



Egg patterns as identity signals in colonial seabirds: a comparison of four alcid species

Lilly Quach | Audrey E. Miller | Benedict G. Hogan | Mary Caswell Stoddard

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey

Correspondence

Mary Caswell Stoddard, Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544.
Email: mstoddard@princeton.edu

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Abstract

The ability to recognize mates, kin, offspring and neighbors by their individually distinctive traits—individual recognition (IR)—is widespread in animals. Much work has investigated IR from the perspective of the recognizer, but less is known about the extent to which signals have evolved to facilitate IR. To explore this, one approach is to compare putative identity signals among species that differ in life history and extent of IR. In Common Murres (*Uria aalge*), a colonially breeding seabird, the eggs of individual females are remarkably variable in terms of color and pattern (maculation). Common Murres also appear to recognize their own eggs, leading to the hypothesis that variable egg phenotypes evolved to promote recognizability. However, we lack a quantitative assessment of the egg pattern information in Common Murres and their close relatives. Here, we analyzed images of eggs laid by four alcid species: Common Murres, Thick-billed Murres (*Uria lomvia*), Razorbills (*Alca torda*) and Dovekies (*Alle alle*). We extracted pattern measures believed to be relevant to bird vision and calculated Beecher's information statistic (H_s), which allowed us to compare the amount of identity information contained in each species' egg patterns. Murres, which nest in dense colonies and can recognize their own eggs, have egg patterns with a relatively large amount of identity information compared to Razorbills and Dovekies. Egg recognition has not been demonstrated in Razorbills and Dovekies, whose colonies are less dense. Our results are consistent with the hypothesis that complex patterns of Murre eggs may have evolved to increase individual recognizability.

KEYWORDS

alcids, Beecher's information statistic, colonial breeding, eggshell patterning, identity signal, individual recognition

1 | INTRODUCTION

The ability to recognize mates, kin, offspring, and neighbors is a hallmark of social behavior. Many animals have evolved individual recognition (IR), a specific form of recognition in which one animal (the receiver) identifies another animal (the signaler) based on its individually distinctive traits (Tibbetts & Dale, 2007). Historically, most work on IR has focused on the receiver's ability to

discriminate individuals, with less work exploring how signalers might actively broadcast their own identity (Dale, 2006; Dale, Lank, & Reeve, 2001; Tibbetts & Dale, 2007). When a signal has evolved to promote recognizability, it is called an identity signal. Although identity signals have had a long history of study (Beecher, 1989), their quantification has been relatively rare outside the acoustic domain, in part because we lack unified metrics (Linhart et al., 2019).

Quach, Miller, and Hogan should be considered joint first authors.

TABLE 1 A comparison of egg recognition ability and breeding ecology characteristics across extant Alcini species.

	Egg discrimination	Qualitative egg pattern variation	Nest site characteristics	Breeding density
Common Murre	Yes, retrieve own egg when presented a choice of own and foreign. If own egg replaced by foreign egg, only incubate if visually similar ^{1,2}	High ^{1,3,4}	Broad and narrow cliff ledges, flat rocky surfaces. Unsheltered ^{3,5-8}	Estimates vary, but very high. 22–34 birds/m ² 4,9 20–70 pairs/m ² 10
Thick-billed Murre	Yes, but more likely to accept foreign egg than Common Murres ¹	High ¹	Some overlap with Common Murre in cliff use, not on flat areas. Unsheltered ^{3,5,6,8}	Few clear estimates, but lower than Common Murre due to avoidance of flat areas ⁸
Razorbill	No ⁴ , but see ^{3,11}	Lower than Murre species ^{3,4}	Transition zones between cliffs and grassy areas, ledges, caves, crevices and burrows ³⁻⁵	Lower density. 0.25–4 pairs/m ² 10,12
Dovekie	Unknown	None	Concealed nests 0.3–1 m below surface in boulder screens ^{13,14}	Low density, estimates vary. 0.45–1.9 pairs/m ² 13–15

Note: 1 (Gaston et al., 1993), 2 (Tschanz, 1959), 3 (Tschanz, 1989), 4 (Birkhead, 1978), 5 (Williams, 1974), 6 (Taylor, Patirana, Birt, & Friesen, 2012), 7 (Birkhead, 1977), 8 (Birkhead & Nettleship, 1987), 9 (Kokko, Harris, & Wanless, 2004), 10 (Birkhead, Thompson, & Montgomerie, 2018), 11 (Shugart, 1987), 12 (Bédard, 1969), 13 (Evans, 1981), 14 (Egevang, Boertmann, Mosbech, & Tamstorf, 2003), 15 (Kampp, Falk, & Egevang Pedersen, 2000).

The distinctive colors, patterns, and shapes of eggs laid by different female Common Murres (*Uria aalge*, also known as the Common Guillemot) are a classic candidate example of a visual identity signal (Birkhead, 1978; Dale et al., 2001; Hauber, Bond, et al., 2019; Tibbetts & Dale, 2007; Tschanz, 1959). In theory, identity signals used for parent-offspring recognition are likely to evolve when animals breed in large, crowded colonies (Buckley & Buckley, 1972; Tibbetts & Dale, 2007). Common Murres nest in extremely dense colonies, with roughly 20 pairs per square meter or higher (Birkhead & Nettleship, 1980; see also Table 1). Female Common Murres lay a single egg, directly on the bare ledges of rocky cliffs, and can distinguish their own egg from a foreign one (Tschanz, 1959). Have the egg characteristics of Common Murres evolved to facilitate individual recognition? To test this, one approach is to determine whether a species' egg traits have the predicted characteristics of identity signals: they should be condition independent, highly variable in a population, and relatively fixed or repeatable over an animal's lifetime (Dale et al., 2001; Tibbetts & Dale, 2007). Common Murre eggs appear to fulfill the last of these predictions. Recent studies show that several aspects of an individual female's egg appearance—including shape (Birkhead, Thompson, & Biggins, 2017), size, background color, and some pattern traits (Hauber, Luro, et al., 2019)—are highly repeatable across multiple breeding attempts. Identity signals are also predicted to comprise multiple uncorrelated components to maximize entropy and thus overall information capacity (Caves, Stevens, Iversen, & Spottiswoode, 2015). Hauber, Bond, et al. (2019) recently showed that background

color and pattern (maculation) density are uncorrelated in Common Murre eggs.

A second approach used to investigate whether traits evolved as identity signals involves comparing traits across closely-related taxa with different cognitive, social, and ecological characteristics (Tibbetts & Dale, 2007). Common Murres and their close relatives belong to the Alcini tribe (family: Alcidae; subfamily: Alcinae), a group of colony-nesting seabirds including four extant species (Figure 1)—Common Murre, Thick-billed Murre (*Uria lomvia*, also known as the Brünnich's Guillemot), Razorbill (*Alca torda*), and Dovekie (*Alle alle*, also known as the Little Auk)—and numerous extinct species, such as the Great Auk (*Pinguinus impennis*). Multiple phylogenetic relationships have been proposed for extant species in this group (see Figure 1; Pereira & Baker, 2008), with the most recent analysis placing Razorbills as sister to a group in which Dovekie is sister to the two *Uria* species (Murres, Figure 1; Smith & Clarke, 2015). All four extant Alcini species are similar in that they typically lay a single egg per breeding attempt, but they vary in some important respects (summarized in Table 1). For example, breeding density is higher in Common Murres and Thick-billed Murres than in Dovekies and Razorbills. In addition, Dovekies lay eggs in concealed burrows, while Murres tend to lay eggs in the open—with Razorbills in between, generally laying in crevices or on open substrate (Table 1). Murres also tend to lay eggs that appear (at least qualitatively) to have a higher degree of color and pattern variation than those of Dovekies and Razorbills (Figure 1; Table 1). This observation led Tschanz (1959, 1989) and Birkhead (1978) to propose that, in

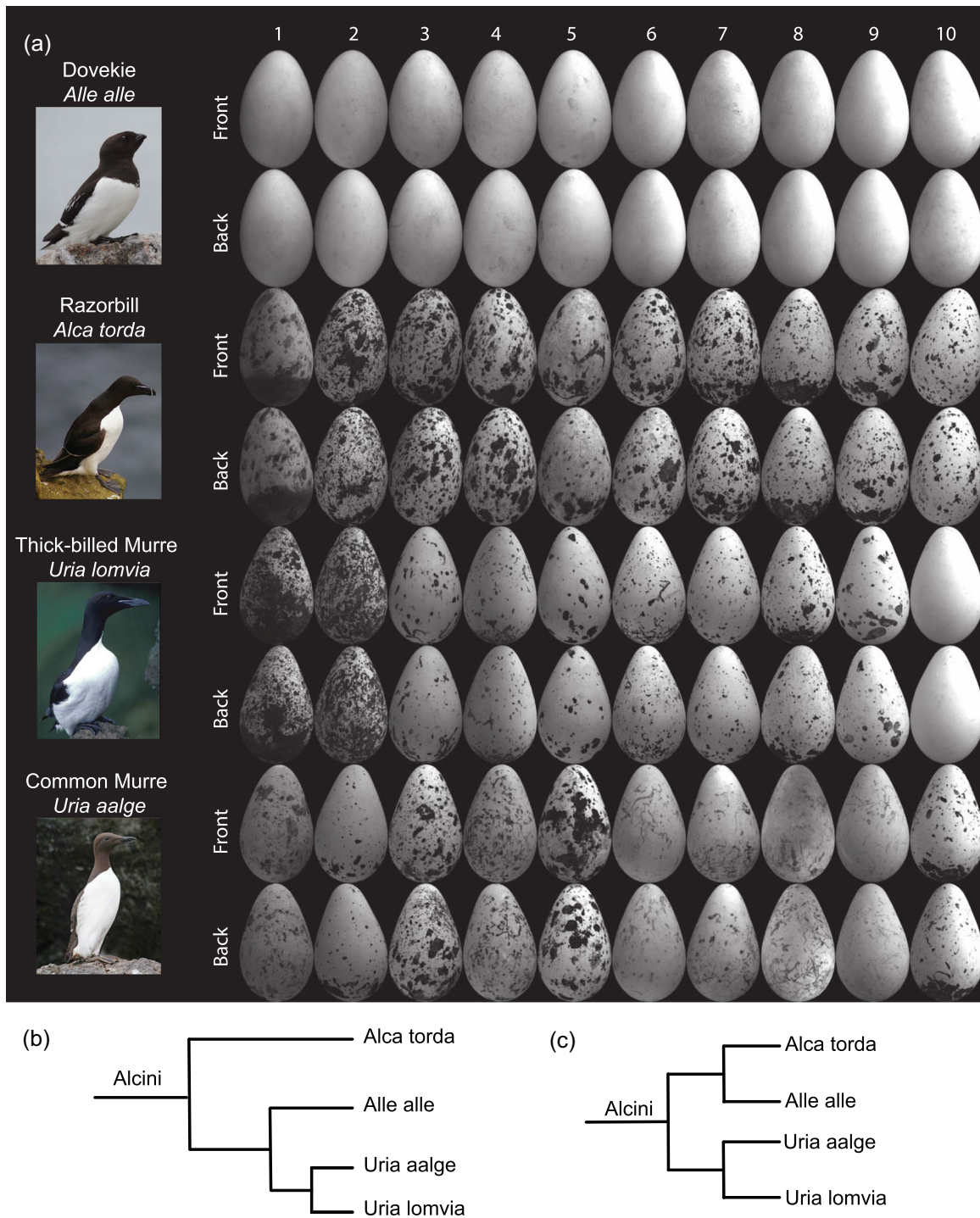


FIGURE 1 (a) Two sides (for convenience, called the “front” and “back” here) of 10 selected eggs are shown here for the four alcini species in this study. We found that the Thick-billed Murre and Common Murre have the highest identity information, with a relatively high degree of between-egg variation compared to within-egg variation. Egg images were generated using estimates of avian double cone stimulation (for luminance/achromatic processing). Images: *Uria aalge* (Dick Daniels), *Uria lomvia* (Vernon Byrd), *Alca torda* (Paul Wordingham) and *Alle alle* (Bernard Scherler). Licenses: CC BY-SA 3.0, public domain, CC BY 2.0, and CC BY 2.0, respectively. All images cropped to size and not to scale. (b, c) Support exists for various phylogenetic relationships. (b) Topology from the most recent phylogenetic reconstruction (Smith & Clarke, 2015); additional support for this topology comes from Pereira and Baker (2008) and Smith and Clarke (2011). (c) Topology supported by analyses from Pereira and Baker (2008), Mouv, Arnason, and Árnason (2002) and Mouv, Johansen, Erikstad, and Piatt (1994). Thomas, Wills, and Székely (2004) found support for a variety of relationships, and Smith (2011) found a polytomy of *Alca torda*, *Alle alle*, and the *Uria* species. [Color figure can be viewed at wileyonlinelibrary.com].

Common Murres, highly variable egg phenotypes help facilitate egg recognition in the crowded colonies. In a series of experiments, Tschanz (1959) demonstrated that Common Murres can recognize their own eggs. A subsequent study by Gaston, De Forest, and Noble (1993) revealed that Thick-billed Murres are also capable of egg recognition, but they are more likely than Common Murres to incubate a foreign egg if their own had disappeared. By contrast, Razorbills do not appear to show egg discrimination (Birkhead, 1978, but see Shugart, 1987; Tschanz, 1989). Whether or not Dovekies can recognize their eggs is unknown.

Alcid egg patterns are ripe for study using this second approach: we currently lack a quantitative comparison of egg pattern traits across the four extant Alcini species. If egg patterns evolved to promote recognizability in densely breeding species, we predict that Common Murres and Thick-billed Murres (higher breeding density, demonstrated egg recognition ability) will lay more distinctive eggs than Dovekies and Razorbills (lower breeding density, undemonstrated egg recognition ability). How can we best quantify the distinctiveness of Alcini eggs? Determining whether egg traits have some predicted characteristics of identity signals (described above) can provide clues, but ultimately a measure of individual distinctiveness must compare the between- to within-individual variation in traits. Identity signals work best when this ratio is maximized

because an individual will be different from others in the population but highly self-similar (Beecher, 1989; Linhart et al., 2019).

In this study, following an early suggestion by Shugart (1987), we used Beecher's information statistic (H_s ; Beecher, 1989; Linhart et al., 2019) to quantify and compare the egg pattern content of the extant Alcini species. H_s describes the information content (hereafter identity information) of what Beecher (1989) called a signature system, the collection of potential identity signals in a given species or system. It captures, in a single measure, variation within and among individuals. To calculate H_s , we first photographed eggs in museum collections and extracted several pattern measures believed to be important for egg recognition (Spottiswoode & Stevens, 2010; Stoddard & Stevens, 2010; Stoddard, Hogan, Stevens, & Spottiswoode, 2019; Stoddard, Kilner, & Town, 2014). In our analyses, we focused on egg pattern (maculation) rather than on other aspects of the egg phenotype (e.g., shape, color, size). Our goal was to understand the specific contribution (if any) of egg patterns—the intricate scrolls, squiggles, and blotches for which Murre eggs are famous (Figures 1 and 2)—to identity information. Next, we combined these pattern metrics into a single measure (H_s), which quantified the pattern variation within a single egg (variation between two sides of an individual egg) and among individual eggs (laid by different individuals of the same species). We then compared the amount of

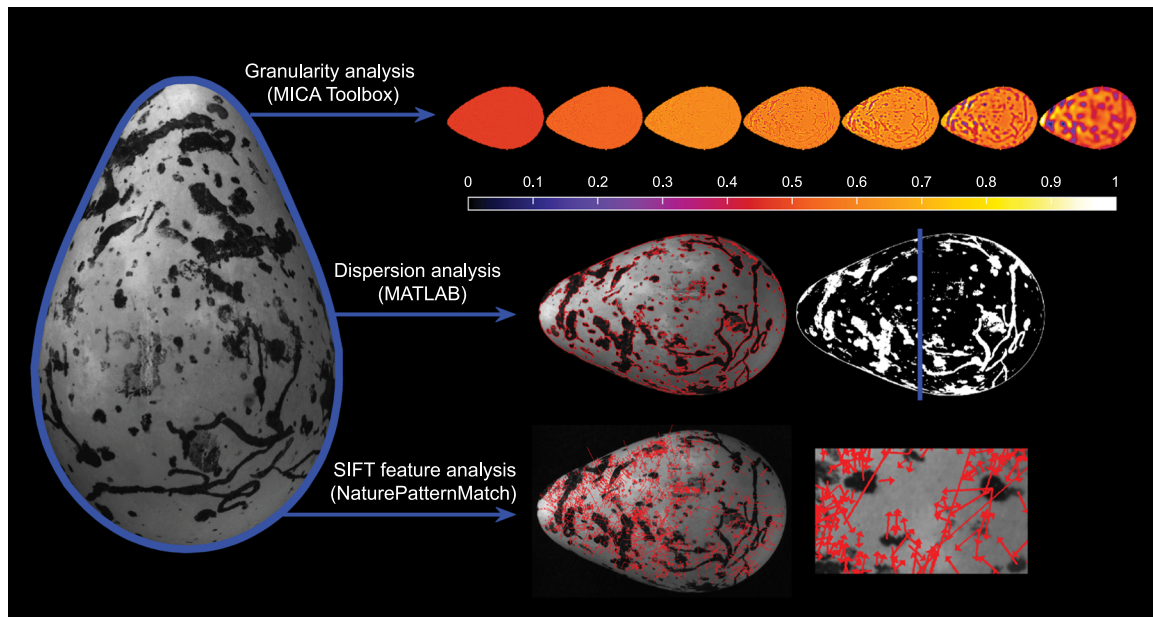


FIGURE 2 Illustration of pattern analysis methods. The luminance image was analyzed using three processes. Top: Granularity analysis measures pattern energy at a series of spatial scales. From the granularity analysis, we derived maxPower (maximum energy at any filter size), maxFreq (filter size containing the maximum energy), propPower (the proportion of total energy contained at maxFreq), and sumPower (sum of pattern energy across all filter sizes). Middle: In dispersion analysis, patterning (maculation) is converted to a binary mask. The proportion of coverage of each hemisphere of the egg (left/right of blue vertical indicated) is measured to give PropTop (proportion of the top part of the egg covered with pattern) and PropBot (proportion of the bottom part of the egg covered with pattern), and the ratio of PropTop to PropBot gives Dispersion. Bottom: NaturePatternMatch (NPM) finds scale-invariant feature transform (SIFT) features in each image, here visualized as red arrows. Note that SIFT features actually encode features as a 128-dimensional vector; arrows only indicate the dominant scale and orientation of each feature. Each image's suite of SIFT features is then compared to all other eggs to generate a similarity matrix, which is inverted and submitted to multi-dimensional scaling (MDS). Each egg is represented by a single location (encoding information about its NPM-based similarity to other eggs) in a 3D MDS space. [Color figure can be viewed at wileyonlinelibrary.com].

identity information among species and investigated whether it is qualitatively correlated with egg discrimination behavior and breeding density (see Table 1). Recent work has highlighted the advantages of H_s over alternative metrics used to quantify identity signals. It is relatively independent of sample size, easy to calculate and compare, and best meets the criteria for an ideal identity metric (Linhart et al., 2019).

2 | METHODS

2.1 | Data collection and imaging

We obtained UV/RGB images of 240 egg specimens held in the collections at the American Museum of Natural History (AMNH), the Academy of Natural Sciences at Drexel University (ANSP), and the Delaware Museum of Natural History (DMNH). We omitted 20 of these eggs from analyses because they were damaged or because images contained writing or the blow hole. Final sample sizes were: Dovekie: ($n = 17$); Razorbill: ($n = 44$); Thick-billed Murre ($n = 72$), and Common Murre ($n = 87$). We opportunistically sampled eggs from these collections. We photographed all available eggs at the AMNH and ANSP, with supplemental eggs from the DMNH. Several different subspecies were included in our samples (Table S6-S7). An analysis that split species to subspecies level revealed qualitatively similar results (Table S6), so we report here results in which the subspecies distinctions are ignored. In some cases, eggs were collected from the same geographic location in multiple years, so it is possible that our sample contained more than one egg from an individual female. However, we consider this to be a very slight possibility. We assume that our sample for each species roughly captured the egg pattern variation that might exist in a hypothetical population. We acknowledge that this is a simplifying assumption and future studies should explore interpopulation and geographic variation in egg patterning within each species and subspecies.

We photographed eggs in RAW format with a converted UV-sensitive Nikon (Minato, Japan) D7000 camera, with a Nikkor 105 mm fixed lens (ISO Sensitivity of 400, f/13 aperture). We took images sequentially using a Baader (Mammendorf, Germany) UV/IR-Cut/L filter (420–680 nm pass) and a Baader U-Filter (320–380 nm pass) to capture a (human-) visible light image and a UV image, respectively. Each image contained Labsphere (North Sutton, NH) 2% and 99% Spectralon reflectance standards, as well as a scale bar. Specimens were illuminated by a 50 W Exo-Terra SunRay halogen lamp (Hagen Inc./Exo-Terra, Montreal, Quebec, Canada) and light was diffused through PTFE. We took each image from a fixed distance, with the camera positioned directly above the stage. The egg was supported by a small ring, and adjustments were made to ensure that the major axis of the egg was orthogonal to the camera (parallel to the stage; Biggins, Thompson, & Birkhead, 2018; Birkhead et al., 2017). We photographed each egg in this manner on two sides (i.e., two images—front and back—per egg were obtained, via rotation of the egg by 180° rotation around its major axis). From each image,

we extracted a number of pattern metrics (see Figure 2 and Section 2.3).

2.2 | Processing images

We linearized, standardized, and converted images to multi-spectral image stacks using the MICA toolbox (Troscianko & Stevens, 2015) for ImageJ (Schneider, Rasband, & Eliceiri, 2012). In addition, we scaled all images to 34 pixels/mm (based on the longest axis of the smallest egg to avoid scaling up any images). In MICA, we generated a mapping from the known camera sensitivities to a model of avian vision. We modeled the images from camera space using Nikon D7000 Nikor 105 mm sensor sensitivities and the emission spectra of the SunRay lamp to a Peafowl visual system (*Pavo cristatus*; Hart, 2002) under D65 illumination. Based on analyses of Common and Thick-billed Murres, it is likely that members of the Alcidae family are violet-sensitive (VS) rather than ultraviolet-sensitive (Ödeen, Håstad, & Alström, 2010). We chose to model our images using a Peafowl visual system because this is a representative VS system provided in MICA. This process resulted in an image stack of predicted cone stimulations for each side of each egg specimen, from which we extracted various pattern measures (see below). All analyses of pattern information (see below) were performed using the double cone (“luminance”) channel, from a region of interest (ROI) that contained the entire (visible) egg in each image. In birds, the double cones are believed to mediate achromatic (including pattern) perception (Jones & Osorio, 2004). All color and double cone measurements were sampled from a small rectangular ROI, which contained only the background color and luminance of the egg. Background color and luminance analyses were not the main focus of the paper and are included in the Supporting Information.

2.3 | Pattern analysis

2.3.1 | Granularity

Using the luminance images described above, we performed “granularity” (Fast Fourier bandpass filtering) analysis, which measures pattern energy at a range of spatial scales, capturing low-level information about the pattern (Figure 2; Stoddard & Stevens, 2010; Troscianko & Stevens, 2015). This process results in a granularity (or pattern energy) spectrum for each egg image, which describes overall amounts of pattern and the contribution of various marking sizes to that pattern. We selected a minimum filter size of 2 pixels, with a 1.414 multiplier, resulting in 14 filter sizes of exponentially increasing size, from 2 to 181 pixels in width. From the resulting granularity spectra, we calculated the following measures: maxPower (maximum energy at any filter size), maxFreq (filter size containing the maximum energy), propPower (the proportion of total energy contained at maxFreq), and sumPower (sum of pattern energy across all filter sizes). maxFreq indicates the dominant marking size of the pattern, while

maxPower indicates the amount of pattern at that marking size. sumPower measures the total amount of pattern across all marking sizes. propPower is the ratio of maxPower to sumPower, so it measures the relative contribution of the most dominant marking size to the overall pattern. An analysis replacing these extracted measures with the entire granularity spectrum did not qualitatively affect results (see Supporting Information).

2.3.2 | NaturePatternMatch

We analyzed luminance images using NaturePatternMatch (NPM; Figure 2; Stoddard et al., 2014), a scale-invariant feature transform (SIFT; Lowe, 1999, 2004)-based algorithm that compares the texture of two images. For this analysis, full-resolution 16-bit TIFF format versions of the (32-bit) luminance images were exported and cropped to size (with 100 pixels space on each side). We then masked these images to remove all background information (using MATLAB code from Stoddard et al., 2017) and enhanced them with a combination of median filtering and histogram equalization; these are methods to reduce noise and increase local contrast in images (Stoddard et al., 2019). We repeated all analyses omitting image enhancement and the results were qualitatively unchanged (see Supporting Information). We then submitted the images to NPM feature extraction and matching. This process resulted in a matrix of pairwise similarities between all egg images. To generate image-level data, (i.e., one value that describes features of a given image, rather than pairwise data), we inverted this similarity matrix to generate a distance matrix and submitted this to classical multi-dimensional scaling (MDS; using command `cmdscale` in R Statistics) for each species. MDS is a dimensionality reduction technique that attempts to find a lower-dimensional embedding of points in Cartesian space that maintains the pairwise distances of the input. In this analysis, we used three MDS dimensions.

NPM analysis produced spurious results for the immaculate eggs of Dovekies because eggs that have no or few extractable features cannot be accurately compared to others, resulting in high distances for clearly near-identical immaculate eggs. To eliminate this spurious variance, the MDS coordinates for all Dovekie eggs were set to the same point (zero in all three MDS dimensions). The same approach was not taken with the immaculate eggs of Common Murres or Thick-billed Murres, because here the relatively high distances between maculated and immaculate eggs is appropriate (analysis omitting immaculate or near-immaculate eggs from these species yielded the same qualitative results, see Supporting Information; also see subsampling analysis below).

2.3.3 | Dispersion

Egg patterning is often non-uniformly distributed across the egg surface. To account for this, we adopted methods from Stoddard and Stevens (2010) and semi-manually thresholded egg images into

binary images where pigmentation is white and background is black (Figure 2). We then used this binary mask to measure dispersion of pigment across the egg image. This resulted in the following measures: PropTop (proportion of pigmented pixels on the narrower half of egg), PropBot (proportion of pigmented pixels on broader half of egg), and Dispersion (ratio of PropTop to PropBot).

2.4 | Calculating identity information

The above approaches yielded a number of pattern measures for each image (10 for Common Murres, Thick-billed Murres, Razorbills and 3 for Dovekies, see below). We then compared the within-individual variance (i.e., within the egg, using the two images of the same egg) in pattern measures to the between-individual variance (i.e., intra-species egg, using all images of all eggs). We expected recognizable eggs to be those in which the pattern is similar on both sides of the egg but different from the patterns of other eggs. Thus, we considered pattern measures extracted from both sides of a single egg to be samples of that egg's overall pattern. To analyze these samples, we calculated Beecher's information statistic (H_s), a measure of the amount of information in a signature system that is available to convey individual identity (Beecher, 1989; Linhart et al., 2019). Its value is proportional to the number of individuals that can be discriminated in a population, given the assumption that a receiver can distinguish within-individual variation (Beecher, 1989). H_s provides a convenient metric for comparing signature systems among species.

To calculate H_s for each species, pattern measures must be independent of one another (to avoid double-counting of correlated variance between pattern measures). To accomplish this, we used principal component analysis (PCA; using R statistics function `prcomp`, with scaling and centering; R Core Team, 2017) on the pattern measures extracted on all images for each species, before calculating H_s on the calculated principal components (using function `calcHS` in R package `IDmeasurer`; Linhart et al., 2019). We retained all principal components for each species except for Dovekies (maxFreq, Dispersion, PropTop and PropBot dropped because of zero variance). Finally, we calculated a version of H_s that accounts for multiple observations per individual (Linhart et al., 2019); here, we had two observations (the "front" and "back" of an individual's egg). For completeness, we also included in all analyses a version of the H_s calculation that retains only those principal components that significantly predict individual identity (see Beecher, 1989; Linhart et al., 2019). These values should be similar because by definition those parameters that do not predict individual identity well will not contribute much to H_s . To facilitate comparisons among the H_s values, we report the mean and (sample) standard deviation of H_s from 100 random bootstraps for each species. In each bootstrap, we sampled egg pairs randomly with replacement until we reached the original sample size for each species. We then used this bootstrap sample to calculate PCA and H_s . Because sample size varied among species, we also include in the Supporting Information a version of

this analysis in which each species is repeatedly randomly subsampled (without replacement) to match the sample size of the least-sampled species (Dovekies, Table S1). This analysis had qualitatively similar results. Note that the PCA axes shown in Figure 3 were generated with the original sample without any random sampling.

We note that H_s is inherently focused on the signaler. This means that it does not explicitly describe the sensory-perceptual systems of the receiver or the behaviors expressed in recognition (Beecher, 1989). This also means that we do not distinguish between-egg recognition as simple discrimination (i.e., one egg discriminated from all other eggs) and “true” individual recognition (i.e., all eggs discriminated from one another). As Beecher (1989) noted, however, the requirements for identity signals do not differ between these alternatives: in both cases, all eggs must be distinguishable from

other eggs. For a further discussion of what constitutes “true” individual recognition, see Tibbetts and Dale (2007).

3 | RESULTS

The amount of information available to signal identity (identity information) contained in Common Murre, Thick-billed Murre, Razorbill, and Dovekie egg patterns differs (Table 2). Differences between the immaculate white eggs of Dovekies (which lay their eggs in concealed nests and have the lowest breeding density of the Alcini species) and the other species are unsurprising. More noteworthy is the difference between Razorbills and the Murre species (Figures 1 and 3). Razorbills’ value of H_s is approximately 60–70% of that of Common Murres and Thick-billed Murres (Table 2; see also

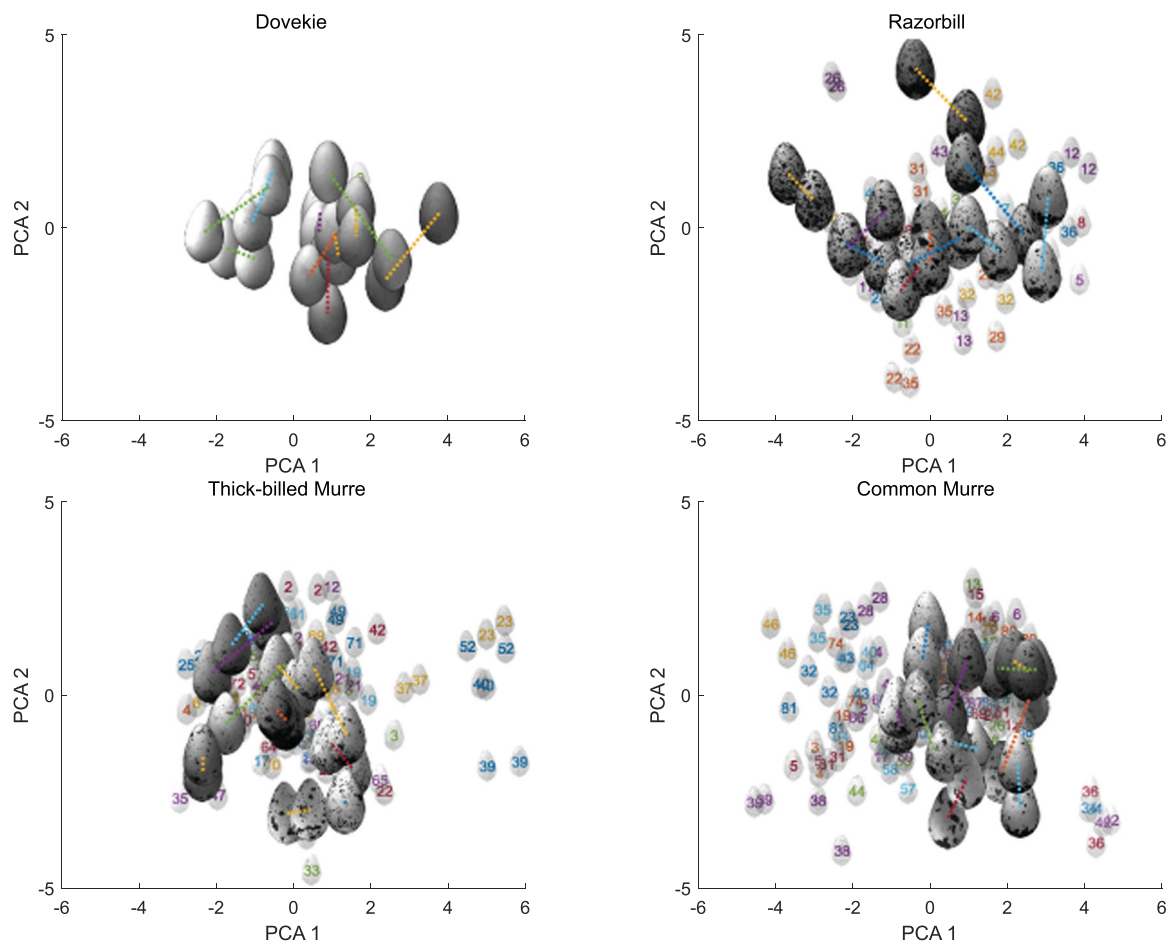


FIGURE 3 Plot of egg images embedded in principal component analysis (PCA) axes. Here all egg images for each species are embedded in their respective first two PCA axes, calculated with all samples from each species. In each case, 10 randomly selected pairs of eggs are enlarged and opaque. Colored dotted lines on this subset link the “front” and “back” images of each pair. All other egg pairings are denoted with numbers. Note that some eggs are occluded by the selected subset. High individual recognizability is characterized by large inter-pair variation and low intra-pair variation. Note also some small clusters (outliers) of egg pattern types in Razorbills, Thick-billed Murres, and Common Murres. The influence of these outliers is explored in the Supporting Information. Separation of Dovekie eggs along the two PCA axes is likely due to artifacts of lighting during photography in combination with little or no pattern information. The three-dimensional geometry of eggs can produce image artifacts when lighting is not perfectly diffuse. These artifacts appear as crescent-shaped shadows most easily seen in the Dovekie eggs at the left side of the top left panel. Other differences in the apparent brightness of the eggs (all four species) are a product of real variation in egg pigmentation. [Color figure can be viewed at wileyonlinelibrary.com].

TABLE 2 Beecher's information statistic (H_s) values for each species.

Species	Mean H_s All Vars	SD H_s All Vars	Mean H_s Sig. Vars	SD H_s Sig. Vars
Dovekie	1.440	0.463	1.394	0.303
Razorbill	5.752	0.633	5.562	0.697
Thick-billed Murre	9.354	0.662	9.351	0.664
Common Murre	10.116	0.750	10.116	0.750

Note: All Vars, H_s summed over all PCA axes for each species; Sig. Vars, H_s summed over PCA axes found to differ significantly between individuals (see IDmeasurer documentation; Linhart et al., 2019). Mean and standard deviation from 100 random bootstrap calculations of PCA and H_s .

Supporting Information). This indicates that the egg patterns of Murre species are able to convey more identity information to a potential discriminator. Both Common Murres and Thick-billed Murres have egg recognition capabilities (Gaston et al., 1993; Tschanz, 1959), which Razorbills apparently lack (Birkhead, 1978). These results are qualitatively robust to subsampling (to the sample size of the smallest sample of 17 egg image pairs) and to variations in image processing, inclusion of color measures, and exclusion of immaculate and near-immaculate eggs from Thick-billed Murres and Common Murres (see Tables S1–S6).

The higher identity information in Murre eggs relative to Razorbill eggs is likely due to some combination of higher inter-egg differences and lower intra-egg differences (Figures 1, 3, and S1–3) and/or decreased correlation between different pattern variables (Figures S4–7; Caves et al., 2015). The increase in the inter-egg variability of Murre eggs could be driven in part by increased complexity of maculation on their eggs (Figure 1; Gaston et al., 1993). In our sample, Razorbill eggs were lightly to moderately speckled and blotched with uniform dark pigmentation, whereas Murre eggs appeared to have greater variation in the degree of pigmentation (immaculate to heavily pigmented), type of pigmentation (including squiggles), and pigment intensity (shades of pigmentation).

4 | DISCUSSION

Using Beecher's information statistic (H_s), we quantified the amount of identity information contained in the egg patterns (e.g., the size, shape, orientation and dispersion of markings and features) of four seabird species. Eggs of the Common Murre and Thick-billed Murre possessed the most identity information ($H_s > 9$ for each species), with intermediate information in the Razorbill ($H_s \approx 5.5$) and very little information in the Dovekie ($H_s \approx 1.5$; Table 2). Our findings are consistent with the idea that egg patterns in the Common Murre and the Thick-billed Murre may have evolved to signal identity. As hypothesized by Tschanz (1959) and Birkhead (1978), selection on

females to produce recognizable eggs in very dense breeding colonies may have resulted in the information-rich egg patterns we observe in these species. An alternative hypothesis is that Murre eggs evolved to be highly variable for some other purpose (e.g., due to drift, for camouflage), and Murres use that phenotypic variability for IR without it having evolved to signal identity *per se*. Or perhaps Murres have simply evolved to be better at the visual and cognitive demands of recognition than Dovekies and Razorbills, irrespective of the available signal content. We cannot rule out these possibilities. However, because all four species have similar phylogenetic history and similar breeding ecologies—except with respect to breeding density, nest characteristics and egg recognition behavior—these alternatives seem less likely. This is an advantage of the comparative approach: it can identify factors (here, differences in breeding density) that might favor the evolution of identity signals (Tibbetts & Dale, 2007). An important next step will be to understand how phylogenetic history has shaped the evolution of egg patterning across the entire Alcidae family. Our analysis did not account for phylogenetic relatedness (i.e., we did not perform correlative analyses that would require phylogenetic correction), which was not practical due to small sample size and some uncertainty about the evolutionary relationships (Figure 1). Moving forward, it will be productive to assess the degrees to which phylogeny, ecology and cognition/behavior influence phenotypic variation in eggs in this group.

To our knowledge, this is the first quantitative analysis of egg pattern identity signals across multiple colonial seabird species. Most previous comparative work on egg pattern signatures has been performed in another context: the coevolutionary arms races between brood parasites and their hosts. Hosts are under strong selection to recognize and reject parasitic eggs, which can lead to the evolution of host egg patterns that are highly recognizable (reviewed in Langmore & Spottiswoode, 2012; Stoddard & Hauber, 2017). For example, many host species intensely targeted by the parasitic Common Cuckoo (*Cuculus canorus*) in Europe appear to have evolved highly recognizable egg pattern signatures as a defense against cuckoo egg mimicry (Stoddard et al., 2014). In Asia, some cuckoo hosts also appear to use egg pattern information to reject odd eggs (Liu, Yang, Yu, Wang, & Liang, 2019), possibly because their own eggs provide signature information. In addition, passerine host species parasitized by Australian brood parasites have evolved higher within-species egg pattern variation than non-hosts (Medina, Troscianko, Stevens, & Langmore, 2016). Finally, in two African bird families, parasitized hosts have higher entropy (the quantity of information encoded by combinations of egg pattern and color traits at a population level without respect to within-individual variation) in egg traits than unparasitized hosts (Caves et al., 2015).

The ultimate test of whether egg patterns in Murres evolved as identity signals will be to demonstrate that more distinctive eggs in a population have a selective advantage over less distinctive eggs. Are the most recognizable eggs those most likely to survive to hatching? Future behavioral work could test this hypothesis. Even in the parasite-host systems mentioned above, experiments testing

whether distinctive host egg patterns carry a selective advantage are rare—and evidence so far has been mixed; see, for example, Cherry, Bennett, and Moskát (2007) and Moskát, Avilés, Bán, Hargitai, and Zölei (2008), but note that these studies only tested the effect of intraclutch variation (rather than identity information *per se*) on egg rejection behavior. In hosts of the parasitic Cuckoo Finch (*Anomalouspiza imberbis*), behavioral experiments showed that neither the intra- nor interclutch (higher-level) pattern variation in the host's clutch predicted whether host birds would reject a foreign egg (Stoddard et al., 2019).

Beyond detailed behavioral experiments, there are several additional avenues for future research. First, the intermediate amount of identity information in Razorbill eggs (Table 2) is intriguing. Although egg discrimination has not been shown in Razorbills (Birkhead, 1978), some authors alluded to unpublished data suggesting that they may show some recognition (Shugart, 1987; Tschanz, 1989). If future work reveals that Razorbills do show some crude egg recognition, one possible explanation is that Razorbills benefit from IR and egg identity signals—but selection on these traits is relaxed compared to the Murres. Perhaps in the comparatively sparse Razorbill colonies (Table 1)—where physical location might be a more reliable cue of egg identity—only a modest degree of IR, facilitated by intermediate egg pattern identity content, is required.

Another puzzle is the reported difference in egg recognition abilities between the Murre species (with Common Murre showing more refined discrimination; Table 1), given the similar identity content of their eggs (Gaston et al., 1993). Perhaps the higher colony density in Common Murres (driven by their propensity to breed densely on flat areas avoided by Thick-billed Murres; Birkhead & Nettleship, 1987) has led to greater selection for egg recognition, irrespective of egg patterning. Common Murres, in this case, are more discriminating than Thick-billed Murres not because their eggs are more informative but because they have enhanced cognitive abilities. This raises many questions. What are the costs of evolving complex egg patterns versus more elaborate cognitive processes? Can eggs reach an upper limit of identity information, after which selection for increased cognitive abilities becomes more common? Alternatively, perhaps both Murre species are equally able to recognize eggs but differ in their acceptance thresholds, potentially for reasons related to their breeding ecology. Finally, the mechanisms responsible for egg pattern production are still poorly understood in birds (Sparks, 2011). Deciphering the genetic, developmental and physiological processes responsible for egg pattern formation will be an important step toward appreciating how identity signals evolve and persist.

In their recent review of identity signal metrics, Linhart et al. (2019) urged researchers to begin quantifying and comparing identity signals in diverse systems and in multiple sensory modalities. Beecher's information statistic (H_s) will be a powerful measure for such a project because it is relatively independent of sample size and can be calculated at the population (system, species) level. To our knowledge, our study is the first to use H_s to quantify the identity information in egg patterns. Our finding that egg pattern identity information is qualitatively correlated with IR in Alcini seabirds is

consistent with discoveries in other taxa. For example, swallow species capable of IR and nesting in dense colonies tend to have more distinctive vocalizations than closely-related species that lack IR and live alone or in small groups (Beecher, Medvin, Stoddard, & Loesche, 1986). In addition, a highly social paper wasp species with IR has more variable face patterns than two closely-related species lacking IR (Sheehan & Tibbetts, 2010). In these diverse systems, it appears that increased phenotypic variation evolved via selection for identity signals. Unraveling the extent to which this is a general phenomenon across animal taxa will be an exciting goal for future research, and a unified metric (H_s) will make broad comparisons possible.

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DATA AVAILABILITY STATEMENT

The data for pattern analyses are available upon request.

ORCID

Lilly Quach  <http://orcid.org/0000-0003-1833-0561>

Audrey E. Miller  <http://orcid.org/0000-0003-2048-6856>

Benedict G. Hogan  <http://orcid.org/0000-0001-6762-7738>

Mary Caswell Stoddard  <http://orcid.org/0000-0001-8264-3170>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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