

Interannual repeatability of eggshell phenotype in individual female Common Murres (*Uria aalge*)

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Abstract: The recognition of own progeny is critical in group-living organisms that provide parental care for their young. The colonial seabird Common Murre (*Uria aalge* (Pontoppidan, 1763); also known as the Common Guillemot) does not build a nest, so direct cues must be available for the parents to recognize their own egg. However, only anecdotal evidence exists that, as seen in other avian lineages where examined, eggshells of Common Murres are also consistent in most aspects of their appearance between different breeding attempts by each female. Using digital photography, we quantified several eggshell traits of a handful of captive Common Murres across multiple years. Individual female Common Murre eggs were significantly repeatable in background colour, maculation coverage, spot shape, and shell size. Laying individually consistent and recognizable eggshells across breeding attempts may benefit Common Murres by reducing both the cost of relearning and the risk of misidentifying their own eggs. More generally, these data also add to the growing knowledge of individually consistent eggshell genesis by the avian reproductive system.

Key words: coloniality, Common Murre, colouration, discrimination, egg recognition, maculation, *Uria aalge*.

Résumé : La reconnaissance de leur propre progéniture est d'importance clé pour les organismes vivant en groupe qui prodiguent des soins parentaux à leurs jeunes. Le guillemot marmette (*Uria aalge* (Pontoppidan, 1763), aussi appelé marmette commune), un oiseau marin colonial, ne construit pas de nid, de sorte qu'il doit y avoir des signaux directs permettant aux parents de reconnaître leur œuf. Comme pour d'autres lignées d'oiseaux, il n'existe toutefois que des preuves anecdotiques de la similitude de la plupart des aspects de l'apparence des coquilles d'œuf d'une même femelle de guillemot marmette produites lors de différentes tentatives de reproduction. En utilisant la photographie numérique, nous quantifions plusieurs caractères des coquilles d'œuf de quelques guillemots marmettes en captivité sur plusieurs années. Les œufs d'une même femelle sont significativement similaires en ce qui concerne leur couleur de fond, la couverture des maculations, la taille des maculations et la taille de la coquille. La ponte par une femelle donnée de coquilles similaires et reconnaissables pour différentes tentatives de reproduction pourrait avantager les guillemots marmettes en réduisant les coûts d'apprentissage et le risque d'identification erronée de leurs propres œufs. Plus généralement, ces données s'ajoutent aux connaissances croissantes sur la genèse cohérente au plan individuel des coquilles d'œuf par le système reproducteur des oiseaux. [Traduit par la Rédaction]

Mots-clés : colonialité, guillemot marmette, coloration, discrimination, reconnaissance des œufs, maculation, *Uria aalge*.

Introduction

In many lineages of animals, parental investment often involves a costly period of provisioning dependent young (Clutton-Brock 1991). In group-living species, it is critical that parents direct care towards their own genetic progeny for adaptive benefits to accrue. Parents may identify and provision their own offspring via indirect cues, often using location (e.g., the site of the egg mass, den, or nest) as a reliable proxy to recognize genetic progeny (Hauber and Sherman 2001). However, in species where young are precocial, or can (be) move(d) between dens or nests, using direct recognition cues may be needed to discriminate between foreign and own young (Medvin et al. 1993).

For example, in group-breeding birds, including colonial seabirds that do not build nests, the identification of own eggs and

dependent young can be challenging (Hauber 2014). This is because indirect cues, such as egg or chick location in high-density colonies, may not be specific or consistent enough for accurate offspring recognition (Birkhead 2016). In the face of natural selection for accurate identification of their own eggs across their long life span (over 40+ years in the wild; Fransson et al. 2010), Common Murres (*Uria aalge* (Pontoppidan, 1763); also known as Common Guillemots) have evolved highly variable egg appearances between individual females (Ainley et al. 2002) (Fig. 1). This is adaptive for this colonial seabird that nests at high densities (mean: 20 pairs/m²; Birkhead and Nettleship 1980) by laying its sole egg directly on rock cliffs because nests cannot serve a reliable cue to locate and identify a pair's own single egg

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Fig. 1. Representative colour and pattern variations between eggs, as viewed from the blunt end, collected from different individual Common Murres (*Uria aalge*) in Iceland. Photo credit: K.B. Colour version online.



(Birkhead 1978). Indeed, Common Murres have become a textbook exemplar (e.g., Faaborg 1988) of individually distinctive eggshell traits, including a diverse mix of background colouration and maculation patterns and variation in egg size and shape (Dale 2006; Birkhead et al. 2017a, 2017b). In turn, when given the choice of multiple eggs, Common Murre parents accurately select their own eggs for retrieval and incubation (Tschanz 1959). In contrast, even closely related, but less densely nesting, colonial seabird species show both less egg variability and poorer egg recognition abilities compared with Common Murres (Gaston et al. 1993).

Here we test whether high levels of phenotypic individuality in Common Murre egg appearance may be the result of prominent interindividual variation coupled with low levels of intraindividual variation. Across many avian lineages, egg phenotypes show strong repeatability when laid by the same females (e.g., colouration, maculation, and size; Hauber 2014), although for species laying multiple eggs per nest such repeatability can also decline with advancing incubation stage or differences in viability (e.g., Randall and Dawson 2017) and between clutches or across breeding seasons (e.g., Honza et al. 2012). No data on quantitative eggshell trait repeatability exist for bird species that typically lay a single egg per season. Regarding Common Murres specifically, only qualitative accounts have been available on eggshell traits' individual repeatability within the same season or across different seasons for eggs laid putatively by putatively the same females (Storer 1952; Marsault 1975; Ainley et al. 2002; Birkhead and Montgomerie 2018). The only exception is Common Murre egg shape, where quantitative, statistically significant within-individual repeatability was demonstrated by Birkhead et al. (2017a). Because quantitative assessments of intraindividual egg trait phenotypes

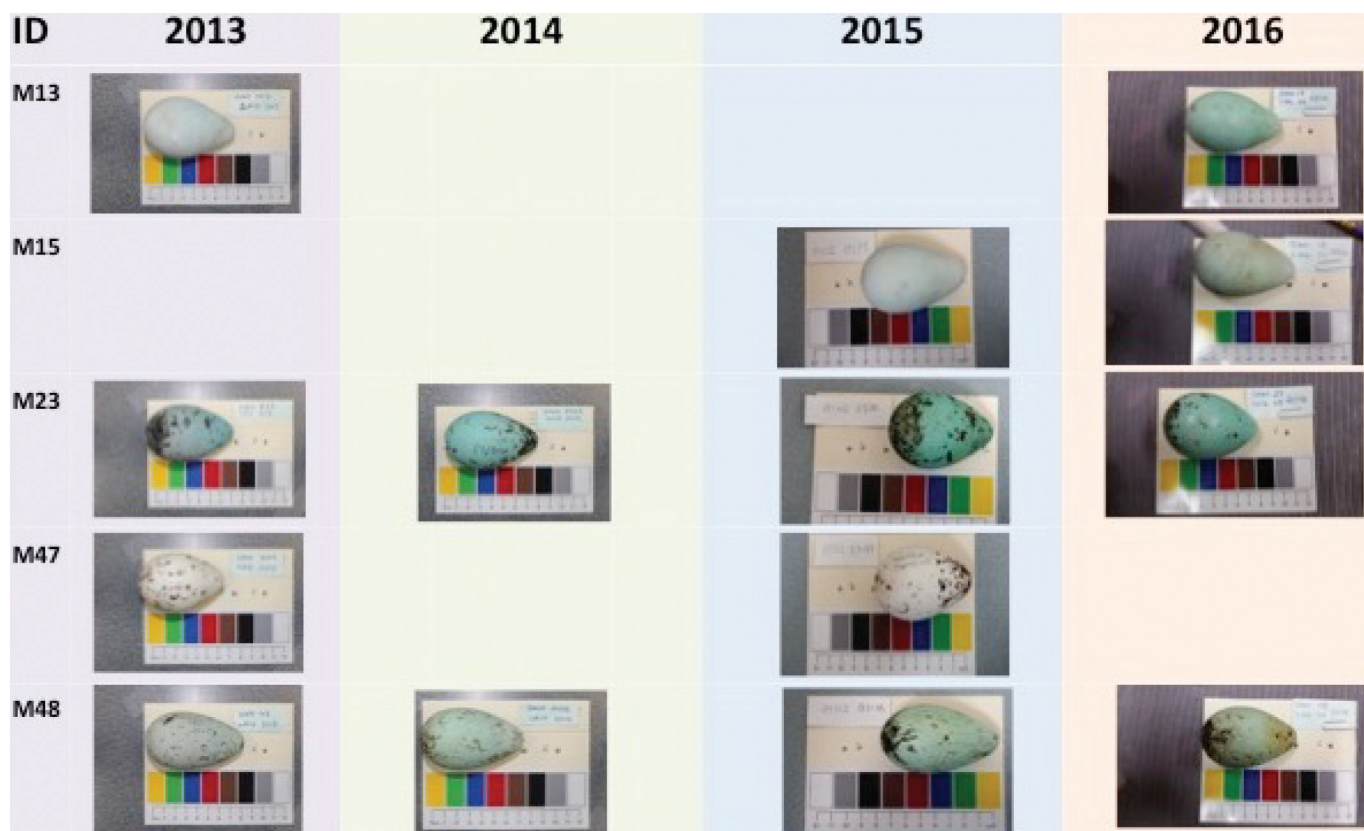
are mostly lacking, we use statistical tests to assess the repeatability of eggshell appearance when laid by the same female Common Murres. Here we analyzed the colouration and maculation patterns, as well as the size and shape metrics taken from standardized digital photographs of Common Murre eggs laid by individually marked females ($n = 8$), in a captive colony across multiple breeding seasons. Our data set, although admittedly small, provides an independent complement to studying other eggs known to be laid by the same marked females across (and not within the same) years that are available for research from museum collections (a total of $n = 9$ such females identified and analyzed by Birkhead et al. 2017a).

Materials and methods

Subjects and photography

Common Murres are long-lived seabirds that nest in dense colonies and typically return annually to breed with the same mate; they provide obligate biparental care, with at least one parent present from egg laying to fledging (Moody et al. 2005). For this study, we opportunistically tapped into the rare resource of a captive bred Common Murre colony. First, we made contact with Oregon Coast Aquarium (Newport, Oregon, USA) personnel in charge of birds including Common Murres (C.J.M.). We asked and arranged for the caretaker team to take multiple photographs of Common Murre eggs ($n = 17$) laid by each female ($n = 8$) that had been collected at the onset of staff-detected incubation behaviour, as part of regular animal husbandry, during the 2013–2016 breeding seasons. Each egg was photographed in the same year as laid, so as to control for fading across years (e.g., Cassey et al. 2010), and

Fig. 2. Photographic documentation of the representative appearance of only those captive female Common Murres (*Uria aalge*) that laid multiple (two or more) eggs across the different years of data collection at the Oregon Coast Aquarium (Newport, Oregon, USA). Photo credit: C.J.M.



was assigned to a female Common Murre based on which individual was incubating that egg; we did not conduct genetic analyses of parentage. Five of the eight females laid eggs in two or more years of the study (Fig. 2). Digital photographs, saved as JPG files, were taken of eggs lying horizontally along their length against a colour and size standard, with four photographs per egg, each after a 90° rotation around the long axis. We acknowledge that although digital photography is suitable for the analysis of egg shape (e.g., Troscianko 2014; Stoddard et al. 2017), it does not capture all data relevant for avian colour perception, including UV reflectance (Dale et al. 2015). Instead, we used photographs to quantify the physical appearance of the eggshells (see below for spectrometric validation of this approach).

Background colour quantification

All colour scoring of eggs was conducted blind to the laying female's identity. For each photograph, we scored background colour by measuring red, green, and blue (RGB) values with the image analysis software package colorZapper (Valcu and Dale 2014). Scores were taken on a polygon subjectively selected that encompassed the characteristic background colouration in that particular photograph. We excluded any obvious areas of glare and selected an area of the egg that did not contain any spotting. The colorZapper software then calculated the mean values for red (R), green (G), and blue (B), on scales of 0 to 255, for 400 randomly chosen pixels within the selected polygon. In addition, we scored the RGB values on a colour standard present in each image. We then normalized the RGB egg scores with respect to the colour standard included in each photograph (Laucht et al. 2010). Our final RGB scores for each egg were calculated as the mean of the four separate images.

Validating digital photography based background colour data with avian-visible spectrophotometry data

We validated our digital photography's background colour measurements against full-spectrum avian-visible reflectance data suitable for the analysis of avian visual perception (e.g., Cassey et al. 2008). For this purpose, we used Common Murre eggshells collected for commercial (sale) purposes on the south Langanes cliffs (66°18'41.2"N, 14°49'15.9"W (66.311448, -14.821074)) in northeastern Iceland, but obtained for scientific purposes by us in the 2014 breeding season. For $n = 21$ eggshells, we took digital photos of eggshells ($n = 4$ photos per shell; see above) with a colour standard visible in each photo, as well as collected avian-visible spectrum (300–700 nm) reflectance data ($n = 3$ of the shell's background colour per egg) with an Ocean Optics spectrometer directly from the same eggshells (following Igc et al. 2012). We then calculated brightness and blue chroma (sensu Cassey et al. 2008) for the reflectance spectra and used linear regressions, respectively, against principal component (PC) 1 and PC2 (see below) of the RGB values obtained from the photographs in the same manner as described for the captive eggs above.

Maculation coverage quantification

We quantified maculation (spotting) coverage by cropping out the pointy-end third, middle-region third, and blunt-end third of each egg along its long axis. For each cropped third, the image was converted to a bitmap in Adobe Photoshop and the spotted area was transformed to black (RGB = 0,0,0) and the non-spotted area was transformed to white (RGB = 255,255,255). We then measured the percentage of black pixels in each third as a measure of spot coverage. We did not quantify avian-perceivable spotting patterns of Common Murre eggs (sensu Stoddard et al. 2014), because there

Table 1. Principal component (PC) eigenvectors for the analyzed Common Murre (*Uria aalge*) egg feature variables.

Background colour		
Egg feature variable	PC1: background brightness	PC2: background colour
RGB: standardized R	0.54	0.83
RGB: standardized G	0.60	-0.29
RGB: standardized B	0.59	-0.47
Explained variance (%)	86.10	11.70
∑ Explained variance (%)	97.80	
Spot coverage		
Egg feature variable	PC1: spottiness	PC2: spot gradient
Blunt-end spot (%)	0.54	-0.65
Mid-spot (%)	0.70	-0.01
Pointy-end spot (%)	0.47	0.76
Explained variance (%)	61.30	31.60
∑ Explained variance (%)	92.90	
Spot colour		
Egg feature variable	PC1: spot brightness	PC2: spot colour
RGB: standardized R	0.55	0.82
RGB: standardized G	0.60	-0.25
RGB: standardized B	0.58	-0.52
Explained variance (%)	89.40	8.77
∑ Explained variance (%)	98.17	
Spot profile		
Egg feature variable	PC1: spot shape	PC2: spot shape gradient
Blunt-end spot shape index	0.57	0.73
Mid-spot shape index	0.57	-0.69
Pointy-end spot shape index	0.59	-0.03
Explained variance (%)	84.70	9.96
∑ Explained variance (%)	94.66	
Egg dimensions		
Egg feature variable	PC1: egg shape	PC2: egg size
Egg length	0.71	0.71
Egg width	-0.71	0.71
Explained variance (%)	51.60	48.40
∑ Explained variance (%)	100.00	

Note: Principal component analyses were performed using correlation matrices.

are no data on the species-specific sensory abilities of Common Murres to perceive such patterns (Caves and Johnsen 2018).

Spot colour quantification

We also quantified spot colour in the same way as for background colour (see above). In this case, however, we selected a polygon around a representative spot located on the photos of each egg, calculated the mean RGB of the pixels in that polygon, normalized the RGB spot scores with respect to the colour standard included in each photograph, and then took the mean values across the four replicate photos for the final spot colour RGB score.

Spot profile quantification

For the subset of Common Murre eggs with any maculation ($n = 13$), we randomly selected five spots on each third of each egg photo, measured the length and width of each spot in pixels, and then calculated the ratio of the length to width as a spot profile index, with higher values corresponding to longer, narrower spots. Our final spot profile index for each egg was the mean within each third of the shell, averaged across the photographs for each egg.

Egg dimensions quantification

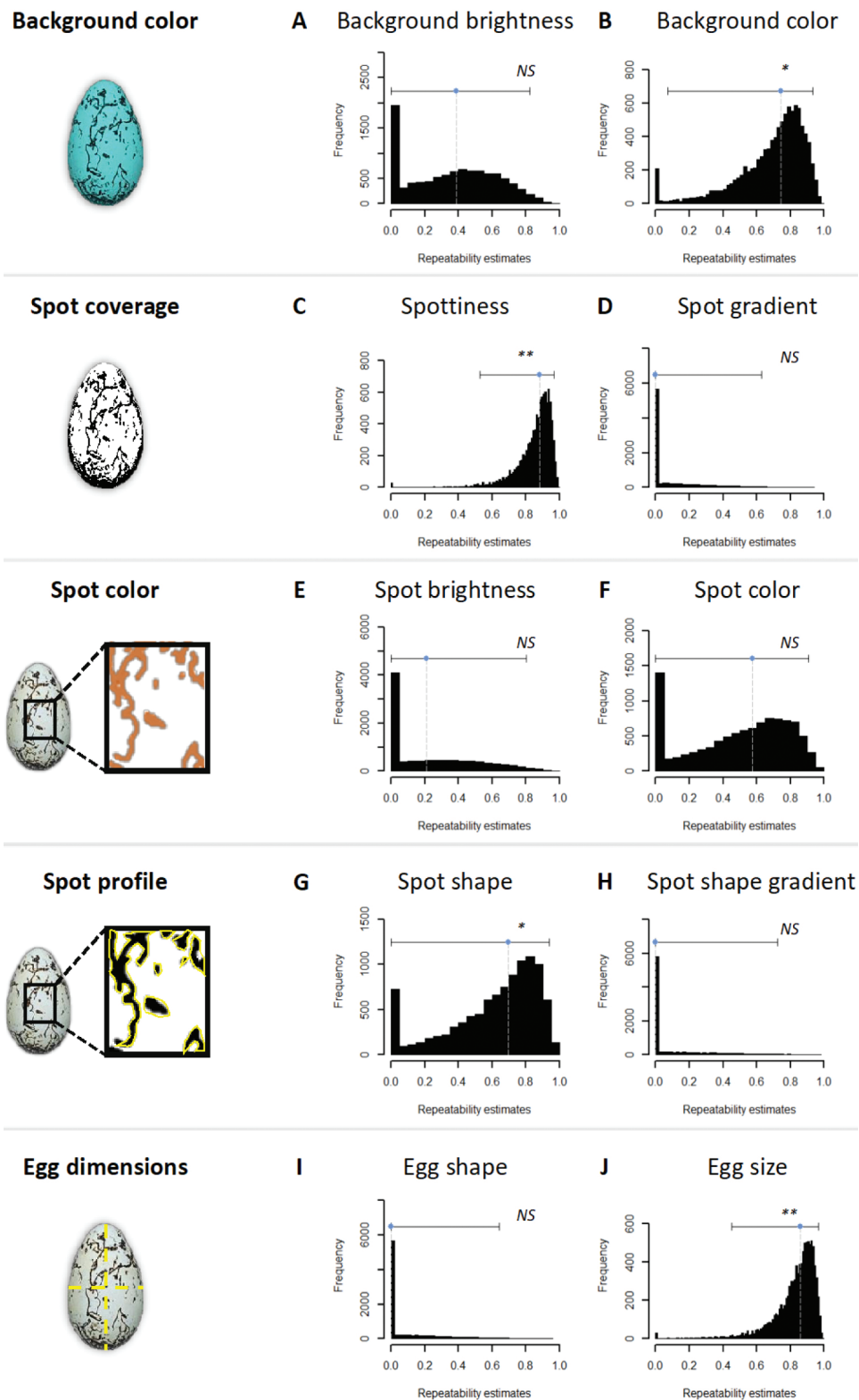
Common Murre eggs have interspecifically unique (Stoddard et al. 2017) and intraspecifically highly variable shell shapes

(Birkhead et al. 2017a), and we quantitatively approximated size and shape metrics by measuring the length and width of each egg from the photographs and running these data through a principal component analysis (PCA; see below). Again, data were averaged from each photograph to calculate a single length and width metric per egg.

Statistical analyses

To eliminate collinearity between our measured egg traits and reduce the dataset into independent axes of variation, we conducted a set of unrotated PCA with correlation matrices in JMP version 12 (Table 1). For those metrics where data were collected for each third along the long axis of the egg and these differences entered into the PC scores (Table 1), we used the term “gradient” to indicate such egg-location-dependent variability. We then calculated the repeatability of (i) Common Murre egg colour (PC1: background brightness; PC2: background colour), (ii) spot coverage (PC1: spottiness; PC2: spot gradient), (iii) spot colour (PC1: spot brightness; PC2: spot colour), (iv) spot profile (PC1: egg shape; PC2: egg size gradient), and (v) egg dimensions (PC1: egg size; PC2: egg shape) to determine the consistency of unique within-individual egg phenotypes by the separate egg traits. In a preliminary analysis, we detected no year-of-collection effects in any of these response metrics (least squares fit, all $P \geq 0.27$; sensu Cassey et al. 2010), implying a lack of effect on egg morphology due to subject

Fig. 3. Ninety-five percent distribution (*y* axes) and confidence intervals of within-individual Common Murre (*Uria aalge*) egg feature repeatability estimates (*x* axes) from 10 000 bootstrap samples for principal component scores for egg background colour (A, B), spot coverage (C, D), spot colour (E, F), spot shape (G, H), and egg dimension (I, J). Permutation significance test (*P* values from 15 000 permutations): NS (not significant), $P > 0.05$; *, $P < 0.05$; **, $P < 0.005$. Colour version online.



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age, nutrition, or other husbandry-related interannual variation in captivity. We also visually confirmed that each of our PC scores formed Gaussian distributions.

Repeatability, or the intraclass correlation (ICC), is a metric calculated by partitioning within-group and between-group variances and is often used for estimating the maximum theoretical value of the heritability of a trait (Bell et al. 2009) and relative heritabilities across different traits (Wolak et al. 2012). Repeatabilities for the within-individual female consistencies of all Common Murre egg trait PC values were calculated using the rptR function and package (Stoffel et al. 2017) in R version 3.4.2 (R Core Team 2017). Permutation significance tests of repeatabilities for Gaussian data distribution, using individual female bird ID as a grouping factor, were done for each PC by comparing a reference null distribution of $n = 15\ 000$ randomly permuted sample repeatabilities with the actual repeatability of the observed data. Given 15 000 permutations, the achievable P value of the repeatability significance tests can never be lower than $1/15\ 000$, or 0.000067, well within the generally accepted type I error level of $\alpha = 0.05$ for parametric statistical tests (Ernst 2004). Finally, 95% confidence intervals of the egg feature PC repeatabilities were estimated using $n = 10\ 000$ bootstrap samples.

Results

Regarding the validation of the digital photography based background colour data with reflectance spectrometry across the avian-perceivable range, we predicted and found a strong positive linear correlation between spectral reflectance brightness and PC1 of RGB scores ($R = 0.66$, $n = 21$ eggs, $P = 0.0007$) and a strong negative correlation between blue chroma and PC2 of RGB scores ($R = -0.72$, $P = 0.0001$). Background colour was highly repeatable within individual Common Murres, but egg background brightness was not (Figs. 3A, 3B). Spottiness was also highly repeatable, but spot gradient was not (Figs. 3C, 3D). Neither spot brightness nor spot colour was statistically repeatable (Figs. 3E, 3F). Spot shape was repeatable, but spot shape gradient was not (Figs. 3G, 3H). Finally, egg size was highly repeatable, whereas egg shape was not (Figs. 3I, 3J).

Discussion

In Common Murres, the recognition cues for each female's eggs may be reliably based on interindividual variation in specific eggshell morphology traits (Dale 2006). Here we show that such differences are further reinforced by statistically repeatable intraindividual patterns of eggshell background colour, maculation coverage, and spot shape, as well as overall size. In contrast, our limited sample sizes indicate that any nonsignificant patterns must be interpreted conservatively; for example, in an analysis of a much larger data set ($n = 78$ eggs laid by $n = 34$ females), Birkhead et al. (2017a) showed consistent repeatability of intraindividual eggshell shape in Common Murres. Similarly, using a subset of only those of our eggs that had any maculation at all in our samples, spot colouration showed no significant repeatability even though the shape of the repeatability frequency plot (Fig. 3F) resembled more closely those of the significant patterns rather than all the other nonsignificant ones. Therefore, we advocate for further and collaborative research across teams to generate and use larger sample sizes and comparisons of within year (i.e., the relaying of lost or removed eggs; Birkhead et al. 2017a) and between year (i.e., interseasonal) traits of eggs laid by the same, individually marked female Common Murres in the wild.

How and why are Common Murre eggs consistently coloured and patterned when laid by the same female? Aspects of the individual consistency and interannual repeatability reported here regarding eggshell phenotypes also suggest that Common Murres are similar to many other studied bird species from several avian orders (e.g., Galliformes: Sezer and Tekelioglu 2009; Gruiformes:

Petrie et al. 2009; Passeriformes: Cherry et al. 2007; Croston and Hauber 2015) in that avian egg morphology is reliably associated with female identity within and between breeding attempts and between breeding seasons. A proximate explanation may be that genomic, transcriptomic, and physiological processes associated with the formation and pigmentation of eggs laid by the same female birds yield more consistency in colouration and maculation across eggs within, rather than between, individuals (Stoddard et al. 2017). This is especially likely for a simple, two-pigment based system of eggshell appearance that is shared across all known living and even some extinct birds (Igic et al. 2010), whereby biliverdin is responsible for the blue–green hues of the shell surface and its matrix and protoporphyrin IX is responsible for the rusty-brown background and the maculation colours (Hanley et al. 2015).

In turn, an ultimate explanation may be that egg consistency by each female is favored by natural selection if female Common Murres benefit from remembering their own eggs' phenotypes from prior breeding attempts and use such memories as mental templates to assist in the accurate learning and the error-proof recognition of each newly laid egg (Dale 2006). Furthermore, with a low and reproductively costly divorce rate ($\sim 8\%$ between years; Moody et al. 2005), even mated males could benefit from learning and remembering the appearance of their long-term mate's prior eggs to aid accurate recognition of her subsequent eggs for each year's incubation period. Overall, however, it remains to be assessed experimentally, this time focusing on the perceptual and behavioural responses of individuals to experimental eggs which have carefully manipulated colours, spotting patterns, and shapes designed (sensu Hauber et al. 2015), to tease apart the relative biological importance of egg each feature in egg recognition by Common Murres.

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