

# Landscape-mediated variation in diet is associated with egg size and maculation in a generalist forager

NINA J. O'HANLON,<sup>1,2,\*†</sup> SARAH ALONSO,<sup>3</sup> JULIE A. O. MILLER,<sup>2</sup> RONA A. R. MCGILL<sup>4</sup> & RUEDI G. NAGER<sup>2</sup>

<sup>1</sup>Institute of Biodiversity, Animal Health and Comparative Medicine, The Scottish Centre for Ecology and the Natural Environment, University of Glasgow, Rowardennan, Drymen, Glasgow, G63 0AW, UK

<sup>2</sup>Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Graham Kerr Building, Glasgow, G12 8QQ, UK

<sup>3</sup>Department of Science and Technology, University of Bordeaux, 351 Cours de la Libération, 33400, Talence, France

<sup>4</sup>NERC Life Sciences Mass Spectrometry Facility, Scottish Universities Environmental Research Centre, East Kilbride, G75 0QF, UK

Human impacts alter landscapes with consequences for the distribution and availability of high-quality food resources to populations inhabiting those landscapes, which may impact on the reproductive output of individuals in those populations. The sensitivity of wild populations to changes in food resources may vary among stages of the annual cycle. For example, in birds, effects are likely to be greater during costly stages such as egg production. Here we compare assimilated diet (from stable isotope analysis of chick feathers) and egg traits (egg size, shape, eggshell colour and maculation, using pattern-analysis software) in Herring Gulls *Larus argentatus*, across seven colonies in southwest Scotland and Northern Ireland. The Herring Gull is an opportunistic, generalist forager on both marine and terrestrial resources which frequently exploits anthropogenic food sources such as fishery discards and human refuse. We found that larger eggs were laid in colonies where females consumed either a higher proportion of marine resources or terrestrial resources; smaller eggs were laid in colonies where females had an intermediate diet. In colonies where females consumed more marine items, they also laid eggs with higher maculation (intensity and size of spots) compared with colonies where females mainly consumed terrestrial food. We also found smaller and more pointed eggs, suggestive of resource shortages, in larger colonies. Generalist foragers are often thought to have the capacity to buffer themselves against changes in the food web, provided that enough alternative food is available. However, this study highlights that specializing on the most profitable or available resources has consequences for egg traits even in an opportunistic generalist forager exploiting a large range of habitats. If variation in egg traits is related to reproductive output, then understanding the impact of assimilated diet on reproduction early in the breeding season can provide important insights into how populations will respond to landscapes altered by human impact.

**Keywords:** conservation, gull, intertidal, *Larus*, marine, pattern-analysis software, resource use, stable isotopes.

<sup>†</sup>Present address: Environmental Research Institute, North Highland College – UHI, University of the Highlands and Islands, Castle Street, Thurso, Caithness, KW14 7JD, UK

\*Corresponding author.  
Email: nina.ohanlon@uhi.ac.uk  
Twitter: @Nina\_OHanlon

Human impact on the landscape can affect the quantity, quality and configuration of resources on which animals depend (Benton *et al.* 2003, Chace & Walsh 2006, Halpern *et al.* 2008). Landscape composition can affect fitness-related traits with potential consequences for demographic parameters (e.g. Kurki *et al.* 2000, Penteriani *et al.* 2002, Bond *et al.* 2004). Understanding the relationship

between landscape characteristics and fitness-related traits can therefore provide insights into the conservation and management of populations inhabiting human-impacted landscapes.

Human-impacted landscapes can have reduced or degraded foraging habitat but may also provide new foraging opportunities. Consequent changes in resource availability may influence a consumer's diet and thus the composition of energy and nutrients consumed (Amar & Redpath 2005, Palma *et al.* 2006). The quantity and quality of consumed resources can have important consequences for survival and reproductive performance (Alverson 1992, Grémillet *et al.* 2008, Österblom *et al.* 2008, White 2008). Optimal foraging theory predicts that energy gain, and associated fitness, is maximized by specializing on the single most abundant and/or highest quality food (Stephens & Krebs 1986). However, specialist foragers may be negatively affected when landscape changes impact their food availability (Montevecchi 1993, Davoren & Montevecchi 2003, Vucetich & Peterson 2004, Millon & Bretagnolle 2008). Conversely, generalist foragers are thought to buffer themselves against changes in food availability by switching to alternatives (Schoener 1971, Pyke *et al.* 1977). However, how human-impacted landscapes influence generalists' resource consumption and hence their reproduction is not known in many wild populations (Yohannes *et al.* 2016).

Sensitivity to resource availability may vary among stages of the annual cycle (Lindstrom *et al.* 1993, Perrins 1996, Wikelski & Tarlow 2003) and is likely to be greater during nutritionally and energetically demanding periods. Egg formation in birds is a particularly demanding stage (Robbins 1981, Monaghan & Nager 1997). Egg size is positively related to the abundance and quality of resources during egg formation in birds (Bolton *et al.* 1992, Christians 2002, Nager 2006, Sorensen *et al.* 2009, Barrett *et al.* 2012, Kouwenberg *et al.* 2013, Bennett *et al.* 2017). Egg shape may also depend on resource availability during egg formation (Ardendt 2004, Górski *et al.* 2015). Furthermore, food availability and quality has been shown to influence variation in egg pigmentation (eggshell colour and maculation) in several bird species, with less pigment deposited at low availability of overall (Avilés *et al.* 2006, Duval *et al.* 2013) or specific resources (i.e. calcium, Gosler *et al.* 2005). There is evidence that offspring development and survival can depend on egg size (reviewed by Krist

2011) and egg pigmentation (Maurer *et al.* 2011, Lahti & Ardia 2016, Hargitai *et al.* 2018). Thus, female birds living in human-impacted landscapes may find their preferred food reduced or may need to rely on alternatives of different quality which may affect egg quality and, ultimately, demographic rates.

One group of generalist foragers that increasingly use human-impacted landscapes are the large gulls, Laridae (Rock 2005). Even when breeding, and constrained to a central nesting site, gulls can move over a large area and exploit a variety of resources from marine food, consisting of pelagic fish and intertidal invertebrates, to terrestrial food sources, including those derived from human refuse and farming (Hunt 1972, Götmark 1984, O'Hanlon *et al.* 2017). As their marine food webs have been simplified and impoverished by human impact (Halpern *et al.* 2008), many European gull populations are consuming anthropogenic terrestrial food from farmland and built-up areas (Pons & Migot 1995, Coulson & Coulson 2008, Schwemmer *et al.* 2008, Garthe *et al.* 2016, Gyimesi *et al.* 2016). Marine foods, in particular fish, are thought to best meet the high energy and nutrient requirements of laying female gulls (Hiom *et al.* 1991), but some populations now rely on anthropogenic, terrestrial food resources (e.g. Pons & Migot 1995, Steigerwald *et al.* 2015, Gyimesi *et al.* 2016). Across southwest Scotland and Northern Ireland, there is a strong relationship between the local landscape and diet of breeding Herring Gulls *Larus argentatus*. Gulls predominantly forage on the locally most available resources, and colonies with a higher proportion of marine resources in their diet have a higher breeding success (O'Hanlon *et al.* 2017). The marine diet consists mainly of intertidal invertebrates (crustaceans and bivalves) with few marine fish, consistent with the absence of any significant fin fishery in the region, and therefore limited access to discards. Terrestrial food consists mainly of grain, although terrestrial invertebrates and anthropogenic food waste are also consumed (O'Hanlon *et al.* 2017). Here we test the relationship between assimilated diet during egg formation, based on stable isotope analyses of chick down feathers, and egg traits from seven Herring Gull colonies across southwest Scotland and Northern Ireland. These colonies occupy different landscapes, with varying availability of marine and terrestrial resources. We predict that colonies consuming a more marine diet, at a higher

trophic level, produce larger and more pigmented eggs, measured as more intense eggshell colour and maculation (intensity and size of spots). This study aims to contribute to our understanding of how altered landscapes impact egg formation of a generalist seabird.

## METHODS

Fieldwork was carried out between 5 May and 11 July 2014 across seven Herring Gull colonies located in southwest Scotland and Northern Ireland covering an approximate area of  $200 \times 250$  km (Fig. 1, Table 1). In this region, we selected colonies that had within their foraging ranges low ( $1\text{--}2$  km<sup>2</sup> built-up area  $> 10$  km away) to high human population density (over 400 km<sup>2</sup> built-up area as close as 2–3 km), and rocky intertidal habitat with low wave fetch, supporting a diverse and abundant invertebrate community (Burrows 2012), to resource-poorer, exposed coastlines with high wave fetch (Table 1). The colonies typically contained several gull species and we identified Herring Gull nests by direct observations of attending adults. Within our study colonies, clutch initiation spread over approximately 3 weeks starting in early May, with the incubation period lasting 4 weeks. We visited each colony for a few days every 2 weeks (Table 1). Thus, at each visit only a snapshot of clutches and chicks were available that were suitable for taking egg measurements during incubation and for sampling down of chicks in their first week of life for stable isotope analysis. Consequently, we could not take assimilated diet and egg measurements from the same nests. There was no bias that a colony visited during early egg-laying was also visited during early chick-rearing (Spearman rank correlation:  $r_s = 0.16$ ,  $n = 7$ ,  $P = 0.73$ ).

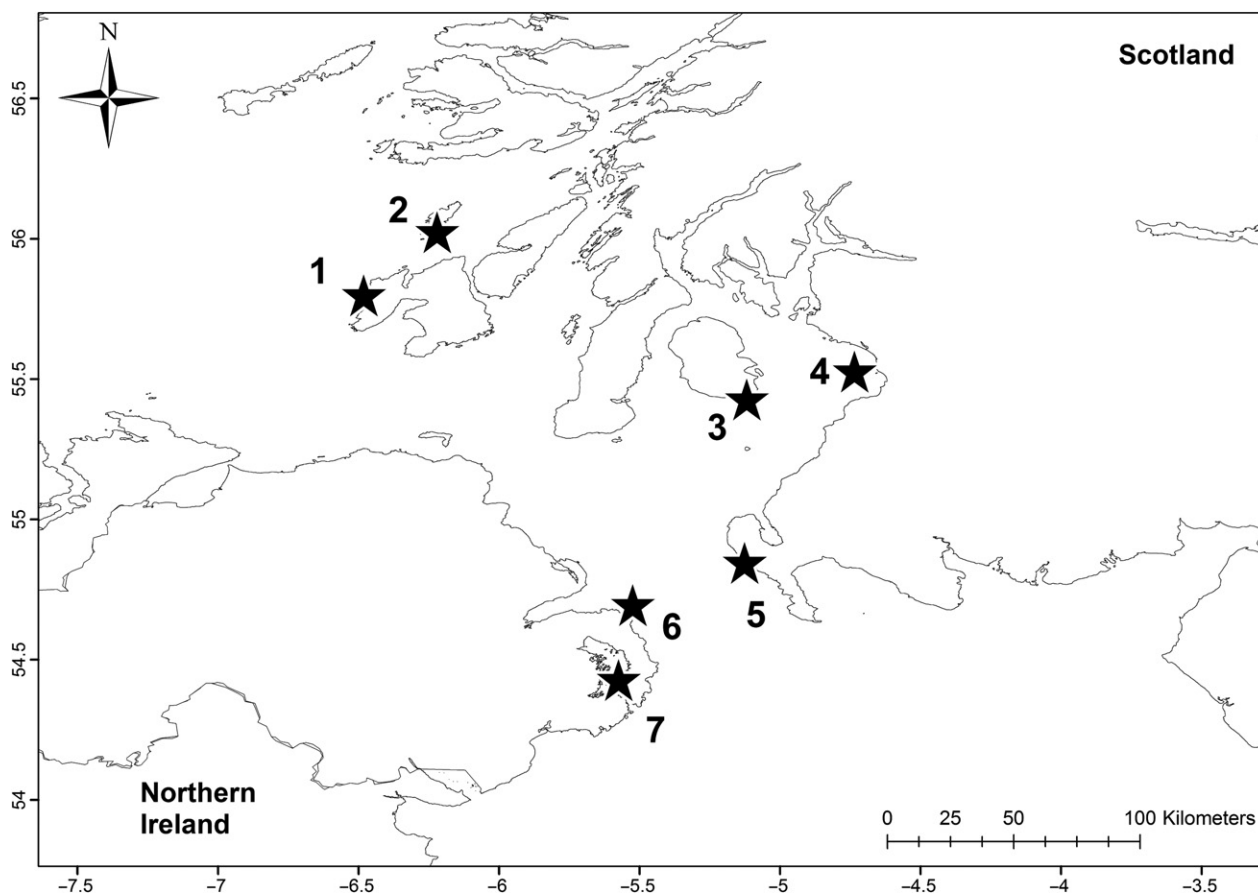
### Egg measurements

During short colony visits during the incubation period between 5 May and 3 June, we took digital photographs of Herring Gull clutches *in situ*, under standardized conditions, to minimize the duration of disturbance (Fig. S1). The modal clutch size of Herring Gulls is three eggs (Pierotti 1982). In this study it was unknown whether smaller clutches had been subject to partial nest predation, so we did not know clutch size at laying. Thus, we include clutch size in data analyses. From these digital photographs

we measured four egg traits: size, shape, eggshell colour and maculation (a more detailed account of how we did this is provided in Appendix S1). Egg size, measured as egg volume, and shape were measured using the *Egg Measurement Tool* plugin developed by Troscianko (2014) in IMAGEJ (Schneider *et al.* 2012). We measured egg length ( $l$ ) and width ( $w$ ) to calculate egg volume ( $V$ ), using  $V = klw^2$  (Hoyt 1976) where  $k$  is a species-specific shape constant, here taken as 0.000476 (Harris 1964). Egg shape was calculated as the deviation from a perfect ellipse, with a higher shape index indicating more pointed eggs (Fig. S2). We measured eggshell colour from the background, excluding maculation, as red (R), blue (B) and green (G) values in IMAGEJ. Eggshell colour was represented by the green/blue (G/B) ratio, with a high G/B ratio indicating brown-coloured and a low G/B ratio paler, green-blueish coloured eggs (Fig. S3). We also measured maculation, which is a complex trait comprising the distribution, intensity and size of spots (Gosler *et al.* 2000). A range of approaches have been developed to measure maculation (Gosler *et al.* 2005, Stoddard *et al.* 2014, Wegmann *et al.* 2015, Brulez *et al.* 2016, Gómez & Liñán-Cembrano 2016). We used *NaturePatternMatch* (Stoddard *et al.* 2014), which determined the similarity of an egg to an unmaculated reference (duck) egg. This measure considers the intensity and size of spots but not distribution, with the less maculated eggs (fewer and lighter spots) having a higher similarity score (Fig. S4). The number of sampled nests varied among colonies owing to differences in colony size, the proportion of nests that were accessible and the time available to take photographs (Table 1). Egg size, shape and eggshell colour were determined for a total of 514 eggs from 194 clutches. Maculation could only be determined for 318 eggs from 128 clutches; 66 clutches (34%) were excluded as one or more eggs within the clutch were dirty or had started to pip, which would have biased the estimate of the similarity score, or contained eggs that returned no maculation score, as the software rejected images due to insufficient contrasts. The proportion of eggs rejected for maculation scoring did not differ across colonies (Chi-square test:  $\chi^2_6 = 0.62$ ,  $P = 0.996$ ).

### Assessment of assimilated diet

We collected samples of several down feathers from different areas of the body (head, back and sides) from chicks from accessible nests in each



**Figure 1.** Study region and location of the seven Herring Gull breeding colonies across southwestern Scotland and Northern Ireland: 1 Islay, 2 Oronsay, 3 Pladda, 4 Lady Isle, 5 Portpatrick, 6 Copeland Islands, 7 Strangford.

colony at the appropriate developmental stage (see Table 1 for sample sizes). Sampled chicks needed to be less than 1 week old based on known age or judged from chick development (Kadlec *et al.* 1969) to ensure that we collected only feather material that was grown by the chicks while developing in the egg. Thus, their carbon and nitrogen stable isotope signature reflects the resources that the female gulls consumed during egg formation (Klaassen *et al.* 2004).

Collected feathers were washed in liquid detergent (Ecover) diluted with deionized water (approximate 1 : 99 dilution), followed by a wash in a 2 : 1 mixture of chloroform/methanol. Dried samples were then homogenized. Where more than one chick from the same brood was sampled, feather material from all chicks of that brood were homogenized together to provide one sample per brood. Homogenized samples of feathers were weighed (mass between 0.7 and 0.8 mg) and

sealed in tin capsules, combusted and analysed for carbon and nitrogen isotopes by continuous-flow isotope ratio mass spectrometry (using a Costech Elemental Analyser (Milan, Italy) linked to a Thermo Finnigan Delta Plus XP Mass Spectrometer (Bremen Germany)) at the NERC Life Sciences Mass Spectrometry Facility in East Kilbride (UK). The stable isotope ratios are expressed as  $\delta^{13}\text{C}$  ( $^{13}\text{C}/^{12}\text{C}$ ) and  $\delta^{15}\text{N}$  ( $^{15}\text{N}/^{14}\text{N}$ ) in parts per thousand (‰) relative to the international references Vienna PeeDee belemnite (V-PDB) marine fossil limestone for carbon, and atmospheric  $\text{N}_2$  for nitrogen, respectively. Measurement accuracy was  $\pm 0.09\text{‰}$  for  $\delta^{13}\text{C}$  and  $\pm 0.12\text{‰}$  for  $\delta^{15}\text{N}$  based on the standard deviation of the repeated analyses of tryptophan as a lab standard. The nitrogen ratio reflects trophic level while the carbon ratio varies along a gradient from marine, coastal to terrestrial habitats (Hobson & Wassenaar 1999). For our study area, the isotopic analysis of

**Table 1.** Information on the land use around the Herring Gull study colonies across southwest Scotland and Northern Ireland (Fig. 1), sample sizes of eggs and clutches photographed, and broods from which down feathers were collected for stable isotope analyses.

Colony	Dates egg photographs were taken	Latitude (°N)	Longitude (°W)	Amount of built-up area within 50 km of the colony (km <sup>2</sup> ) and nearest distance (km) in parentheses	Average wave fetch within 50 km of the colony (km) <sup>a</sup>	Colony size <sup>b</sup>	Number of eggs (clutches)	Number of broods down feathers were sampled from	Dates down feathers were sampled
1. Islay	18 May 2014	55.8	6.48	1 (12)	1044	25	24 (9)	11	27 May 2014
2. Oronsay	3 June 2014	55.43	5.12	2 (28)	743	95	75 (31)	33	6 June 2014, 17 June 2014, 2 July 2014
3. Pladda	31 May 2014	54.84	5.13	89 (29)	840	150	38 (15)	24	20 June 2014, 28 June 2014
4. Lady Isle	13 May 2014	55.53	4.73	473 (3.5)	957	830	72 (24)	28	30 May 2014, 11 June 2014, 18 June 2014
5. Portpatrick	5 May 2014	54.43	5.57	222 (8)	1243	175	58 (28)	2	9 June 2014
6. Copeland	11 May 2014 & 23 May 2014	54.69	5.52	405 (3.5)	993	683	141 (48)	22	15 June 2014, 29 June 2014
7. Strangford	14 May 2014	54.40	5.61	406 (2)	1004	190	106 (39)	13	11 June 2014
Total		–	–	–	–	–	514 (194)	133	

<sup>a</sup>Wave fetch is calculated based on the exposure of a coastline depending on its topography (Burrows *et al.* 2008). A low (or short) wave fetch value reflects a more sheltered intertidal habitat, with short distances to the nearest land mass, whereas high (or long) 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). <sup>b</sup>Colony size is the count of apparently occupied nests (AON) in 2012 or 2013 using standard monitoring techniques (Walsh *et al.* 1995).

these two elements captured the continuum from marine to terrestrial resource use by gulls (O'Hanlon *et al.* 2017). Although down feathers could only be obtained from two broods at Portpatrick (Fig. 1), we are confident that these feathers provide a representative reflection of resource use at this colony, as pellets and stable isotope analyses of feathers from older chicks from this colony indicated a similar diet (O'Hanlon 2016).

### Statistical analyses

We performed all statistical analyses in R, Version 2.12.0 (R Development Core Team 2014). For each egg trait (eggshell colour, maculation, shape and size) we used the mean value of all eggs measured in a clutch as the unit of analysis, as the exact order of laying was unknown. To determine whether the egg traits were related to one another, we performed linear mixed effect models using *lme4* with one egg trait as the response variable and the other egg traits as the explanatory variables, so that all combinations were tested. To account for the data

being representative of a population, these models included colony as a random effect and included only clutches where all four egg traits were measured ( $n = 128$  clutches). As our visits were not standardized to the phenology of each colony, we performed Spearman rank correlation tests between egg sampling dates and each egg trait, and chick down sampling dates and resource assimilation.

Resource assimilation of a colony was characterized by the first principal component of the stable isotope ratios  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  from chick down feathers collected in that colony (isotope-PC1) using the R package *prcomp*. Isotope-PC1 explained 84.6% of the variation in isotope ratios, with an eigenvalue of 7.13 and factor loadings for  $\delta^{13}\text{C} = 0.90$  and  $\delta^{15}\text{N} = 0.44$ . Hence, isotope-PC1 reflected where on the marine–terrestrial gradient birds from a colony foraged, with low isotope-PC1 values when a terrestrial diet was consumed and high values for marine diets, and also reflected trophic level, which increased from terrestrial to marine diets (Fig. S5).

To explore the effect of variation in assimilated resources (isotope-PC1) prior to egg-laying on

among-colony differences in egg traits we used linear mixed effect models. We ran separate models for each egg trait, with the mean egg trait of each clutch as the response variable. Mean isotope-PC1, colony size and clutch size were included as explanatory variables. We included colony size, as the study colonies varied in size from 25 and 830 apparently occupied nests (Table 1). Larger colonies can exert increased levels of competition and deplete local resources (Furness & Birkhead 1984, Birt *et al.* 1987, Lewis *et al.* 2001), which could affect egg traits. We included clutch size as the number of eggs in each clutch varied between one and three, which might also influence the egg trait measurements (see above). The variable isotope-PC1 only varied among colonies, so the power of our mixed model to find an effect of assimilated diet on egg traits is reduced, and hence we applied a conservative test. Colony identity was again included as a random effect to account for the non-independence of clutches from the same colony. We tested the main effects (mean isotope-PC1, colony size and clutch size) and all two-way interactions between them using an information theoretic approach (Burnham & Anderson 2002) to determine the best-fitting model across all competing models. Akaike's information criterion ( $AIC_c$ ), corrected for small sample sizes, and Akaike weights ( $w_i$ ) were calculated for all models in the R package *MuMIn* (Barton 2012) and compared across candidate models. To account for model uncertainty, we retained all competing models with  $\Delta AIC_c \leq 2$  compared with the model with the lowest  $AIC_c$  (Burnham & Anderson 2002). We calculated the weighted average of each supported explanatory variable across all retained models to obtain parameter estimates and 95% confidence intervals. The fact that the 95% confidence intervals did not overlap with zero supports that variable is important.

We checked all diagnostic plots to ensure model assumptions were met; colony size had to be *ln*-transformed. We visually inspected all relationships for linearity and, where plots suggested a non-linear relationship, we also tested the fit of a second-order polynomial function. The significance threshold was set at a two-tailed  $P < 0.05$ .

## RESULTS

All four egg traits (eggshell colour, maculation, shape and size) varied independently of each other with no significant relationships among any of the

traits across colonies (linear mixed effect models, all  $P > 0.10$ ,  $n = 128$ ). We found no seasonal change in mean egg traits ( $P > 0.62$ ) or assimilated diet ( $r_s = 0.003$ ,  $n = 132$ ,  $P = 0.98$ ) among colonies. Female Herring Gulls' assimilated diet during the pre-laying period, reflected in chick's down feather isotope-PC1, varied significantly across the seven colonies ( $F_{6,126} = 15.73$ ,  $P < 0.001$ ,  $R^2 = 0.40$ ). Variation in assimilated diet among colonies during egg formation was important in explaining variation in Herring Gull egg size and maculation, with 95% confidence intervals that did not overlap zero (Tables 2 and 3). In colonies with the most terrestrial, low trophic level diets (low values of  $\delta^{13}C$  and  $\delta^{15}N$  contribute to a negative isotope-PC1 value representing grain, terrestrial invertebrates and some human refuse; Islay and Portpatrick) or the most marine, high trophic level diets (high values of  $\delta^{13}C$  and  $\delta^{15}N$  contribute to a positive isotope-PC1 representing intertidal invertebrates, fish and occasional mammal and bird prey; Oronsay and Pladda) eggs were larger than in the remaining colonies which had an intermediate diet (Table 3, Fig. 2a). Furthermore, egg size declined with increasing colony size (Table 3, Fig. S6a). In colonies with a more marine, higher trophic level diet, eggs were also more maculated (Table 3, Fig. 2b). We found no relationship between isotope-PC1 and eggshell colour or egg shape; however, eggs in larger colonies were more pointed (Table 3, Fig. S6b). There was no support for clutch size explaining any of the observed variation in egg traits.

## DISCUSSION

Colonies of Herring Gulls, generalist foragers inhabiting landscapes with a range of marine and terrestrial foraging opportunities, differed in their assimilated diet during egg formation. These differences explained a significant part of the among-colony variation in egg size and maculation, but not in eggshell colour or egg shape. Based on previous work in the study region, this variation would be expected to be related to local availability of foraging habitats (O'Hanlon *et al.* 2017). Our results thus indicate that egg traits of Herring Gulls are sensitive to variation in landscape structure reflecting relative local availabilities of marine and terrestrial resources.

In our study region, breeding Herring Gulls during incubation and chick-rearing generally

**Table 2.** Rank of general linear multivariate regression models explaining variation in Herring Gull egg traits by isotope\_PC1 (proxy for assimilated diet), colony size and clutch size using Akaike's information criterion corrected for small sample size ( $AIC_c$ ):  $k$  is the number of estimated parameters included,  $w_i$  is the Akaike weight, and  $\Delta AIC_c$  is the  $AIC_c$  difference. Supported models ( $\Delta AIC_c < 2$ ) are shown in bold and were used in the model averaging to obtain parameter estimates (Table 3).

Variables included within model	$k$	$AIC_c$	$\Delta AIC_c$	$w_i$
<b>(A) Eggshell colour</b>				
<b>Intercept only</b>	<b>1</b>	<b>-913.3</b>	<b>0.00</b>	<b>0.320</b>
<b>Clutch Size</b>	<b>2</b>	<b>-912.6</b>	<b>0.70</b>	<b>0.225</b>
<b>Colony Size</b>	<b>2</b>	<b>-911.3</b>	<b>1.98</b>	<b>0.119</b>
Isotope_PC1	2	-911.2	2.06	0.114
Clutch Size, Isotope_PC1	3	-910.5	2.78	0.080
Clutch Size, Colony Size	3	-910.4	2.86	0.077
Colony Size, Isotope_PC1	3	-909.1	4.12	0.041
Clutch Size, Colony Size, Isotope_PC1	4	-908.3	5.03	0.026
<b>(B) Maculation</b>				
<b>Colony Size, Isotope_PC1</b>	<b>3</b>	<b>-601.3</b>	<b>0.00</b>	<b>0.487</b>
<b>Isotope_PC1</b>	<b>2</b>	<b>-599.9</b>	<b>1.44</b>	<b>0.238</b>
Clutch Size, Colony Size, Isotope_PC1	4	-598.4	2.92	0.113
Clutch Size, Isotope_PC1	3	-598.2	3.13	0.102
Clutch Size	2	-595.1	6.25	0.021
Intercept only	1	-594.9	6.45	0.019
Colony Size	2	-593.5	7.78	0.010
Clutch Size, Colony Size	3	-593.4	7.90	0.009
<b>(C) Shape</b>				
<b>Colony Size</b>	<b>2</b>	<b>-254.8</b>	<b>0.00</b>	<b>0.432</b>
<b>Colony Size, Isotope_PC1</b>	<b>3</b>	<b>-253.6</b>	<b>1.24</b>	<b>0.232</b>
<b>Clutch Size, Colony Size</b>	<b>3</b>	<b>-253.0</b>	<b>1.86</b>	<b>0.171</b>
Clutch Size, Colony Size, Isotope_PC1	4	-251.6	3.27	0.084
Intercept only	1	-249.9	4.93	0.037
Clutch Size	2	-249.2	5.59	0.026
Isotope_PC1	2	-247.5	7.36	0.011
Clutch Size, Isotope_PC1	3	-246.6	8.18	0.007
<b>(D) Size</b>				
<b>Clutch Size, Colony Size, Isotope_PC1<sup>2</sup></b>	<b>4</b>	<b>1234.3</b>	<b>0.00</b>	<b>0.474</b>
<b>Colony Size, Isotope_PC1<sup>2</sup></b>	<b>3</b>	<b>1234.8</b>	<b>0.46</b>	<b>0.377</b>
Colony Size	2	1238.2	3.88	0.068
Clutch Size, Colony Size	3	1238.9	4.60	0.048
Isotope_PC1 <sup>2</sup>	2	1241.4	7.05	0.014
Clutch Size, Isotope_PC1 <sup>2</sup>	3	1241.6	7.23	0.013
Intercept only	1	1243.8	9.49	0.004
Clutch Size	2	1244.6	10.25	0.003

The superscript 2 refers to the quadratic term in the model as Isotope\_PC1 was not linear so was fit to a second order polynomial. Isotope\_PC1 without the subscript in the linear term.

consumed the most abundant resources in the local landscape, which varied among colonies (O'Hanlon *et al.* 2017). Female Herring Gulls also probably consumed resources gathered locally for egg formation as they depend largely on exogenous resources for egg formation (income breeders, Kilpi *et al.* 1996). Although Herring Gulls can make regional movements in the non-breeding season (Coulson & Butterfield 1985, Camphuysen *et al.* 2011), they return to their breeding area 1–2 months prior to the start of egg-laying (N. J. O'Hanlon unpubl. data). Some stored lipid

reserves can be used for egg formation (Hario *et al.* 1991) but it is not known when they are accumulated and whether they are differentially allocated among the eggs of a clutch. Furthermore, down feathers are thought to reflect the protein more than the lipid stores deposited into the egg (Hobson 2006). Consequently, the isotope values of chick down feathers are thought to provide an accurate reflection of the diet of females prior to egg-laying.

At the colony level, Herring Gulls foraging more on either marine or terrestrial resources laid

**Table 3.** Final model-averaged parameter estimates for each egg trait with standard error and 95% confidence intervals. Effects are model-averaged slope estimates derived from the supported models in Table 2, ranked by relative importance of each explanatory variable to explain variation in changes in Herring Gull egg traits.

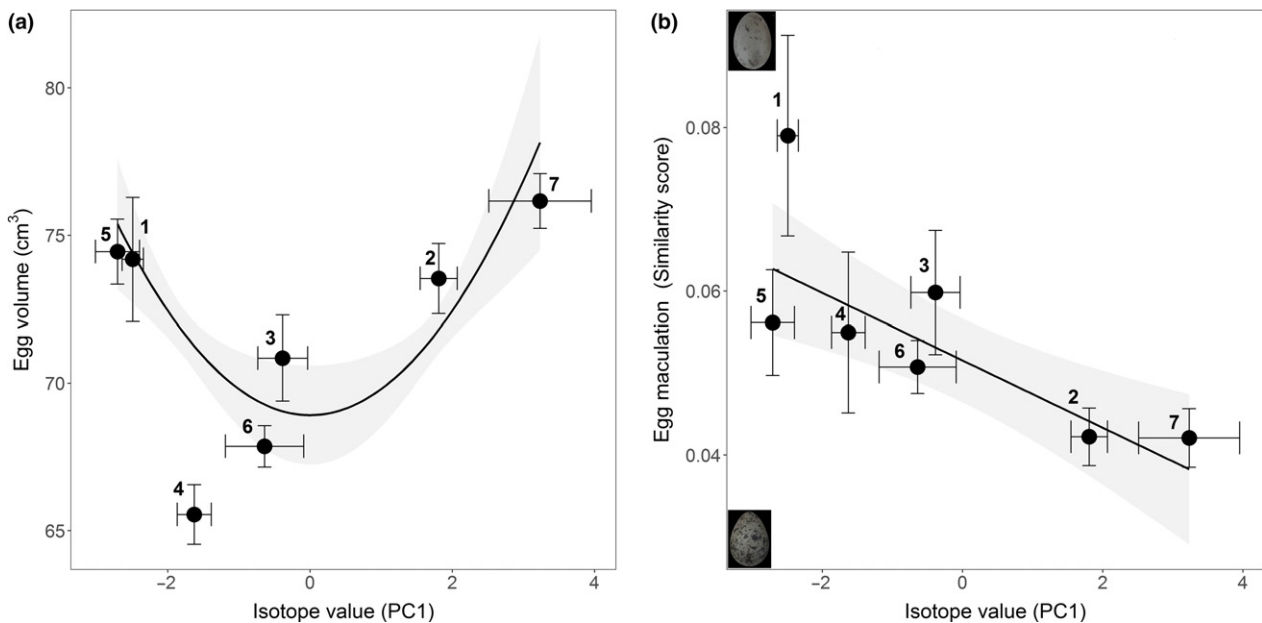
Parameter	Effect	se	95% confidence intervals		Relative importance <sup>a</sup>
			Lower	Upper	
(A) Eggshell colour					
Intercept	1.113				
Clutch Size	0.001	0.002	-0.002	0.008	0.408
Colony Size	0.0003	0.001	-0.005	0.007	0.263
(B) Maculation					
Intercept	0.068				
Isotope_PC1	-0.004	0.0012	-0.007	-0.002	0.940
Colony Size	-0.003	0.0029	-0.009	0.001	0.619
(C) Shape					
Intercept	0.3233				
Colony Size	0.025	0.010	0.006	0.043	0.919
Isotope_PC1	0.001	0.003	-0.005	0.013	0.334
Clutch Size	0.001	0.007	-0.021	0.035	0.288
(D) Size					
Intercept	84.388				
Colony Size	-2.068	0.533	-3.119	-1.018	0.967
Isotope_PC1	16.115	6.301	3.684	28.539	
Isotope_PC1 <sup>2</sup>	20.864	6.548	7.946	33.782	0.878
Clutch Size	-0.594	0.723	-2.367	0.232	0.538

<sup>a</sup>Relative importance refers to the sum of all model weights in which a given parameter occurs. The superscript 2 refers to the quadratic term in the model as Isotope\_PC1 was not linear so was fit to a second order polynomial. Isotope\_PC1 without the subscript in the linear term.

on average larger eggs than those with an intermediate diet. A positive relationship between egg size and food quantity and quality has been observed in several gull species (Hiom *et al.* 1991, Bolton *et al.* 1992, Blight 2011, Svagelj *et al.* 2015, Bennett *et al.* 2017). The observed association of assimilated diet with egg size may reflect differences in resource quality and availability (Sibly & McCleery 1983, Pierotti & Annett 1991). Foraging on marine resources at a higher trophic level, especially fish, is generally thought to provide more energy and protein than foraging on lower trophic and terrestrial items (Hiom *et al.* 1991, Pierotti & Annett 1991, Ronconi *et al.* 2014, Blight *et al.* 2015). For example, among-colony differences in egg size in Balearic Shearwaters *Puffinus mauretanicus* over a relatively small spatial scale were attributed to differences in trophic level (Louzao *et al.* 2008). In our study, Herring Gulls at colonies where they consumed more marine items (Oronsay, Strangford) laid the largest eggs, although the Gulls only rarely consumed fish (O'Hanlon *et al.* 2017). More marine items were consumed in colonies along sheltered coastlines (O'Hanlon *et al.*

2017) harbouring a higher abundance and diversity of marine invertebrates (Burrows 2012). In contrast, terrestrial and low trophic level resources have been considered a lower quality diet for gulls (Murphy *et al.* 1984, Pierotti & Annett 1991, Pons 1992, Belant *et al.* 1993, Duhem *et al.* 2008, Weiser & Powell 2010, Hobson *et al.* 2015, O'Hanlon *et al.* 2017), although some resources, for example refuse from landfills, can have a high energy and protein content (Sibly & McCleery 1983, Pierotti & Annett 1987, 1991, Pons & Migot 1995). In our study region, grain was the main terrestrial food (O'Hanlon *et al.* 2017), and its source (farmland) was the dominant terrestrial habitat (86.2–99.7% of all potential terrestrial foraging habitat), close to all study colonies. However, female Gulls in colonies with a mainly terrestrial diet (Islay, Portpatrick) also laid large eggs, possibly because terrestrial resources are thought to be more predictably available compared with intertidal resources that may only be available at low tide (Van Donk *et al.* 2017), which may compensate for small differences in resource quality (Pierotti & Annett 1991, Steigerwald *et al.* 2015). Future





**Figure 2.** Relationship between mean (a) egg size and (b) egg maculation (higher similarity scores relate to less maculated eggs) with mean assimilated diets during egg formation from feather isotope analyses at the colony level. Assimilated diet is expressed by the isotope value (PC1 score from  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , see Methods), ranging from low isotopic scores on the left, reflecting low trophic, terrestrial resources, to high isotopic scores on the right, reflecting high trophic, marine resources. Solid lines indicate the trend line with 95% confidence intervals (dashed lines) predicted from a linear model, which also included colony size (Table 2B). Shown are means  $\pm$  1 se for each colony. Number refers to colony numbers as shown in Fig. 1.

work should test whether terrestrial resources are relatively more predictable and abundant than intertidal food resources in our region. Intermediate diets probably represent a mixed diet of terrestrial and marine food consumed by an individual. As specialized behavioural, physiological or morphological adaptations are often required to obtain or digest particular food items, these individuals may be less efficient (Bolnick *et al.* 2003). If Herring Gulls show such specializations, this could result in smaller eggs laid by individuals consuming a mixed diet. Thus, it may be advantageous to Herring Gulls to select a specific resource, either because they exploit the most abundant or profitable resource or because they become efficient in using that resource.

Several studies have investigated the association between egg pigmentation (eggshell colour and maculation) and female condition or environmental conditions experienced during egg formation, but the relationship is not clear (Moreno & Osorno 2003, Osorno *et al.* 2004, Siefferman *et al.* 2006, Krist & Grim 2007, Martinez-de la Puente *et al.* 2007, Morales *et al.* 2008, Soler *et al.* 2008, Sanz & García-Navas 2009, López de Hierro & De

Neve 2010, De Coster *et al.* 2013, Duval *et al.* 2013, Hargitai *et al.* 2016, 2018). Different studies have measured different components of eggshell pigmentation using different approaches, and it is likely that each measurement provides different information (Badás *et al.* 2017). Background eggshell colour did not vary with consumed diet in our study. This is consistent with experimental food restriction in Japanese Quails *Coturnix coturnix japonica* not affecting eggshell colour, although it did increase the amount of pigment in the shell (Duval *et al.* 2013). Background colour of Herring Gull eggs has been shown to vary with the egg's contamination load (Hanley & Doucet 2012). The results from our analysis of eggshell colour cannot support any differences in food limitation between colonies or potential systematically different contamination loads associated with different diets. We also measured maculation (size and intensity of spots) with less maculated eggs (fewer and lighter spots) laid in colonies with a low trophic level, terrestrial diet. Previous studies found that less maculated eggs were associated with poorer foraging and female condition (Christians 2002, Reynolds *et al.* 2009, Duval *et al.* 2014), whereas

Martinez-de la Puente *et al.* (2007) and Hargitai *et al.* (2016) found the opposite association. The relationships between diet, female condition and foraging conditions in Herring Gulls need further study before a clear conclusion can be drawn. Including a measure of the distribution of spots, which also can be associated with female condition (Sanz & García-Navas 2009), may provide further information that we missed by only looking at size and intensity of spots.

Interestingly, female Herring Gulls in colonies consuming the most terrestrial diet, largely composed of grain (Islay, Portpatrick) and in colonies consuming the most marine diet (mostly intertidal invertebrates) laid similarly large eggs, but differed in maculation. As maculation possibly reflects differences in egg or parental quality as discussed above, the quality of Herring Gull eggs may vary with assimilated diet, independent of egg size. However, the existing information on the association between maculation and environmental and fitness-related traits is still unclear. Therefore, to elucidate further the observed maculation relationship, and test whether eggs formed on one diet are of higher quality than those formed on the other diet would require a study of hatching and fledgling success. Larger eggs can more probably result in surviving offspring (reviewed by Krist 2011), and egg pigmentation can play an important role in the successful development of the embryo (Maurer *et al.* 2011, Lahti & Ardia 2016). Unfortunately, due to the logistical constraints of studying seven colonies, we do not have measures of success for individual eggs or nests. Future studies should consider relationships between egg traits, diet and breeding success among nests within a colony. These logistical constraints also meant that we were unable to standardize our colony visits to specific times of breeding. However, we did not sample eggs or down feathers consistently early or late, and egg traits and diet were not related to sampling date. Therefore, differences in breeding phenology related to parental quality are unlikely to have influenced the relationships we found among egg traits and Herring Gull diet.

We found that egg size and shape, but not pigmentation, were associated with colony size. In larger colonies, Herring Gulls laid smaller eggs (also observed by Coulson *et al.* 1982, Bennett *et al.* 2017) and more pointed eggs. Individuals nesting in larger colonies may experience increased competition for limited resources (Ashmole 1963, Lewis *et al.* 2001, Wakefield *et al.* 2013), resulting

in smaller and more pointed eggs (Houston *et al.* 1983, Kilpi *et al.* 1996, Nager *et al.* 2000). If the larger colonies are expanding, there may be more young, inexperienced birds that lay smaller eggs (Coulson *et al.* 1982), whereas in declining colonies larger eggs may be attributed to reduced resource depletion or disproportionately more older individuals breeding (Bennett *et al.* 2017). In this study region, colony size was unrelated to population trends (O'Hanlon & Nager 2018), which makes it unlikely that the colonies differed in age structure; instead, female Gulls in larger colonies are likely to have experienced greater resource competition.

## CONCLUSION

At the colony level, Herring Gull egg traits measured by digital photography in the field, which was an efficient tool to measure multiple egg traits with minimal disturbance to the colony, were related to differences in resources consumed when eggs were formed. As Herring Gulls, at least in our study region, used the resources from habitats that were most readily available to them (O'Hanlon *et al.* 2017), differences in resource use during egg formation among colonies with different composition of habitats in their landscape also affected egg traits. Anthropogenic changes in local landscapes that alter the resources available to generalist birds such as Herring Gulls may therefore affect reproduction from the earliest stage in the breeding cycle.

This work was supported by funding from the European Union INTERREG IVA Programme (project 2859 'IBIS') managed by the Special EU Programmes Body, a grant from NERC and Department for Environment, Food and Rural Affairs (NE/L003090/1/1, Marine Ecosystems Research Program) and a grant from the NERC Life Sciences Mass Spectrometry Facility for the stable isotope analysis (EK228-07/14). We thank Paul Jerem and several volunteers for help with photographing Herring Gull clutches and Paul Johnson for statistical advice. We also thank Pat Monaghan for helpful comments on a previous version of the manuscript and the anonymous reviewers for their constructive comments that improved the manuscript.

## AUTHOR CONTRIBUTIONS

R.G.N. and N.J.O'H. originally formulated the idea and developed the methodology. N.J.O'H., J.A.O.M. and S.A. conducted fieldwork and

extracted data from the images. R.A.R.M. carried out the stable isotope analysis. N.J.O'H. analysed the data. N.J.O'H. and R.G.N. wrote the manuscript, with all authors providing editorial advice.

## REFERENCES

- Alverson, D.L.** 1992. Commercial fisheries and the Steller Sea Lion (*Eumetopias jubatus*): the conflict arena. *Rev. Aquat. Sci.* **6**: 203–256.
- Amar, A. & Redpath, S.M.** 2005. Habitat use by Hen Harriers *Circus cyaneus* on Orkney: implications of land-use change for this declining population. *Ibis* **147**: 37–47.
- Arendt, W.J.** 2004. A quarter century of variation in color and allometric characteristics of eggs from a rain forest population of the Pearly-eyed Thrasher (*Margarops fuscatus*). *Caribb. J. Sci.* **40**: 204–217.
- Ashmole, N.P.** 1963. The regulation of numbers of tropical oceanic birds. *Ibis* **103**: 458–473.
- Avilés, J.M., Stokke, B.G., Moksnes, A., Røskaft, E. & Møller, A.P.** 2006. Environmental conditions influence egg color of Reed Warblers *Acrocephalus scirpaceus* and their parasite, the Common Cuckoo *Cuculus canorus*. *Behav. Ecol. Sociobiol.* **61**: 475–485.
- Badás, E.P., Martínez, J., Rivero-de Aguilar, J., Stevens, M., van der Velde, M., Komdeur, J. & Merino, S.** 2017. Eggshell pigmentation in the Blue Tit: male quality matters. *Behav. Ecol. Sociobiol.* **71**: 57.
- Barrett, R.T., Nilsen, E.B. & Anker-Nilssen, T.** 2012. Long-term decline in egg size of Atlantic Puffins *Fratercula arctica* is related to changes in forage fish stocks and climate conditions. *Mar. Ecol. Prog. Ser.* **457**: 1–10.
- Barton, K.** 2012. *MuMIn: Multi-Model Inference*. R package version 1.13.4.
- Belant, J.L., Seamans, T.W., Gabrey, S.W. & Ickes, S.K.** 1993. Importance of landfills to nesting Herring Gulls. *Condor* **95**: 817–830.
- Bennett, J.L., Jamieson, E.G., Ronconi, R.A. & Wong, S.N.P.** 2017. Variability in egg size and population declines of Herring Gulls in relation to fisheries and climate conditions. *Avian Conserv. Ecol.* **12**: 16.
- Benton, T.G., Vickery, J.A. & Wilson, J.D.** 2003. Farmland biodiversity: Is habitat heterogeneity the key?. *Trends Ecol. Evol.* **18**: 182–188.
- Birt, V.L., Birt, T.P., Goulet, D., Cairns, D.K. & Montevecchi, W.A.** 1987. Ashmole's halo: direct evidence for prey depletion by a seabird. *Mar. Ecol. Prog. Ser.* **40**: 205–208.
- Blight, L.K.** 2011. Egg production in a coastal seabird, the Glaucous-winged Gull (*Larus glaucescens*), declines during the last century. *PLoS One* **6**: e22027.
- Blight, L.K., Drever, M.C. & Arcese, P.** 2015. A century of change in Glaucous-winged Gull (*Larus glaucescens*) populations in a dynamic coastal environment. *Condor* **117**: 108–120.
- Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D. & Forister, M.L.** 2003. The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.* **161**: 1–28.
- Bolton, M., Houston, D. & Monaghan, P.** 1992. Nutritional constraints on egg formation in the lesser black-backed gull: an experimental study. *J. Anim. Ecol.* **61**: 521–532.
- Bond, G., Burnside, N.G., Metcalfe, D.J., Scott, D.M. & Blamire, J.** 2004. The effects of land-use and landscape structure on Barn Owl (*Tyto alba*) breeding success in southern England, U.K. *Landsch. Ecol.* **20**: 555–566.
- Burlez, K., Mikšik, I., Cooney, C.R., Hauber, M.E., Lovell, P.G., Maurer, G., Portugal, S.J., Russell, D., Reynolds, S.J. & Cassey, P.** 2016. Eggshell pigment composition covaries with phylogeny but not with life history or with nesting ecology traits of British passerines. *Ecol. Evol.* **6**: 1637–1645.
- Burnham, K.P. & Anderson, D.R.** 2002. *Model Selection and Multimodel Inference*. New York, NY: Springer.
- Burrows, M.T.** 2012. Influences of wave fetch, tidal flow and ocean colour on subtidal rocky communities. *Mar. Ecol. Prog. Ser.* **445**: 193–207.
- Burrows, M.T., 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, C.J., Vercrujssse, H.J.P. & Spaans, A.L.** 2011. Colony- and age-specific seasonal dispersal of Herring Gulls *Larus argentatus* breeding in The Netherlands. *J. Ornithol.* **152**: 849–868.
- Chace, J.F. & Walsh, J.J.** 2006. Urban effects on native avifauna: a review. *Landsch. Urban Plan.* **74**: 46–69.
- Christians, J.K.** 2002. Avian egg size: variation within species and inflexibility within individuals. *Biol. Rev. Camb. Philos. Soc.* **77**: 1–26.
- Coulson, J.C. & Butterfield, J.** 1985. Movements of British Herring Gulls. *Bird Study* **32**: 91–103.
- Coulson, J.C. & Coulson, B.A.** 2008. Lesser Black-backed Gulls *Larus fuscus* nesting in an inland urban colony: the importance of earthworms (Lumbricidae) in their diet. *Bird Study* **55**: 37–41.
- Coulson, J.C., Duncan, N. & Thomas, C.** 1982. Changes in the breeding biology of the Herring Gull (*Larus argentatus*) induced by reduction in the size and density of the colony. *J. Anim. Ecol.* **51**: 739–756.
- Davoren, G.K. & Montevecchi, W.A.** 2003. Signals from seabirds indicate changing biology of capelin stocks. *Mar. Ecol. Prog. Ser.* **258**: 253–261.
- De Coster, G., De Neve, L. & Lens, L.** 2013. Intra-clutch variation in avian eggshell pigmentation covaries with female quality. *J. Ornithol.* **154**: 1057–1065.
- 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.
- Duval, C., Cassey, P., Mikšik, I., Reynolds, S.J. & Spencer, K.A.** 2013. Condition-dependent strategies of eggshell pigmentation: an experimental study of Japanese Quail (*Coturnix coturnix japonica*). *J. Exp. Biol.* **216**: 700–708.
- Duval, C., Zimmer, C., Mikšik, I., Cassey, P. & Spencer, K.A.** 2014. Early life stress shapes female reproductive strategy through eggshell pigmentation in Japanese Quail. *Gen. Comp. Endocrinol.* **208**: 146–153.

- Furness, R.W. & Birkhead, T.R. 1984. Seabird colony distributions suggest competition for food supplies during the breeding season. *Nature* **311**: 655–656.
- Garthe, S., Schwemmer, P., Paiva, V.H., Corman, A., Fock, H.O., Voigt, C.C. & Adler, S. 2016. Terrestrial and marine foraging strategies of an opportunistic seabird species breeding in the Wadden Sea. *PLoS One* **11**: e0159630.
- Gómez, J. & Liñán-Cembrano, G. 2016. SpotEgg: an image-processing tool for automatized analysis of colouration and spottiness. *J. Avian Biol.* **48**: 502–512.
- Górski, A., Nowakowski, J.J. & Bańbura, J. 2015. Variation in egg-size traits of the European Roller (*Coracias garrulus*) in Eastern Poland. *Ornis Fenn.* **92**: 213–220.
- Gosler, A.G., Barnett, P.R. & Reynolds, S.J. 2000. Inheritance and variation in eggshell patterning in the Great Tit *Parus major*. *Proc. R. Soc. Lond. B* **267**: 2469–2473.
- Gosler, A.G., Higham, J.P. & Reynolds, S.J. 2005. Why are birds' eggs speckled? *Ecol. Lett.* **8**: 1105–1113.
- Götmark, F. 1984. Food and foraging in five European Larus gulls in the breeding season: a comparative review. *Ornis Fenn.* **61**: 9–18.
- Grémillet, D., Pichegru, L., Kuntz, G., Woakes, A.G., Wilkinson, S., Crawford, R.J.M. & Ryan, P.G. 2008. A junk-food hypothesis for gannets feeding on fishery waste. *Proc. R. Soc. Lond. B* **275**: 1149–1156.
- Gyimesi, A., Boudewijn, T.J., Buijs, R.J., Shamoun-Baranes, J.Z., de Jong, J.W., Fijn, R.C., van Horsen, P.W. & Poot, M.J.M. 2016. Lesser Black-backed Gulls *Larus fuscus* thriving on a non-marine diet. *Bird Study* **63**: 241–249.
- Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R. & Watson, R. 2008. A global map of human impact on marine ecosystems. *Science* **319**: 948–952.
- Hanley, D. & Doucet, S.M. 2012. Does environmental contamination influence egg coloration? A long-term study in Herring Gulls. *J. Appl. Ecol.* **49**: 1055–1063.
- Hargitai, R., Nagy, G., Herényi, M., Nyiri, Z., Laczi, M., Hegyi, G., Eke, Z. & Török, J. 2016. Darker eggshell spotting indicates lower yolk antioxidant level and poorer female quality in the Eurasian Great Tit (*Parus major*). *Auk* **133**: 131–146.
- Hargitai, R., Herényi, M., Nagy, G. & Török, J. 2018. Eggshell spotting pattern is related to hatching asynchrony, hematocrit value and growth of nestling Great Tits (*Parus major*). *J. Avian Biol.* **49**: e01827.
- Hario, M., Kilpi, M. & Selin, K. 1991. Parental investment by the sexes in the Herring Gull: the use of energy reserves during early breeding. *Ornis Scand.* **22**: 308–312.
- Harris, M.P. 1964. Aspects of the breeding biology of gulls. *Ibis* **106**: 432–456.
- Hiom, L., Bolton, M., Monaghan, P. & Worrall, D. 1991. Experimental evidence for food limitation of egg production in gulls. *Ornis Scand.* **22**: 94–97.
- Hobson, K.A. 2006. Using stable isotopes to quantitatively track endogenous and exogenous nutrient allocations to eggs of birds that travel to breed. *Ardea* **94**: 359–369.
- Hobson, K.A. & Wassenaar, L.I. 1999. Stable isotope ecology: an introduction. *Oecologia* **120**: 312–313.
- Hobson, K.A., Blight, L.K. & 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.
- Houston, D.C., Jones, P.J. & Sibly, R.M. 1983. The effect of female body condition on egg laying in Lesser Black-backed gulls *Larus fuscus*. *J. Zool. Soc.* **200**: 509–520.
- Hoyt, D.F. 1976. The effect of shape on the surface-volume relationships of birds' eggs. *Condor* **78**: 343–349.
- Hunt, G.L. 1972. Influence of food distribution and human disturbance on the reproductive success of Herring Gulls. *Ecology* **53**: 1051–1061.
- Kadlec, J.A., William, H., Drury, W.J.H. & Onion, D.K. 1969. Growth and mortality of Herring Gull chicks. *Bird-Banding* **40**: 222–233.
- Kilpi, M., Hillstrom, L. & Lindstrom, K. 1996. Egg-size variation and reproductive success in the Herring Gull *Larus argentatus*: adaptive or constrained size of the last egg? *Ibis* **138**: 212–217.
- Klaassen, M., Baarspul, T., Dekkers, T. & van Tienen, P. 2004. The relationship between carbon stable isotope ratios of hatching down and egg yolk in Black-headed Gulls. *J. Field Ornithol.* **75**: 196–199.
- Kouwenberg, A., Hipfner, J.M., Kay, D.W.M.C. & Storey, A.E. 2013. Corticosterone and stable isotopes in feathers predict egg size in Atlantic Puffins *Fratercula arctica*. *Ibis* **155**: 413–418.
- Krist, M. 2011. Egg size and offspring quality: a meta-analysis in birds. *Biol. Rev. Camb. Philos. Soc.* **86**: 692–716.
- Krist, M. & Grim, T. 2007. Are blue eggs a sexually selected signal of female Collared Flycatchers? A cross-fostering experiment. *Behav. Ecol. Sociobiol.* **61**: 863–876.
- Kurki, S., Nikula, A., Helle, P. & Lindon, H. 2000. Landscape fragmentation and forest composition effects on grouse breeding success in Boreal forests. *Ecology* **81**: 1985–1997.
- Lahti, D.C. & Ardia, D.R. 2016. Shedding light on bird egg color: pigment as parasol and the dark car effect. *Am. Nat.* **187**: 547–563.
- Lewis, S., Sherratt, T.N., Hamer, K.C. & Wanless, S. 2001. Evidence of intra-specific competition for food in a pelagic seabird. *Nature* **412**: 816–819.
- Lindstrom, A., Visser, G.H. & Daan, S. 1993. The energetic cost of feather synthesis to basal metabolic rate is proportional. *Physiol. Zool.* **66**: 490–510.
- López de Hierro, M.D.G. & De Neve, L. 2010. Pigment limitation and female reproductive characteristics influence egg shell spottiness and ground colour variation in the House Sparrow (*Passer domesticus*). *J. Ornithol.* **151**: 833–840.
- Louzao, M., Igual, J.M., Genovart, M., Forero, M.G., Hobson, K.A. & Oro, D. 2008. Spatial variation in egg size of a top predator: interplay of body size and environmental factors? *Acta Oecol.* **34**: 186–193.
- Martinez-de la Puente, J., Merino, S., Moreno, J., Moreno, J., Tomas, G., Morales, J., Lobato, E., Garcia-Fraile, S. & Martinez, J. 2007. Are eggshell spottiness and colour indicators of health and condition in Blue Tits *Cyanistes caeruleus*? *J. Avian Biol.* **38**: 377–384.
- Maurer, G., Portugal, S.J., Miksik, I. & Cassey, P. 2011. Speckles of cryptic black-headed gull eggs show no

- mechanical or conductance structural function. *J. Zool.* **285**: 194–204.
- Millon, A. & Bretagnolle, V.** 2008. Predator population dynamics under a cyclic prey regime: numerical responses, demographic parameters and growth rates. *Oikos* **117**: 1500–1510.
- Monaghan, P. & Nager, R.G.** 1997. Why don't birds lay more eggs?. *Trends Ecol. Evol.* **12**: 270–274.
- Montevicchi, W.A.** 1993. Birds as indicators of change in marine prey stocks. In Furness, R.W. & Greenwood, J.J.J. (eds) *Birds as Monitors of Environmental Change*: 217–266. London: Chapman & Hall.
- Morales, J., Velando, A. & Moreno, J.** 2008. Pigment allocation to eggs decreases plasma antioxidants in a songbird. *Behav. Ecol. Sociobiol.* **63**: 227–233.
- Moreno, J. & Osorno, J.L.** 2003. Avian egg colour and sexual selection: does eggshell pigmentation reflect female condition and genetic quality? *Ecol. Lett.* **6**: 803–806.
- Murphy, E.C., Day, R.H., Oakley, K.L. & Hoover, A.A.** 1984. Dietary changes and poor reproductive performance in Glaucous-winged Gulls. *Auk* **101**: 532–541.
- Nager, R.G.** 2006. The challenges of making eggs. *Ardea* **94**: 323–346.
- Nager, R.G., Monaghan, P. & Houston, D.C.** 2000. Within-clutch trade-offs between the number and quality of eggs: Experimental manipulations in gulls. *Ecology* **81**: 1339–1350.
- O'Hanlon, N.J.** 2016. *Spatial variation in herring gull traits and their potential as monitors of the coastal environment*. PhD Thesis, University of Glasgow.
- O'Hanlon, N.J. & Nager, R.G.** 2018. Identifying habitat-driven spatial variation in colony size of Herring Gulls *Larus argentatus*. *Bird Study* **65**: 306–316.
- O'Hanlon, N.J., McGill, R.A.R. & Nager, R.G.** 2017. Increased use of marine resources benefits breeding success in a generalist gull species. *Mar. Ecol. Prog. Ser.* **574**: 193–210.
- Osorno, L., Morales, J., Merino, S., Toma, G. & Moreno, J.** 2004. Egg colouration and male parental effort in the Pied Flycatcher *Ficedula hypoleuca*. *J. Avian Biol.* **35**: 300–304.
- Österblom, H., Olsson, O., Blenckner, T. & Furness, R.W.** 2008. Junk-food in marine ecosystems. *Oikos* **117**: 967–977.
- Palma, L., Beja, P., Pais, M. & Cancela Da Fonseca, L.** 2006. Why do raptors take domestic prey? The case of Bonelli's Eagles and pigeons. *J. Appl. Ecol.* **43**: 1075–1086.
- Penteriani, V., Gallardo, M. & Roche, P.** 2002. Landscape structure and food supply affect Eagle Owl (*Bubo bubo*) density and breeding performance: a case of intra-population heterogeneity. *J. Zool.* **257**: 365–372.
- Perrins, C.M.** 1996. Eggs, egg formation and the timing of breeding. *Ibis* **138**: 2–15.
- Pierotti, R.** 1982. Habitat selection and its effect on reproductive output in the Herring Gull in Newfoundland. *Ecology* **63**: 854–868.
- Pierotti, R. & Annett, C.** 1987. Reproductive consequences of dietary specialization and switching in an ecological generalist. In Kamil, A.C., Krebs, J.R. & Pulliam, H.R. (eds) *Foraging Behavior*: 417–442. New York, NY: Plenum Press.
- Pierotti, R. & Annett, C.A.** 1991. Diet choice in the Herring Gull: constraints imposed by reproductive and ecological factors. *Ecology* **72**: 319–328.
- 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, J.M. & 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.
- Pyke, G.H., Pulliam, H.R. & Charnov, E.L.** 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*. Vienna: R Foundation for Statistical Computing.
- Reynolds, S.J., Martin, G.R. & Cassey, P.** 2009. Is sexual selection blurring the functional significance of eggshell coloration hypotheses? *Anim. Behav.* **78**: 209–215.
- Robbins, C.T.** 1981. Estimation of the relative protein cost of reproduction in birds. *Condor* **83**: 177–179.
- Rock, P.** 2005. Urban gulls: problems and solutions. *Br. Birds* **98**: 338–355.
- Ronconi, R.A., Steenweg, R.J., Taylor, P.D. & Mallory, M.L.** 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.
- Sanz, J.J. & García-Navas, V.** 2009. Eggshell pigmentation pattern in relation to breeding performance of Blue Tits *Cyanistes caeruleus*. *J. Anim. Ecol.* **78**: 31–41.
- Schneider, C.A., Rasband, W.S. & Eliceiri, K.W.** 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* **9**: 671–675.
- Schoener, T.W.** 1971. Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* **2**: 369–404.
- Schwemmer, P., Garthe, S. & Mundry, R.** 2008. Area utilization of gulls in a coastal farmland landscape: habitat mosaic supports niche segregation of opportunistic species. *Landsc. Ecol.* **23**: 355–367.
- Sibly, R.M. & McCleery, R.H.** 1983. Increase in weight of Herring Gulls while feeding. *J. Anim. Ecol.* **52**: 35–50.
- Siefferman, L., Navara, K.J. & Hill, G.E.** 2006. Egg coloration is correlated with female condition in Eastern Bluebirds (*Sialia sialis*). *Behav. Ecol. Sociobiol.* **59**: 651–656.
- Soler, J.J., Navarro, C., Contreras, T.P., Avilés, J.M. & Cuervo, J.J.** 2008. Sexually selected egg coloration in Spotless Starlings. *Am. Nat.* **171**: 183–194.
- Sorensen, M.C., Hipfner, J.M., Kyser, T.K. & Norris, D.R.** 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.
- Steigerwald, E.C., Igual, J.M., 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, NJ: Princeton University Press.
- Stoddard, M.C., Kilner, R.M. & Town, C.** 2014. Pattern recognition algorithm reveals how birds evolve individual egg pattern signatures. *Nat. Commun.* **5**: 1–10.
- Svagej, W.S., Lisnizer, N., Borboroglu, P.G. & Yorio, P.** 2015. Variation in the size of eggs of Kelp Gulls (*Larus dominicanus*) at two colonies in Patagonia, Argentina. *Waterbirds* **38**: 92–98.

- Troscianko, J.** 2014. A simple tool for calculating egg shape, volume and surface area from digital images. *Ibis* **156**: 874–878.
- Van Donk, S., Camphuysen, C.J., Shamoun-Baranes, J. & Van Der Meer, J.** 2017. The most common diet results in low reproduction in a generalist seabird. *Ecol. Evol.* **7**: 4620–4629.
- Vucetich, J.A. & Peterson, R.O.** 2004. The influence of prey consumption and demographic stochasticity on population growth rate of Isle Royale wolves *Canis lupus*. *Oikos* **107**: 309–320.
- Wakefield, E.D., Bodey, T.W., Bearhop, S., Blackburn, J., Colhoun, K., Davies, R., Dwyer, R.G., Green, J.A., Grémillet, D., Jackson, A.L., Jessopp, M.J., Kane, A., Langston, R.H.W., Lescroël, A., Murray, S., Le Nuz, M., Patrick, S.C., Péron, C., Soanes, L.M., Wanless, S., Votier, S.C. & Hamer, K.C.** 2013. Space partitioning without territoriality in Gannets. *Science* **341**: 68–70.
- Walsh, P.M., Halley, D.J., Harris, M.P., Nevo, A., Sim, I.M.W. & Tasker, M.L.** 1995. *Seabird Monitoring Handbook for Britain and Ireland*. Peterborough: JNCC/RSPB/ITE/Seabird Group.
- Wegmann, M., Vallat-Michel, A. & Richner, H.** 2015. An evaluation of different methods for assessing eggshell pigmentation and pigment concentration using Great Tit eggs. *J. Avian Biol.* **46**: 597–607.
- Weiser, E.L. & Powell, A.N.** 2010. Does garbage in the diet improve reproductive output of Glaucous Gulls? *Condor* **112**: 530–538.
- White, T.C.R.** 2008. The role of food, weather and climate in limiting the abundance of animals. *Biol. Rev.* **83**: 227–248.
- Wikelski, M. & Tarlow, E.M.** 2003. Costs of migration in free-flying songbirds. *Nature* **423**: 704.
- Yohannes, E., Gwinner, H., Lee, R.W. & Schwabl, H.** 2016. Stable isotopes predict reproductive performance of European starlings breeding in anthropogenic environments. *Ecosphere* **7**: e01566.

Received 23 October 2018;  
revision accepted 30 April 2019.  
Associate Editor: Matt Wood.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1.** Photographic determination of egg size, shape, colour and maculation.

**Figure S1.** Egg holder to photograph Herring Gull eggs in the field with the graph paper background and QPcard+201 colour checker panel and scale. Grey squares P03–P09 highlighted on row 1 and colour square P15 highlighted on row 2.

**Figure S2.** Contrasting egg shapes with (a) low egg shape deviation scores describing oval eggs and (b) high deviation scores describing pointy eggs.

**Figure S3.** Contrasting egg colours with (a) low GB ratios reflecting more blue, less brown, eggs and (b) high GB ratios reflecting brown eggs.

**Figure S4.** Contrasting egg maculation with (a) low similarity scores reflecting highly maculated eggs and (b) high similarity scores reflecting less maculated eggs.

**Figure S5.** Relationship between mean ( $\pm$ sd)  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values based on stable isotope analysis of Herring Gull down feather samples.

**Figure S6.** Relationship between Herring Gull mean (a) egg volume and (b) egg size (higher deviation scores relate to pointier eggs) with colony size (natural logarithm). Solid lines indicate the trend line with 95% confidence intervals (dashed lines) predicted from model averaged Mixed Effect Models, which also included isotope\_PC1 and clutch size (Table 2). Shown are means  $\pm 1$  se for each colony. Number refers to colony numbers as in Fig. 1.