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

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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. 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, while 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 to 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 specialising 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, *Larus*, intertidal, resource use, gull, marine, stable isotopes, pattern-analysis software

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, Österblom *et al.* 2008, Grémillet *et al.* 2008, White 2008). Optimal foraging theory predicts that energy gain, and associated fitness, is maximized by specialising 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 (Lindström *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 in 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 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 only 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 for a 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 by 250 km (Fig. 1, Table 1). In this region, we selected colonies that had within their foraging ranges low (1-2 km² built-up area > 10 km away) to high human population density (over 400 km² 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 three weeks starting in early May, with the incubation period lasting four

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weeks. We visited each colony for a few days every two 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 standardised conditions, to minimise the duration of disturbance (Supporting Information 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 the Supporting Information 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 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 (Supporting Information 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 (Supporting Information Fig. S3). We also measured maculation, which is a complex trait comprising 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,

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Wegmann *et al.* 2015, Brulez *et al.* 2016, Gómez & Liñán-Cembrano 2016). We used *NaturePatternMatch* (Stoddard *et al.* 2014) that determined the similarity of an egg to an un-maculated reference (duck) egg. This measure considers intensity and size of spots but not distribution, with less maculated eggs (fewer and lighter spots) having a higher similarity score (Supporting Information Fig. S4). The number of sampled nests varied among colonies owing to differences in colony size, the proportion of nests that was 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; sixty-six 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 colony at the appropriate developmental stage (see Table 1 for sample sizes). Sampled chicks needed to be less than one 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 deionised 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 were sampled, feather material from all chicks of that brood were homogenised together to provide one sample per

brood. Homogenised samples of feathers were weighed (mass between 0.7 - 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 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 whilst the carbon ratio varies along a gradient from marine, coastal to terrestrial habitats (Hobson & Wassenaar 1999). For our study area, the isotopic analysis of 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 standardised 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 characterised 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 (Supporting Information 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 Information Criteria (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 to the model with the lowest AICc (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. 95% confidence intervals, which did not overlap with zero support 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. Significance threshold was set at 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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ contribute to a negative isotope_PC1 value representing grain, terrestrial invertebrates and some human refuge; Islay and Portpatrick) or the most marine, high trophic level diets (high values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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, Supporting Information Fig. S6a). In colonies with a more marine, higher trophic level diet, eggs were also more maculated (Fig. 2b, Table 3). We found no relationship between isotope_PC1 and egg colour or egg

shape, however eggs in larger colonies were more pointed (Table 3, Supporting Information 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 consumed the most abundant resources in the local landscape, which varied among colonies (O'Hanlon *et al.* 2017). Female Herring Gulls also likely consumed resources gathered locally for egg formation as they depend largely on exogeneous resources for egg formation (income breeders, Kilpi *et al.* 1996). Although Herring Gulls can make regional movements in the non-breeding season (Camphuysen *et al.* 2011, Coulson & Butterfield 1985), they return to their breeding area 1-2 months prior to the start of egg laying (NJO'H, unpublished 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 accurately reflect the diet of females prior to egg laying.

At the colony level, Herring Gulls foraging more on either marine or terrestrial resources laid 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 consumed fish only rarely (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 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 also 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. Yet 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 to 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 work should test whether terrestrial resources are relatively more predictable and abundant than intertidal food resources in our region. Intermediate diets most likely represent a mixed diet of terrestrial and marine food consumed by an individual. As specialised 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 specialisations, 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 nor 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 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 & Garcia-Navas 2009), may provide further information that we missed by only looking at size and intensity of spots.

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Interestingly, both female 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 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 the other diet would require a study of hatching and fledgling success. Larger eggs can more likely result in surviving offspring (reviewed in 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 standardise 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) that results 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), whilst in declining colonies larger eggs may be attributed to reduced resource depletion or disproportionately more older individuals breeding (Bennett *et al.* 2017). In

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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.

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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 ²) and nearest distance (km) in parenthesis | Average Wave Fetch within 50 km of the colony (km) ^a | Colony Size ^b | Number of eggs (clutches) | Number of broods down feathers were sampled from | Dates down feathers were sampled |
|----------------|----------------------------------|--------------|---------------|--|---|--------------------------|---------------------------|--|--|
| 1. Islay | 18/05/2014 | 55.8 | 6.48 | 1 (12) | 1044 | 25 | 24 (9) | 11 | 27/05/2014 |
| 2. Oronsay | 03/06/2014 | 55.43 | 5.12 | 2 (28) | 743 | 95 | 75 (31) | 33 | 06/06/2014, 17/06/2014, 02/07/2014 |
| 3. Pladda | 31/05/2014 | 54.84 | 5.13 | 89 (29) | 840 | 150 | 38 (15) | 24 | 20/06/2014, 28/06/2014 |
| 4. Lady Isle | 13/05/2014 | 55.53 | 4.73 | 473 (3.5) | 957 | 830 | 72 (24) | 28 | 30/05/2014, 11/06/2014, 18/06/2014 |
| 5. Portpatrick | 05/05/2014 | 54.43 | 5.57 | 222 (8) | 1243 | 175 | 58 (28) | 2 | 09/06/2014 |

| | | | | | | | | | |
|---------------|----------------------------|-------|------|-----------|------|-----|-----------|-----|---------------------------|
| 6. Copeland | 11/05/2014 & 23/05/2014 | 54.69 | 5.52 | 405 (3.5) | 993 | 683 | 141 (48) | 22 | 15/06/2014, 29/06/2014 |
| 7. Strangford | 14/05/2014 | 54.40 | 5.61 | 406 (2) | 1004 | 190 | 106 (39) | 13 | 11/06/2014 |
| Total | | - | - | - | - | - | 514 (194) | 133 | |

^a 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, whilst 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). ^b Colony size is the count of apparently occupied nests (AON) in 2012 or 2013 using standard monitoring techniques (Walsh *et al.* 1995).

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 (AICc). k is the number of estimated parameters included, w_i is the Akaike weight, and $\Delta AICc$ is the AICc difference. Supported models ($\Delta AICc < 2$) are shown in bold and were used in the model averaging to obtain parameter estimates (Table 3).

| Variables included within model | K | AICc | $\Delta AICc$ | w_i |
|--|----------|---------------|---------------|--------------|
| (A) Eggshell colour | | | | |
| Intercept only | 1 | -913.3 | 0.00 | 0.320 |
| Clutch Size | 2 | -912.6 | 0.70 | 0.225 |
| Colony Size | 2 | -911.3 | 1.98 | 0.119 |
| 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) Maculation | | | | |
| Colony Size, Isotope_PC1 | 3 | -601.3 | 0.00 | 0.487 |
| Isotope_PC1 | 2 | -599.9 | 1.44 | 0.238 |
| 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 |
| (C) Shape | | | | |
| Colony Size | 2 | -254.8 | 0.00 | 0.432 |
| Colony Size, Isotope_PC1 | 3 | -253.6 | 1.24 | 0.232 |
| Clutch Size, Colony Size | 3 | -253.0 | 1.86 | 0.171 |
| 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 |
| (D) Size | | | | |
| Clutch Size, Colony Size, Isotope_PC1² | 4 | 1234.3 | 0.00 | 0.474 |
| Colony Size, Isotope_PC1² | 3 | 1234.8 | 0.46 | 0.377 |
| Colony Size | 2 | 1238.2 | 3.88 | 0.068 |
| Clutch Size, Colony Size | 3 | 1238.9 | 4.60 | 0.048 |
| Isotope_PC1 ² | 2 | 1241.4 | 7.05 | 0.014 |
| Clutch Size, Isotope_PC1 ² | 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 |

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 ^a |
|----------------------------|--------|--------|--------------------------|--------|----------------------------------|
| | | | 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 ² | 20.864 | 6.548 | 7.946 | 33.782 | 0.878 |
| Clutch Size | -0.594 | 0.723 | -2.367 | 0.232 | 0.538 |

^a Relative importance refers to the sum of all model weights in which a given parameter occurs.

Fig. 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.

Fig. 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 in Fig. 1.









