (1) the gulls from each colony would exploit the resources most readily available within their foraging range; and (2) that resource use would differentially affect breeding productivity. These results will help to clarify our understanding on the influence of consuming marine and terrestrial foods on the demography of a generalist seabird, which forages in coastal habitats impacted by humans.

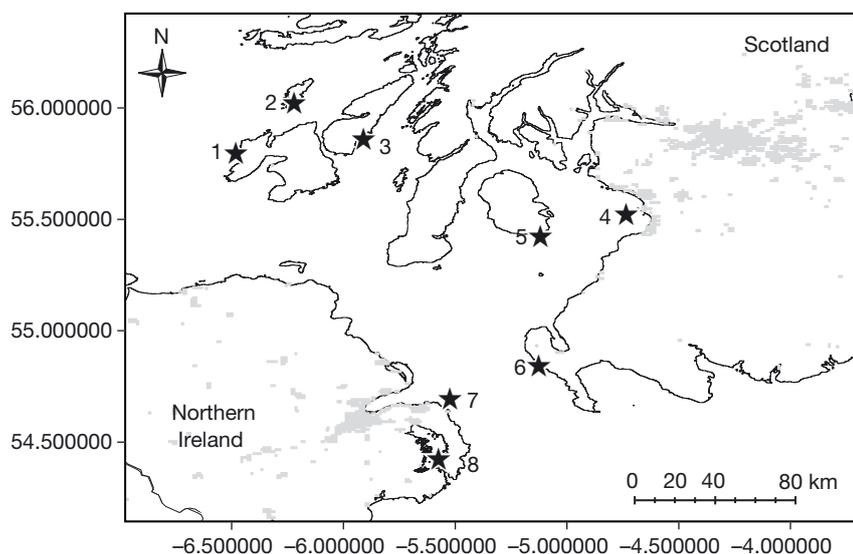


Fig. 1. Study region and location of 8 herring gull *Larus argentatus* breeding colonies across south-west Scotland and Northern Ireland. 1: Islay; 2: Oronsay; 3: Jura; 4: Lady Isle; 5: Pladda; 6: Portpatrick; 7: Copeland Islands; 8: Strangford Lough (Green and Round Islands). Grey shading shows built-up (urban and suburban) areas from Landcover 2000. Map grid reference system: GCS\_WGS\_1984

## MATERIALS AND METHODS

The herring gull *Larus argentatus*, a widespread colonial seabird, is a generalist, opportunistic forager. Traditionally foraging on marine resources (primarily in intertidal habitats), these birds now increasingly forage on terrestrial and anthropogenic resources (e.g. Hunt 1972, Götmark 1984, Pons 1992, Kubetzki & Garthe 2003). To investigate the relationship be-

tween the resources they use and their breeding success, we studied 8 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; 3 in the Southern Hebrides, 2 in Northern Ireland and 3 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 7 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). How-

ever, several studies have shown that diet estimates from pellets are comparable with those 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, but they are less taxonomically resolved (Bond & Jones 2009, Phillips et al. 2014). Where a population consumes a

Table 1. Number of pellet and feather samples collected from 8 herring gull *Larus argentatus* colonies (see Fig. 1) 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>a</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>b</sup>	0	5	24	26	55	13	13	26
Total	91	209	267	214	781	133	126	259

<sup>a</sup>All samples collected from Lighthouse Island; however, colony size is for the 3 Copeland Islands combined due to their close proximity

<sup>b</sup>Pellet samples at Strangford Lough were collected from 2 different sites (Round Island in 2013, Green Island in 2014) that are within 7 km of each other and treated as a single colony

variety of foods with similar stable isotope values, resource use needs to be inferred from stable isotopes cautiously. However, in our case stable isotopes can distinguish between the 2 main resources (marine and terrestrial anthropogenic) that we are interested in for herring gulls. Combining both methods therefore provides complementary information on resource use (Barrett et al. 2007).

### Pellet analysis

We visited each colony 1 to 6 times over the breeding season, to collect pellets, during the pre- and post-hatching period; between 17 May and 12 July 2013 and between 02 May and 13 July 2014. At each visit, we collected complete, fresh pellets from known herring gull territories during incubation (pre-hatching period) and chick rearing (post-hatching period). The timing of breeding was similar across all colonies, and the majority of clutches had hatched by 1 June; therefore, this date was used to distinguish between pre- and post-hatching samples. Territories were identified from nest watches aimed to identify the 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, 1 pellet was collected per territory and visit; when several pellets were col-

lected from the same territory on the same visit, they were combined into 1 pellet sample. As much as possible, pellets were collected from different areas on subsequent visits to minimise disturbance of birds and repeated sampling of the same territories. We collected a total of 300 pellet samples from 6 colonies in 2013 and 481 from 8 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 1 of 3 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, on 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 3 broad foraging habitats. 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

Table 2. Food items, or items that indicate the foraging habitat, identified from herring gull *Larus argentatus* pellets collected during the 2013 and 2014 breeding season from 8 colonies and the 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 is shown. Individual pellet samples may contain multiple food items

Foraging habitat	Food type	FO (%)	Indicator of foraging habitat	FO (%)
Terrestrial	Grain	65.30	Terrestrial vegetation	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 an unidentified wrasse species

period, i.e. whether samples were collected during incubation (pre-hatching: 02 to 31 May) or chick rearing (post-hatching: 1 June 13 July). For 120 pellet samples (15% of total), 2 food items were scored as above 25% and 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 <1 wk old to reflect the resource use of females during egg formation, with nutrients passed into the egg being incorporated into the chicks' down. Feathers from chicks older than 1 wk, that had grown since hatching, were collected to reflect the resources the adults bring back during chick rearing (Klaassen et al. 2004). In chicks older than 1 wk, 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 1 chick was sampled, was homogenised; therefore, all feathers from chicks from the same brood were collated as 1 sample. We collected 133 down samples from 7 colonies, and 126 chick feather samples from 6 colonies (Table 1).

Prior to stable isotope analyses, all feather material was washed in liquid detergent (Ecover<sup>TM</sup>) 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

Table 3. Stable isotope values ( $\pm$  SD) of marine and terrestrial food sources obtained during the 2014 herring gull *Larus argentatus* breeding season to use as reference values in the stable isotope mixing models

Food item	Category	Samples	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
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	Offshore	11	-17.62 $\pm$ 0.65	14.46 $\pm$ 0.83
Blenidae spp.		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</i> spp.		1	-15.96	14.03
Unidentified spp. <sup>a</sup>		2	-17.29 $\pm$ 0.37	15.13 $\pm$ 0.13
<i>Nephrops norvegicus</i>	Offshore	6	-17.41 $\pm$ 0.36	13.08 $\pm$ 2.08

<sup>a</sup>Unidentified fish from chick regurgitates

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 2 roughly equal sub-samples. From 1 sub-sample we extracted lipids using a Soxhlet apparatus with a 2:1 chloroform:methanol mixture until the solvent ran clear, indicating that all lipids were extracted.  $\delta^{13}\text{C}$  values were taken from these lipid-extracted samples. As  $\delta^{15}\text{N}$  can be altered by the lipid extraction,  $\delta^{15}\text{N}$  values were taken from the non-lipid extracted samples (Yurkowski et al. 2015). Dried feather and prey samples were homogenised and weighed (mass between 0.7 and 0.8 mg) into tin capsules before being combusted and analysed by continuous-flow isotope ratio mass spectrometry (Costech Elemental Analyser linked to a Thermo Finnigan Delta Plus XP Mass Spectrometer) at the NERC Life Sciences Mass Spectrometry Facility, East Kilbride. Stable isotope values 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  $\pm 0.09\text{‰}$  for  $\delta^{13}\text{C}$  and  $\pm 0.12\text{‰}$  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 5 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. Eider down feathers were processed and analysed as the herring gull feathers.  $\delta^{13}\text{C}$  did not vary between colonies ( $F_{5,15} = 0.34$ ,  $p = 0.88$ ). 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 differed between the terrestrial and 2 marine food sources (intertidal and offshore) but not between the intertidal and offshore sources (ANOVA:  $F_{2,5} = 38.21$ ,  $p < 0.001$ ; post hoc Tukey HSD pairwise 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 1 marine resource and considered only the 2 sources (marine and terrestrial) for the mixing model. As isotopic discrimination factors are not available for herring gull feathers, we used published values for ring-billed gull *Larus 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 use. Environmental variables were extracted for a foraging range of 50 km around each study colony corresponding to the mean 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 4 colonies in our study region where we observed maximum foraging trips of up to 44 km from the colony (N. O'Hanlon unpubl. data).

We obtained proxies of resource availability reflecting the 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  $22.5^\circ$  is measured and the sum of all wave fetch values from the 16 angular sectors within a 200 m grid cell is 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 2012). For the analysis, we determined the mean '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).

Herring gulls 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). Therefore, we 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 suburban areas; the total area and nearest distances to colonies were calculated from Landcover 2000 (Fuller et al. 2002) 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 the Northern Ireland Environment Agency (NIEA) (E. Kelly pers. comm.).

The main source of food from offshore habitats is likely from fisheries, although this food type was rarely consumed in our study (Table 2). 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 used here. Instead, as a proxy for vari-

ability in conditions in the offshore marine environment, we obtained estimates of sea surface temperature (SST) and chlorophyll *a* (chl *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 chl *a* concentration acts as a proxy for primary productivity at the base of the marine food web (Huot et al. 2007). SST ( $^{\circ}\text{C}$ , from the 11  $\mu$  night-time option) and chl *a* concentration ( $\text{mg m}^{-3}$ ) composites were extracted from Aqua MODIS at 4 km resolution (<https://oceancolor.gsfc.nasa.gov/cgi/13>) separately for May (pre-hatching period) and June (post-hatching period) in each year. For the analysis, the mean values of SST and chl *a* concentration within 50 km of each colony were used. The between-site variability in SST was low ( $\text{CV} = 10.2\%$ ), with site-specific values ranging from 8.94 to 12.08 $^{\circ}\text{C}$ , but was higher for chl *a* ( $\text{CV} = 62.6\%$ ), ranging from 2.39 to 13.31  $\text{mg m}^{-3}$ .

### 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 mean size of broods of chicks of at least 3 wk old; chicks that reach that age are likely to successfully fledge (Bolton et al. 1991). The number and age of chicks were determined from nest watches in each colony (mean of  $16 \pm 9$  SD 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 3 wk old, we took this date into consideration as well as noting the size and feather development of chicks that were of a known age and referring to published information on herring gull chick development (Kadlec et al. 1969). In each colony, multiple nest watches of 3 h were carried out generally every 10 to 14 d throughout the chick-rearing period between 1 June and 16 July 2013 and between 3 June and 4 July 2014 (for individual colony visit dates, see Table S1 in the Supplement at [www.int-res.com/articles/suppl/m574p193\\_supp.pdf](http://www.int-res.com/articles/suppl/m574p193_supp.pdf)). Watches were made from specific vantage points allowing up to 24 focal nests to be observed simultaneously whilst not causing disturbance to the birds, using an observation blind where necessary. Focal nests were selec-

Table 4. Demographic information for target herring gull *Larus argentatus* 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 size is from the most recent colony count (year of count in parentheses) and is given as apparently occupied nests (AON). The number of nests indicates the nests from which the final chick brood size was estimated, with the proportion of total nests with known final chick brood sizes from the total AON of each colony in parentheses

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

<sup>a</sup>Colony size is that of 3 Copeland islands together due to their close proximity  
<sup>b</sup>Colony size is the mean of Green Island (115) and Round Island (265). Final brood size is the mean across both islands

ted 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 1 chick 3 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 Table S2 in the Supplement), we found that the brood size of successful nests was significantly posi-

tively 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 3 wk 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 2-way analysis of variance (ANOVA), with separate models for offshore, intertidal and terrestrial food resources. The 2 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 et al. 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 1 model, and to allow us to investigate the 3 main resource types individually, we ran 3 separate models. The first model reflected conditions in the offshore marine environment (chl *a* concentration and SST); the second reflected the intertidal environment (wave fetch); and the third included variables reflecting the availability of terrestrial resources (distance to and 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 > 3 and were therefore excluded, as both correlated to the nearest distance to built-up area, and so 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. Because the majority of pellets contained 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 mean 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 separate models 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 (no pellet data was available for Portpatrick in 2013). Resource use of pre- and post-hatching stages were pooled as they did not differ (see 'Results'). To calculate the effect sizes of marine resource use on mean brood size, 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. 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 2-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 (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 of 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 ( $F_{5,15} = 7.53$ ,  $p < 0.001$ ,  $R^2 =$

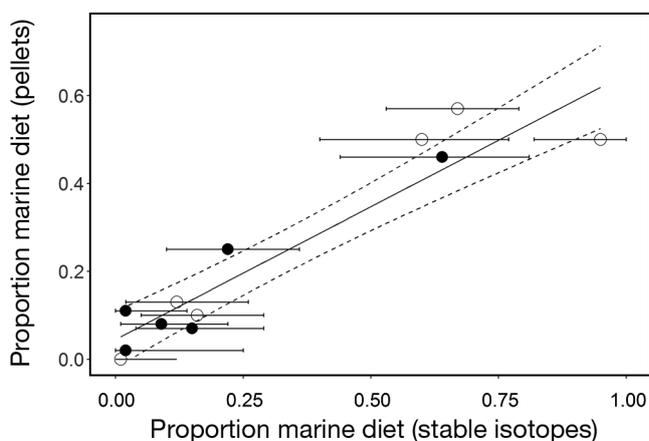


Fig. 2. Relationship between the proportion of use of marine (intertidal and offshore, see Table 2) sources by herring gulls *Larus argentatus* in 2014 estimated as mean frequency of occurrence (FO) from pellets (vertical axis) and the median proportion of marine sources based on stable isotope analysis of feather samples (with 95% Bayesian credible intervals given by MixSIAR (horizontal axis, see 'Materials and 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

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 3 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 were obtained 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 use of marine resources (pooling offshore and intertidal) 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 2 colonies, Oronsay and Pladda (post hoc multiple comparisons:  $p < 0.001$ ).

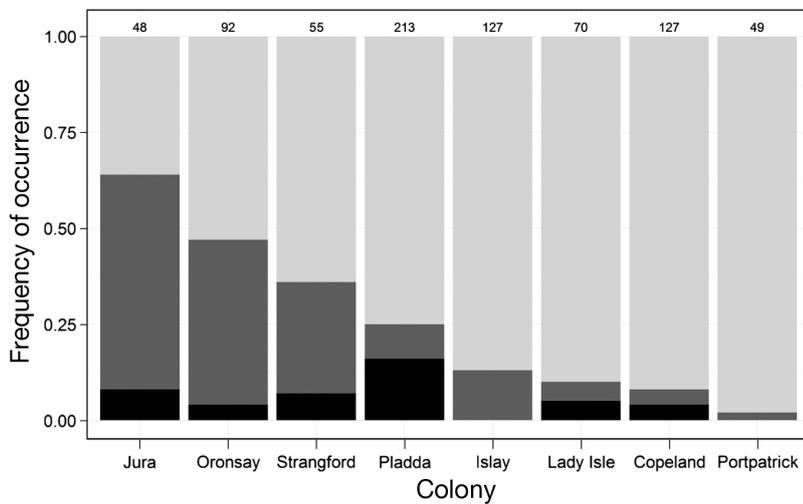


Fig. 3. Frequency of occurrence of herring gull *Larus argentatus* pellets containing offshore (black), intertidal (dark grey) and terrestrial (light grey) food items, pooled for years and breeding stages, as no differences between years or breeding stages were found. The numbers of pellet samples collected in each colony are given above the bars. Colonies are ordered from left to right in decreasing frequency of occurrence of marine (offshore and intertidal combined) food items

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 8 colonies, sampled during both breeding stages of 2013 and 2014, was high for marine food items ( $R_c = 0.87$ , 95% CI: 0.54–0.96,  $p = 0.002$ ) but lower for terrestrial food items ( $R_c = 0.39$ , 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.

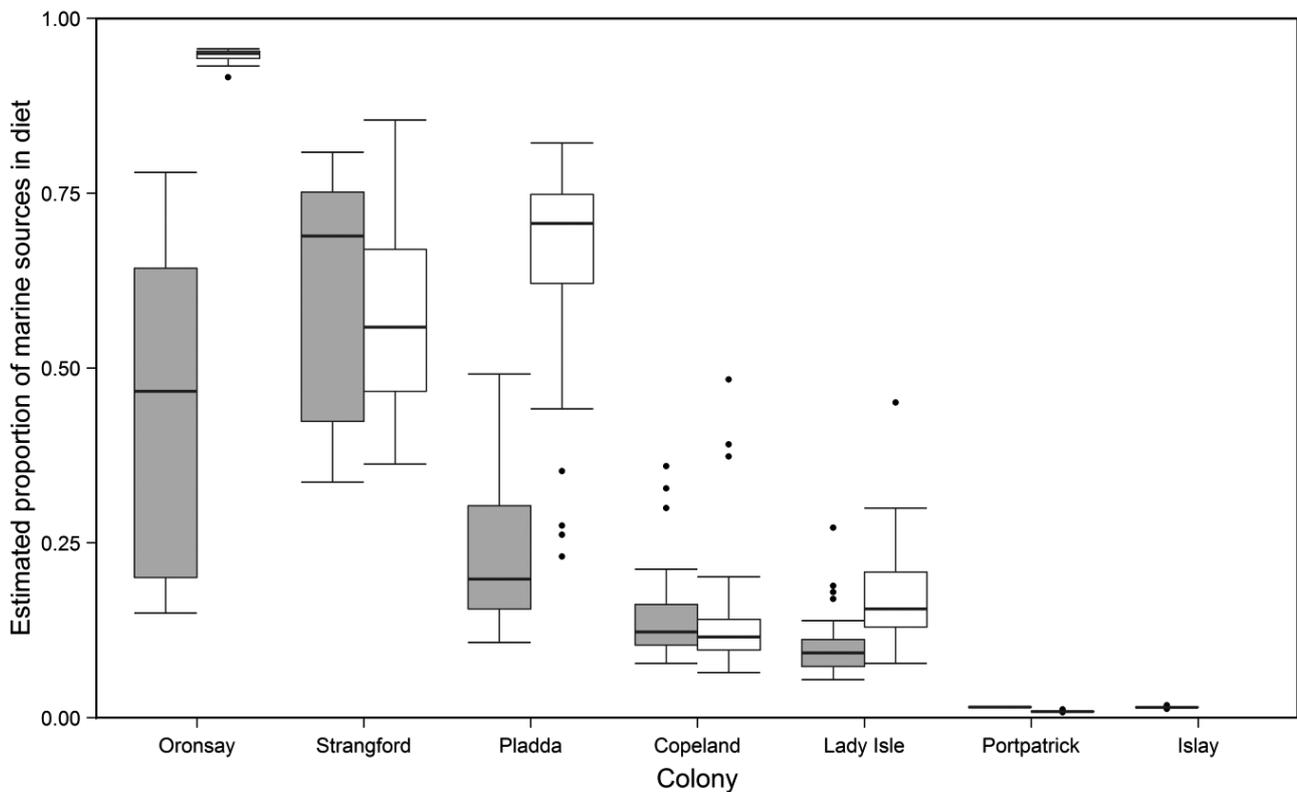


Fig. 4. Estimated proportion of herring gull *Larus argentatus* diet comprised of marine sources (offshore and intertidal resources combined) based on stable isotope analysis of feather samples during the pre- (grey) and post-hatching period (white) over the 2014 breeding season, estimated by MixSIAR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

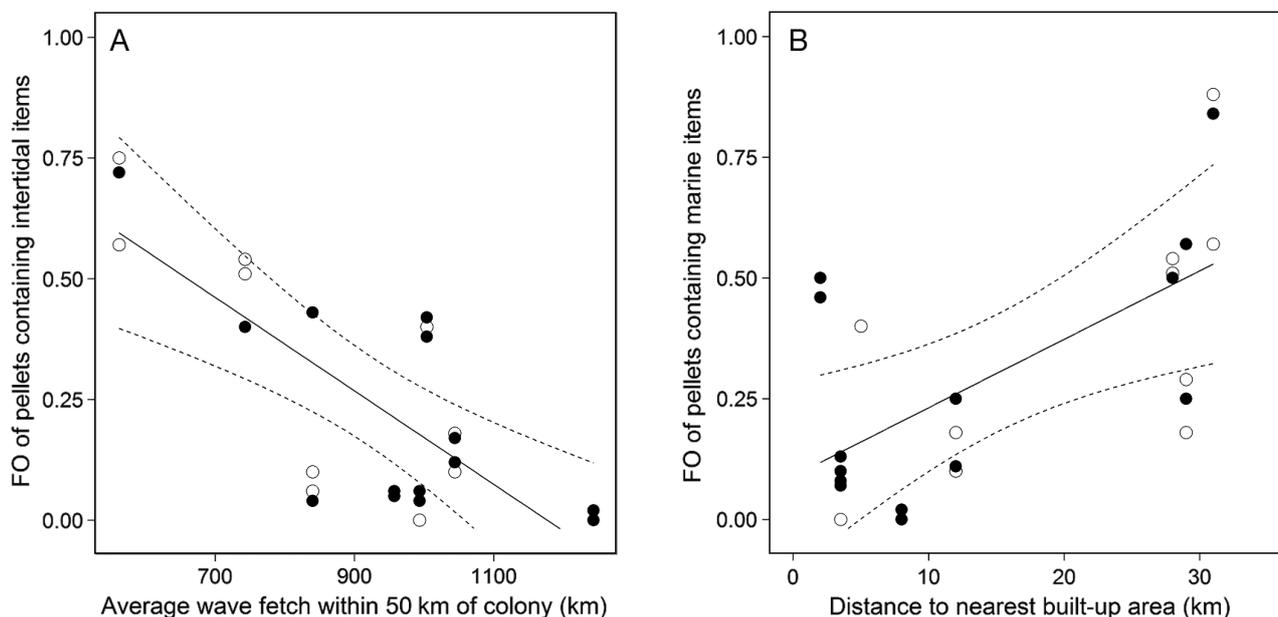


Fig. 5. Relationship between the frequency of occurrence (FO) of intertidal items in pellets collected from each herring gull *Larus argentatus* colony during the 2013 (open circles) and 2014 (filled circles) breeding season and (A) the mean wave fetch within the breeding colony's foraging range and (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

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

The use of intertidal resources by herring gulls was higher in colonies with lower mean 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 2 proxies for conditions in the marine environment (chl *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 breeding success

The frequency of occurrence of intertidal items in pellets, colony size and year all influenced final brood size (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 ( $\pm$  SD) brood sizes were larger in 2014 ( $1.97 \pm 0.29$  chicks) than 2013 ( $1.71 \pm 0.24$  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 showed that spatial variation in resource use is associated with variation in one measure of herring gull demography, viz. 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, consumed more intertidal resources, whilst colonies closer to built-up areas consumed more terrestrial resources, compared to colonies at more exposed coasts and farther away from built-up areas, respectively. Consuming a higher proportion of intertidal food resources was positively associated with the gulls' demogra-

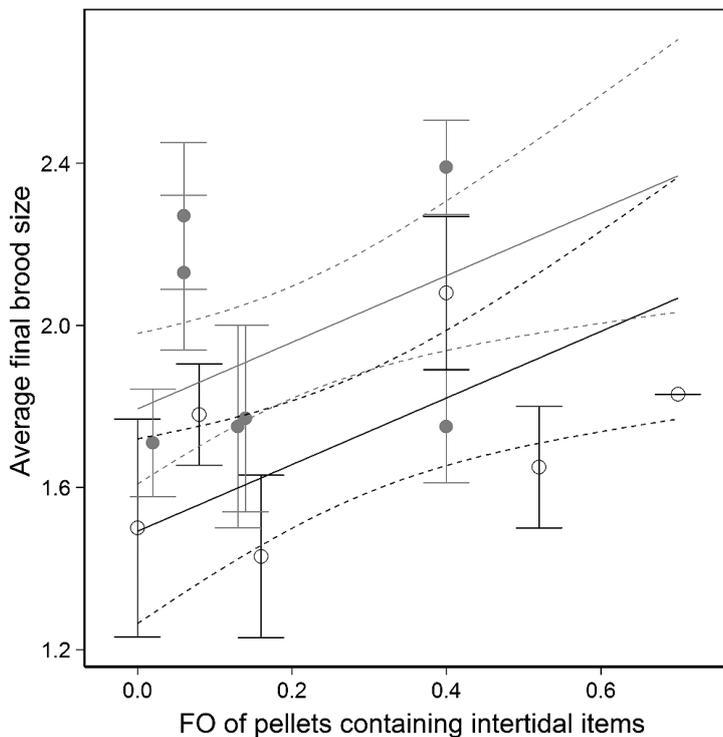


Fig. 6. Herring gull *Larus argentatus* colonies that had a higher frequency of occurrence (FO) of pellets containing intertidal items had larger mean ( $\pm$  SD) brood sizes in both 2013 (open circles) and 2014 (filled circles), with mean brood sizes being larger in 2014 than 2013. Pellet and final brood size information was available for 6 colonies (with no pellet data available for Lady Isle and Portpatrick) in 2013 and 7 colonies (with no brood size data available for Jura) in 2014. Solid lines indicate the trend lines with 95% confidence intervals (dashed lines) predicted from a mixed effect model

phy, 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 1 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 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 ob-

tained 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, which would indicate that fish had been consumed; however, consumption of fish may have been 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 2 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, 2011, 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 snapshot 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, underestimate 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 the outputs of mixing models (Bond & 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, although 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 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 fish typically providing the higher protein and fat content (see Table S3 in the Supplement), required by chicks to build muscle and fuel growth. However, being soft-bodied, fish was the most likely food item to be missed from pellets, although not in the stable isotope data. This might explain the higher bias towards terrestrial resources in the post-hatching period by the pellet data and why these pellet data did not show an effect of breeding stage on marine resource use. It is possible 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 located near *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 strate-

gies. It may also be attributed to variation in the availability of preferred food (Whitfield et al. 2009), or it might 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 chl *a*, our proxies for marine productivity. This may be due to these proxies not accurately reflecting the potential availability of offshore 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 [mean 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 4 of the Scottish study colonies, we know that birds spend very little time foraging offshore or near ports, where they could have scavenged 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 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 was not captured by wave fetch and could explain further variation in intertidal resource use between colonies.

Herring gull colonies that consumed a higher proportion of intertidal resources had larger broods of chicks of at least 3 wk 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; the cost of capturing, handling and transporting it back to the nest; and the assimilation efficiency of extracting the energy and nutrients

from that resource. All of these characteristics may affect the survival of chicks. The quantity and quality of provisioned food can determine whether a chick receives adequate nutrition or will fail due to starvation. The time parents spend away from the nest foraging can also affect chick survival through the risk of conspecific predation when they are left unattended (Hunt & McLoon 1975). Our data cannot distinguish between the different potential causes of mortality.

This positive association between intertidal resource use and breeding success in herring gulls is 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 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 chicks. Herring gulls foraging on intertidal resources may benefit from highly predictable tidal cycles, but neither the energy density nor composition of macro-nutrients of intertidal invertebrates are more favourable than alternative food resources (Table S3). Other micro-nutrients may differ between food resources, which could make intertidal invertebrates particularly suitable for breeding gulls; for example, calcium is important for chick growth (Annett & Pierotti 1989, Noordhuis & Spaans 1992) and is particularly low in grain, the main terrestrial food item consumed (65.30% of pellets containing >25% of grain). Furthermore, grain is relatively low in energy and lipids in comparison to other terrestrial items and to intertidal prey. As previously mentioned, 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 (Table S3) 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, possibly because this resource was not particularly available within the region. Therefore, in 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, particularly where they were located close to built-up areas, potentially because they were attracted by these re-

sources, 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.

We do not have specific foraging rates, processing costs or assimilation efficiencies for the resources within this study. 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 also be underestimated in the pellet data (Coulson & Coulson 2008). Unfortunately, there is no information on the herring gulls' foraging rate on grain. Another point to consider when comparing different diets is the consumer's assimilation efficiency that differs between type of food ingested, but for a given type of food is similar in most bird species (Castro et al. 1989). Assimilation efficiencies are similar between the main marine (intertidal invertebrates with a mean assimilation efficiency of 85%, Kersten & Piersma 1987) and the main terrestrial food type (grain with a mean value of 81%, Green 1978). Less information is available on the assimilation efficiency of different anthropogenic, terrestrial items. Most food items generally have an average assimilation efficiency of around 75%, but these values are considerably lower for some terrestrial items, such as 37% for plants and 41% for fruits (Castro et al. 1989). Therefore, it may be that intertidal prey can be more efficiently assimilated than alternative anthropogenic items, meaning that herring gulls can obtain more energy and nutrients from intertidal resources, which further benefits breeding success.

It may also be that the trips of gulls foraging in terrestrial habitat, and particularly in built-up areas, were longer and more energetically expensive, or were long in duration 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 landfills may be less predictable than they were previously due to management actions to discourage foraging by opportunistic species such as gulls (Baxter & Allan 2006, Cook et al. 2008). We did include distance to nearest farm-

land 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 be worth the effort. Nearest distance to farmland did not play a role, as all colonies were in close proximity to this resource. Reduced feeding rates and longer, or farther, 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 foraging habitats to herring gulls.

In this study, we also found that final brood size was higher in our larger study colonies, potentially suggesting that density-dependent processes were occurring. Typically, reduced productivity is observed in larger colonies due to density-dependent resource depletion; competition for local resources; larger groups being more susceptible to conspecific nest predation; or disease (Hunt et al. 1986). However, it may be that in 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, anthropogenic food. This result may help in understanding the recent declines observed in herring gull numbers across the UK (Mitchell et al. 2004, Eaton et al. 2015).

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#### LITERATURE CITED

- Alverson DL (1992) Commercial fisheries and the Steller sea lion (*Eumetopias jubatus*): the conflict arena. *Rev Aquat Sci* 6:203–256
- Andersson M, Gotmark F, Wiklund CG (1981) Food information in the black-headed gull, *Larus ridibundus*. *Behav Ecol Sociobiol* 9:199–202
- ✦ Annett CA, Pierotti R (1989) Chick hatching as a trigger for dietary switching in the western gull. *Colon Waterbirds* 12:4–11
- ✦ Annett CA, Pierotti R (1999) Long-term reproductive output in western gulls: consequences of alternate tactics in diet choice. *Ecology* 80:288–297
- ✦ Barrett RT, Camphuysen KCJ, Anker-Nilssen T, Chardine JW and others (2007) Diet studies of seabirds: a review and recommendations. *ICES J Mar Sci* 64:1675–1691
- ✦ Barton K (2012) MuMIn: multi-model inference. R package version 1.13.4. <http://cran.r-project.org/package=MuMIn>
- ✦ Bates D, Maechler M, Bolker B, Walker S (2014) lme4: linear mixed-effects models using Eigen and S4. R Package version 1:1–6. <http://CRAN.R-project.org/package=lme4>
- ✦ Baxter AT, Allan JR (2006) Use of raptors to reduce scavenging bird numbers at landfill sites. *Wildl Soc Bull* 34: 1162–1168
- ✦ Belant JL, Seamans TW, Gabrey SW, Ickes SK (1993) Importance of landfills to nesting herring gulls. *Condor* 95: 817–830
- ✦ Biro PA, Stamps JA (2015) Using repeatability to study physiological and behavioural traits: ignore time-related change at your peril. *Anim Behav* 105:223–230
- Birt VL, Birt TP, Goulet D, Cairns DK, Montevecchi WA (1987) Ashmole's halo: direct evidence for prey depletion by a seabird. *Mar Ecol Prog Ser* 40:205–208
- Blight LK, Hobson KA, Kyser TK, Arcese P (2015) Changing gull diet in a changing world: a 150-year stable isotope ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) record from feathers collected in the Pacific Northwest of North America. *Glob Change Biol* 21: 1497–1507
- ✦ Bolton M, Monaghan P, Houston DC (1991) An improved technique for estimating pectoral muscle protein condition from body measurements of live gulls. *Ibis* 133: 264–270
- ✦ Bond AL, Diamond AW (2011) Recent Bayesian stable-isotope mixing models are highly sensitive to variation in discrimination factors. *Ecol Appl* 21:1017–1023
- Bond AL, Jones IANL (2009) A practical introduction to stable-isotope analysis for seabird biologists: approaches, cautions and caveats. *Mar Ornithol* 37:183–188
- ✦ Brousseau P, Lefebvre J, Giroux JF (1996) Diet of ring-billed gull chicks in urban and non-urban colonies in Quebec. *Waterbirds* 19:22–30
- ✦ Burger J, Gochfeld M (1983) Behavior of nine avian species at a Florida garbage dump. *Colon Waterbirds* 6:54–63
- ✦ Burrows MT (2009) Wave fetch model description. The Scottish Association for Marine Science, Argyll. [www.sams.ac.uk/michael-burrows/wave-fetch-model-description](http://www.sams.ac.uk/michael-burrows/wave-fetch-model-description) (accessed June 2014)
- ✦ Burrows MT (2012) Influences of wave fetch, tidal flow and ocean colour on subtidal rocky communities. *Mar Ecol Prog Ser* 445:193–207
- ✦ Burrows MT, Harvey R, Robb L (2008) Wave exposure indices from digital coastlines and the prediction of rocky shore community structure. *Mar Ecol Prog Ser* 353:1–12
- Camphuysen KCJ (1995) Herring gull *Larus argentatus* and lesser black-backed gull *L. fuscus* feeding at fishing vessels in the breeding season: competitive scavenging versus efficient flying. *Ardea* 83:365–380
- ✦ Castro G, Stoyan N, Myers JP (1989) Assimilation efficiency in birds: a function of taxon or food type? *Comp Biochem Physiol Part A Physiol* 92:271–278

- Cherel Y, Hobson KA, Hassani S (2005) Isotopic discrimination between food and blood and feathers of captive penguins: implications for dietary studies in the wild. *Physiol Biochem Zool* 78:106–115
- Cohen J (1988) *Statistical power analysis for the behavioral sciences*, 2<sup>nd</sup> edn. Erlbaum, New York, NY
- Connolly RM, Guest MA, Melville AJ, Oakes JM (2004) Sulphur stable isotopes separate producers in marine food-web analysis. *Oecologia* 138:161–167
- Cook A, Rushton S, Allan J, Baxter A (2008) An evaluation of techniques to control problem bird species on landfill sites. *Environ Manag* 41:834–843
- Coulson JC, Coulson BA (2008) Lesser black-backed gulls *Larus fuscus* nesting in an inland urban colony: the importance of earthworms (Lumbricidae) in their diet. *Bird Study* 55:297–303
- Crawley M (2007) *The R Book*. John Wiley & Sons, Chichester
- Davoren GK, Montevecchi WA (2003) Signals from seabirds indicate changing biology of capelin stocks. *Mar Ecol Prog Ser* 258:253–261
- Duffy DC, Jackson S, Cameron D (1986) Diet studies of seabirds: a review of methods. *Colon Waterbirds* 9:1–17
- Duhem C, Roche P, Vidal E, Tatoni T (2008) Effects of anthropogenic food resources on yellow-legged gull colony size on Mediterranean islands. *Popul Ecol* 50:91–100
- Eaton M, Aebischer N, Brown A, Hearn R and others (2015) Birds of conservation concern 4: the population status of birds in the UK Channel Islands and Isle of Man. *Br Birds* 108:708–746
- Evans RM (1982) Foraging-flock recruitment at a black-billed gull colony: implications for the information center hypothesis. *Auk* 99:24–30
- Fuller RM, Smith GM, Sanderson JM, Hill RA, Thomson AG (2002) The UK Land Cover Map 2000: construction of a parcel-based vector map from satellite images. *Cartogr J* 39:15–25
- Furness RW, Birkhead TR (1984) Seabird colony distributions suggest competition for food supplies during the breeding season. *Nature* 311:655–656
- Gibson D, Cardwell E, Zylich K, Zeller D (2015) Preliminary reconstruction of total marine fisheries catches for the United Kingdom and the Channel Islands in EEZ equivalent waters (1950–2010). Working Paper 2015-76. Fisheries Research Centre, University of British Columbia, Vancouver, BC
- Golet GH, Kuletz KJ, Roby DD, Irons DB (2000) Adult prey choice affects chick growth and reproductive success in pigeon guillemots. *Auk* 117:82–91
- Götmark F (1984) Food and foraging in five European *Larus* gulls in the breeding season: a comparative review. *Ornis Fenn* 61:9–18
- Green R (1978) Factors affecting the diet of farmland skylarks, *Alauda arvensis*. *J Anim Ecol* 47:913–928
- Grémillet D, Pichegru L, Kuntz G, Woakes AG, Wilkinson S, Crawford RJM, Ryan PG (2008) A junk-food hypothesis for gannets feeding on fishery waste. *Proc R Soc Lond B Biol Sci* 275:1149–1156
- Guillemette M, Ydenberg RC, Himmelman JH (1992) The role of energy intake rate in prey and habitat selection of common eiders *Somateria mollissima* in winter: a risk-sensitive interpretation. *J Anim Ecol* 61:599–610
- Harris MP (1965) The food of some *Larus* gulls. *Ibis* 107: 43–53
- Hjernquist B, Hjernquist MB (2010) The effects of quantity and quality of prey on population fluctuations in three seabird species. *Bird Study* 57:19–25
- Hobson KA, Clark RG (1992) Assessing avian diets using stable isotopes II: factors influencing diet-tissue fractionation. *Condor* 94:189–197
- Hobson KA, Piatt JF, Pitocchelli J, Piatt JF, Pitocchelli JAY (1994) Using stable isotopes to determine seabird trophic relationships. *J Anim Ecol* 63:786–798
- Hobson KA, Blight LK, Arcese P (2015) Human-induced long-term shifts in gull diet from marine to terrestrial sources in North America's coastal Pacific: more evidence from more isotopes ( $\delta^2\text{H}$ ,  $\delta^{34}\text{S}$ ). *Environ Sci Technol* 49:10834–10840
- Horton N, Brough T, Rochard JBA (1983) The importance of refuse tips to gulls wintering in an inland area of south-east England. *J Appl Ecol* 20:751–765
- Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biometric J* 50: 346–363
- Hunt GL Jr (1972) Influence of food distribution and human disturbance on the reproductive success of herring gulls. *Ecology* 53:1051–1061
- Hunt GL Jr, Hunt M (1973) Habitat partitioning by foraging gulls in Maine and Northwestern Europe. *Auk* 90: 827–839
- Hunt GL Jr, McLoon SC (1975) Activity patterns of gull chicks in relation to feeding by parents: their potential significance for density-dependent mortality. *Auk* 92: 523–527
- Hunt GL Jr, Eppley ZA, Schneider DC, Url S (1986) Reproductive performance of seabirds: the importance of population and colony size. *Auk* 103:306–317
- Huot Y, Babin M, Bruyant F, Grob C, Twardowski MS, Claustre H (2007) Does chlorophyll *a* provide the best index of phytoplankton biomass for primary productivity studies? *Biogeosci Discuss* 4:707–745
- Jennings S, Cogan SM (2015) Nitrogen and carbon stable isotope variation in northeast Atlantic fishes and squids. *Ecology* 96:2568
- Jodice PGR, Roby DD, Suryan RM, Irons DB and others (2006) Increased energy expenditure by a seabird in response to higher food abundance. *Mar Ecol Prog Ser* 306:283–293
- Johnson PCD (2014) Extension of Nakagawa & Schielzeth's R<sup>2</sup>GLMM to random slopes models. *Methods Ecol Evol* 5:944–946
- Kadin M, Österblom H, Hentati-Sundberg J, Olsson O (2012) Contrasting effects of food quality and quantity on a marine top predator. *Mar Ecol Prog Ser* 444:239–249
- Kadlec JA, Drury WH Jr, Onion DK (1969) Growth and mortality of herring gull chicks. *Bird-Banding* 40:222–233
- Karnovsky NJ, Hobson KA, Iverson SJ (2012) From lavage to lipids: estimating diets of seabirds. *Mar Ecol Prog Ser* 451:263–284
- Kersten M, Piersma T (1987) High levels of energy expenditure in shorebirds; metabolic adaptations to an energetically expensive way of life. *Ardea* 75:175–187
- Kim M, Furness RW, Nager RG (2010) Hatching asynchrony is constrained by parental nest attendance during laying. *Behav Ecol Sociobiol* 64:1087–1097
- Klaassen M, Baarspul T, Dekkers T, van Tienen P (2004) The relationship between carbon stable isotope ratios of hatchling down and egg yolk in black-headed gulls. *J Ornithol* 75:196–199
- Kubetzki U, Garthe S (2003) Distribution, diet and habitat

- selection by four sympatrically breeding gull species in the south-eastern North Sea. *Mar Biol* 143:199–207
- ✦ Lewis S, Sherratt TN, Hamer KC, Wanless S (2001) Evidence of intra-specific competition for food in a pelagic seabird. *Nature* 412:816–819
- ✦ Millon A, Bretagnolle V (2008) Predator population dynamics under a cyclic prey regime: numerical responses, demographic parameters and growth rates. *Oikos* 117:1500–1510
- Mitchell PI, Newton SF, Ratcliffe N, Dunn TE (2004) Seabird populations of Britain and Ireland: results of the Seabird 2000 census (1998–2002). T & AD Poyser, London
- Montevicchi WA (1993) Birds as indicators of change in marine prey stocks. In: Furness RW, Greenwood JJ (eds) *Birds as monitors of environmental change*. Chapman & Hall, London, p 219–266
- ✦ Nakagawa S, Schielzeth H (2010) Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biol Rev Camb Philos Soc* 85:935–956
- Nogales M, Zonfrillo B, Monaghan P (1995) Diets of adult and chick herring gulls *Larus argentatus argenteus* on Ailsa Craig, south-west Scotland. *Seabird* 17:56–63
- Noordhuis R, Spaans AL (1992) Interspecific competition for food between herring *Larus argentatus* and lesser black-backed gulls *L. fuscus* in the Dutch Wadden Sea area. *Ardea* 80:115–132
- O'Hanlon NJ (2016) Spatial variation in herring gull traits and their potential as monitors of the coastal environment. PhD thesis, University of Glasgow
- ✦ Oro D, Genovart X, Ruiz X, Jiménez J, García-Gans J (1996) Differences in diet, population size and reproductive performance between two colonies of Audouin's gull *Larus audouinii* affected by a trawling moratorium. *J Avian Biol* 27:245–251
- ✦ Österblom H, Casini M, Olsson O, Bignert A (2006) Fish, seabirds and trophic cascades in the Baltic Sea. *Mar Ecol Prog Ser* 323:233–238
- ✦ Österblom H, Olsson O, Blenckner T, Furness RW (2008) Junk-food in marine ecosystems. *Oikos* 117:967–977
- ✦ Phillips DL, Inger R, Bearhop S, Jackson AL and others (2014) Best practices for use of stable isotope mixing models in food-web studies. *Can J Zool* 92:823–835
- ✦ Pierotti R, Annett CA (1990) Diet and reproductive output in seabirds. *Bioscience* 40:568–574
- ✦ Pierotti R, Annett CA (1991) Diet choice in the herring gull: constraints imposed by reproductive and ecological factors. *Ecology* 72:319–328
- Player PV (1971) Food and feeding habit of the common eider at Seafield, Edinburgh, in winter. *Wildfowl* 22:100–106
- Pons M (1992) Effects of change in the availability of human refuse on breeding parameters in a herring gull *Larus argentatus* population in Brittany, France. *Ardea* 80:143–150
- ✦ Pons JM, Migot P (1995) Life-history strategy of the herring gull: changes in survival and fecundity in a population subjected to various feeding conditions. *J Anim Ecol* 64:592–599
- ✦ Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montaña CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* 152:179–189
- ✦ Pyke GH, Pulliam HR, Charnov EL (1977) Optimal foraging: a selective review of theory and tests. *Q Rev Biol* 52:137–154
- R Development Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- ✦ Ramos R, Ramírez F, Sanpera C, Jover L, Ruiz X (2009) Feeding ecology of yellow-legged gulls *Larus michahellis* in the western Mediterranean: a comparative assessment using conventional and isotopic methods. *Mar Ecol Prog Ser* 377:289–297
- ✦ Ramos R, Ramírez F, Carrasco JL, Jover L (2011) Insights into the spatiotemporal component of feeding ecology: an isotopic approach for conservation management sciences. *Divers Distrib* 17:338–349
- Resano-Mayor J, Hernández-Matías A, Real J, Parés F, Inger R, Bearhop S (2014) Comparing pellet and stable isotope analyses of nestling Bonelli's eagle *Aquila fasciata* diet. *Ibis* 156:176–188
- ✦ Resano-Mayor J, Real J, Moleón M, Sánchez-Zapata JA, Palma L, Hernández-Matías A (2016) Diet-demography relationships in a long-lived predator: from territories to populations. *Oikos* 125:262–270
- ✦ Romano MD, Piatt JF, Roby DD (2006) Testing the junk-food hypothesis on marine birds: effects of prey type on growth and development. *Waterbirds* 29:407–414
- Ronconi RA, Steenweg RJ, Taylor PD, Mallory ML (2014) Gull diets reveal dietary partitioning, influences of isotopic signatures on body condition, and ecosystem changes at a remote colony. *Mar Ecol Prog Ser* 514:247–261
- ✦ Schoener TW (1971) Theory of feeding strategies. *Annu Rev Ecol Syst* 2:369–404
- ✦ SEPA (Scottish Environment Protection Agency) (2015) Waste sites and capacity information. <https://www.sepa.org.uk/environment/waste/waste-data/waste-data-reporting/waste-site-information/waste-sites-and-capacity-excel/>
- ✦ Sibly RM, McCleery RH (1983) Increase in weight of herring gulls while feeding. *J Anim Ecol* 52:35–50
- ✦ Smith GC, Carlile N (1993) Food and feeding ecology of breeding silver gulls (*Larus novaehollandiae*) in urban Australia. *Colon Waterbirds* 16:9–16
- ✦ Sorensen MC, Hipfner JM, Kyser TK, Norris DR (2009) Carry-over effects in a Pacific seabird: stable isotope evidence that pre-breeding diet quality influences reproductive success. *J Anim Ecol* 78:460–467
- Spaans AL (1971) On the feeding ecology of the herring gull *Larus argentatus* Pont. in the northern part of the Netherlands. *Ardea* 59:73–188
- ✦ Steenweg RJ, Ronconi RA, Leonard ML (2011) Seasonal and age-dependent dietary partitioning between the great black-backed and herring gulls. *Condor* 113:795–805
- ✦ Steigerwald EC, Igual JM, Payo-Payo A, Tavecchia G (2015) Effects of decreased anthropogenic food availability on an opportunistic gull: evidence for a size-mediated response in breeding females. *Ibis* 157:439–448
- Stephens D, Krebs J (1986) *Foraging theory*. Princeton University Press, Princeton, NJ
- ✦ Stock B, Semmens B (2013) MixSIAR GUI user manual. <http://conserver.iugo-cafe.org/user/brice.semmens/MixSIAR>
- ✦ Stratoudakis Y, Fryer RJ, Cook RM, Pierce GJ, Coull KA (2001) Fish bycatch and discarding in *Nephrops* trawlers in the Firth of Clyde (west of Scotland). *Aquat Living Resour* 14:283–291
- ✦ Suddaby D, Ratcliffe N (1997) The effects of fluctuating food availability on breeding Arctic terns (*Sterna paradisaea*). *Auk* 114:524–530
- ✦ Tasker ML, Camphuysen CJK, Cooper J, Garthe S, Montevicchi WA, Blaber SJM (2000) The impacts of fishing on

- marine birds. *ICES J Mar Sci* 57:531–547
- ✦ Thaxter CB, Lascelles B, Sugar K, Cook ASCP and others (2012) Seabird foraging ranges as a preliminary tool for identifying candidate Marine Protected Areas. *Biol Conserv* 156:53–61
- ✦ Uttley J, Monaghan P, White S (1989) Differential effects of reduced sandeel availability on two sympatrically breeding species of tern. *Ornis Scand* 20:273–277
- ✦ Van Heezik Y (1990) Seasonal, geographical, and age-related variations in the diet of the yellow-eyed penguin (*Megadyptes antipodes*). *N Z J Zool* 17:201–212
- ✦ Vucetich JA, Peterson RO (2004) The influence of prey consumption and demographic stochasticity on population growth rate of Isle Royale wolves *Canis lupus*. *Oikos* 107:309–320
- Walsh PM, Halley DJ, Harris MP, del Nevo A, Sim IMW, Tasker ML (1995) Seabird monitoring handbook for Britain and Ireland. JNCC/RSPB/ITE/Seabird Group, Peterborough
- ✦ Wanless S, Harris MP, Redman P, Speakman JR (2005) Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Mar Ecol Prog Ser* 294:1–8
- Ward P, Zahavi A (1979) The importance of certain assemblages of birds as 'information-centres' for food-finding. *Ibis* 115:517–534
- ✦ Washburn BE, Bernhardt GE, Kutschbach-Brohl L, Chipman RB, Francoeur LC (2013) Foraging ecology of four gull species at a coastal–urban interface. *Condor* 115:67–76
- ✦ Weiser EL, Powell AN (2010) Does garbage in the diet improve reproductive output of glaucous gulls? *Condor* 112:530–538
- ✦ White TCR (2008) The role of food, weather and climate in limiting the abundance of animals. *Biol Rev Camb Philos Soc* 83:227–248
- ✦ Whitfield DP, Reid R, Haworth PF, Madders M, Marquiss M, Tingay R, Fielding AH (2009) Diet specificity is not associated with increased reproductive performance of golden eagles *Aquila chrysaetos* in Western Scotland. *Ibis* 151:255–264
- Wilson LJ, Daunt F, Wanless S (2004) Self-feeding and chick provisioning diet differ in the common guillemot *Uria aalge*. *Ardea* 92:197–207
- ✦ Yoda K, Tomita N, Mizutani Y, Narita A, Niizuma Y (2012) Spatio-temporal responses of black-tailed gulls to natural and anthropogenic food resources. *Mar Ecol Prog Ser* 466:249–259
- Yurkowski DJ, Hussey NE, Semeniuk C, Ferguson SH, Fisk AT (2015) Effects of lipid extraction and the utility of lipid normalization models on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in Arctic marine mammal tissues. *Polar Biol* 38:131–143
- ✦ Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. *Methods Ecol Evol* 1:3–14

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