

# Kittiwake eggs viewed by conspecifics and predators: implications for colour signal evolution

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Colour traits evolve under the antagonistic selective pressures of increasing detectability to intended receivers (e.g. conspecifics) while minimizing detectability to unintended receivers (e.g. predators). Primarily selected for camouflage, avian egg coloration has also been suggested to have intraspecific signalling functions. A first step in assessing the relative importance of camouflage/communication requires quantifying detectability for different visual systems, which is rarely done. Here, we compared brightness and colour contrasts of black-legged kittiwake (*Rissa tridactyla*) speckled and soiled eggs as seen from a distance by conspecifics and their main avian predator, the common raven (*Corvus corax*). We also examined how egg speckling and soiling deposition on incubated eggs affected egg detectability and egg coloration variability. We found that eggs were detectable by both species, but were more conspicuous to conspecifics than to predators. Egg speckling reduced brightness contrast and increased colour contrast, contributing to reducing detectability by predators while maintaining potential for intraspecific communication, respectively. Soiling reduced egg detectability for both perceivers, but soiled eggs remained more conspicuous to conspecifics than predators. Moreover, soiling did not homogenize the clutch signature of egg colour and speckling, thus allowing intraspecific exploitation of information on female quality that egg coloration may convey or individual clutch recognition. We suggest that further studies of egg colour adaptive functions and evolution should consider all perceivers as well as soiling deposition, an overlooked mechanism that may be favoured by selection against predation.

ADDITIONAL KEYWORDS: crypsis – predation – *Rissa tridactyla* – sexual selection – soiling – visual modelling.

## INTRODUCTION

Signal evolution arises from antagonist selective forces (Maynard Smith & Harper, 2003; Gomez & Théry, 2007), among which selection for maximal crypsis, usually by predators, and selection for maximal conspicuousness, usually by conspecifics (Andersson, 1994). Prey that contrast more against the background are generally easier to detect, and consequently more often captured by predators (Montgomerie, Lyon & Holder, 2001; Schaefer *et al.*, 2006). Hence, signals are selected for minimal detectability – that is minimal visual contrast to the background – by predators. Conversely, colours used in intraspecific communication are selected to convey reliable information about

individual identity, intentions or quality (sex, age or condition) (McGregor, 2005; Osorio & Vorobyev, 2008; Carazo & Font, 2010). These signals are selected for maximal conspicuousness to the background so that the information they convey can be easily deciphered and interpreted.

Solving this conflict can yield many strategies. Prey can conceal their signals with patches temporarily exposed to conspecifics (Gomez & Théry, 2007) or exploit distance-dependent visual detection (Janson, Monzón & Baldovino, 2014) with small coloured patches, which decrease predator detectability from a distance while maintaining close-range conspicuousness to conspecifics (Gomez & Théry, 2007). In extreme cases, 'hidden messages' are traits that can be perceived by conspecifics while remaining undetectable by predators, like ultraviolet (UV) signals in swordtail fish invisible to its UV-blind predator (Cummings, Rosenthal & Ryan, 2003). In less extreme cases, when both conspecifics

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and predators can detect signals, lower contrast yields lower detectability and predation risk (Montgomerie *et al.*, 2001; Schaefer *et al.*, 2006). To date, few studies have estimated whether variation in detectability is common or rare in nature (Kelber, Vorobyev & Osorio, 2003), which requires considering prey and predators simultaneously as well as the long distance for visual detection by predators.

Bird eggs are a pertinent and timely model to compare detectability by predators and conspecifics because there is a debate on whether eggshell colour could evolve through other processes than selection against predation. Eggs are largely submitted to predation (Martin, 1995), which drives egg colour evolution at broad evolutionary scale (Kilner, 2006). Yet, at the genus or species level, the survival advantage of egg camouflage has received mixed support, which can be partly explained by neglecting to account for predator vision (Stoddard, Marshall & Kilner, 2011; Stoddard *et al.*, 2016). Two strategies have been proposed to contribute to camouflage: (1) egg pigmentation can blend the egg into the background on which it rests (background matching; Stevens & Merilaita, 2009a), reduce its edge detection through patterning (disruptive coloration; Stevens & Merilaita, 2009b) or create within-clutch colour variation confusing to predators (Hockey, 1982; Lloyd *et al.*, 2000) and (2) soiling can conceal eggs through adherence of nest material to the shell (Mayani-Parás *et al.*, 2015), a strategy which camouflage value needs to be confirmed.

Egg pigmentation is potentially affected by several other selective pressures than predation, pertaining more to mechanical, physiological and/or signalling functions of coloration (Underwood & Sealy, 2002; Kilner, 2006; Maurer, Portugal & Cassey, 2011). The hypothesis that eggshell coloration can be a sexually-selected signal (Moreno & Osorno, 2003) is lively debated and has hitherto received mixed support (reviewed in Reynolds, Martin & Cassey, 2009; Cherry & Gosler, 2010; Avilés, Soler & Hart, 2011; Cassey *et al.*, 2011; Riehl, 2011; Holveck *et al.*, 2012). Under this hypothesis, the two major eggshell pigments biliverdin (antioxidant giving blue-green coloration) and protoporphyrin (pro-oxidant giving brown coloration), involved in oxidative stress regulation in laying females (McGraw, 2005), would signal female antioxidant capacity and health at laying time (Morales, Velando & Moreno, 2008; Giordano *et al.*, 2015). Egg coloration may thus give information on egg or female heritable quality (Morales *et al.*, 2010a), and males may accordingly adjust their investment in paternal care to offspring (Soler *et al.*, 2008) or their future remating decisions (e.g. divorces). To be a reliable signal of female quality to males, egg colour and patterning should characterize a clutch and thus are expected to

show high variability and provide a clutch signature, that is be relatively consistent among eggs within each clutch (Holveck *et al.*, 2010). This rarely tested assumption needs to be checked because it may be in conflict with the need of an efficient camouflage.

We addressed the questions raised above in the black-legged kittiwake (*Rissa tridactyla*). This cliff-nesting colonially breeding seabird lays whitish-bluish eggs speckled with brown and grey spots in open nests built on narrow ledges or rock outcrops (Coulson, 2011). In this species, as in some other bird species presenting open nests, eggs are clean in the first day(s) after laying and then soiled (Morales, Torres & Velando, 2012). Kittiwake eggshell coloration is a well-suited model to address the simultaneous effect of sexual and natural selection for the following reasons. First, in favour of selection for crypsis, egg predation is common (Coulson, 2011). Second, in favour of selection for female quality signalling, males invest a lot in parental care (Coulson & Porter, 1985) and strongly vary in their parental effort (Coulson & Johnson, 1993; Leclaire *et al.*, 2010). In addition, divorces are frequent (*c.* 17% of the pairs of a colony in Alaska divorced in 3 years: Hatch, Roberts & Fadely, 1993) in this socially and genetically monogamous, long-lived species. Third, eggs are visible: males have ample opportunities to view the eggs of their mate and of the neighbouring females as both sexes incubate in turn, breeding is highly synchronized in colonies (Coulson & Wooller, 1984), and eggs (between one and three eggs) are uncovered by nesting material in cups of vegetation and mud (Coulson, 2011; Burger *et al.*, 2016). Alternative hypotheses on the evolution of other signalling functions of egg coloration are less likely in kittiwakes. Selection for individual clutch recognition is commonly expected under the occurrence of egg/nest disturbance or destruction by conspecifics, or of conspecific or heterospecific parasitic egg laying (Underwood & Sealy, 2002; Evans, Votier & Dall, 2016), but neither of which has been reported in kittiwakes (Yom-Tov, 2001; Helfenstein *et al.*, 2004; Coulson, 2011). The palatability of kittiwake eggs and their cryptic phenotype do not support selection for aposematism and for coercing ('blackmailing') males into helping at keeping conspicuous eggs concealed during incubation (Kilner, 2006; Hanley, Doucet & Dearborn, 2010).

The common raven (*Corvus corax*) is the main egg predator in most kittiwake populations including in the study population (Boulinier *et al.*, 2008). While both bird species are sensitive to the same wavelength range (300–700 nm), they differ in their spectral sensitivity to UV wavelengths: kittiwakes are more sensitive to UV (peak at 370 nm, UVS system, Håstad, Ernstdotter & Ödeen, 2005a) than common ravens (peak at 405 nm, VS system, Ödeen & Håstad, 2003).

Their sensitivity also differs in the short-wavelength range, with a peak of the SWS at 453 nm for the kittiwake and 475 nm for the common raven. These differences give opportunity for differentially detectable signals to be selected in eggshell coloration.

Detectability primarily depends on the contrast between an object and its visual surrounding; it therefore depends on the distance at which an object is seen. Ravens (as well as Laridae predators of kittiwakes' eggs/chicks, [Coulson, 2011](#)) reach kittiwake nests from the air and often hover many metres above the nests alongside cliffs ([Regehr, 1994](#)). They approach the eggs upon attack, but only for a reduced time span. Kittiwakes can also see conspecific eggs from a distance when prospecting ([Boulinier \*et al.\*, 1996](#)). Yet, kittiwakes certainly also see eggs at a closer distance given nest proximity (nest density can exceed 1 nest/m<sup>2</sup>) and high reproduction synchrony in colonies ([Danchin, 1988](#)). Therefore, kittiwakes are certainly able to detect some fine details of the contrasts between the coloration of eggshell spots, eggshell ground and nest, but ravens in their egg-prey search may not.

To assess if intraspecific communication signals can evolve despite selection for predation avoidance, we consider long-distance egg-viewing as it is likely the only distance common to both species. At long viewing distance, both bird species are expected to perceive the contrast between nest and eggs seen as their average coloration or in other words seen as a unique patch against the background (e.g. as shown in reef fishes in which, at long viewing distances, conspecifics see the average coloration, but not the small spots covering the fish body, [Marshall \*et al.\*, 2003](#)).

To advance our understanding on the potential for egg coloration to bear a signal for conspecifics despite predation pressure, we explore whether egg coloration provides high conspicuousness for conspecifics while preventing predator detection through clutch camouflage by egg soiling and spottiness, and examine whether the variability in egg coloration (i.e. within-clutch repeatability), with and without soiling, provides a clutch signature or a camouflage function. If eggshell coloration conveys information for kittiwake conspecifics, we predict (1) that kittiwake eggshell coloration should be more visible for an UV-sensitive (kittiwakes) than for a violet-sensitive visual system (predators) and that this differential visibility should exploit the UV and short-wavelength range. If the selection to avoid predation is strong, we predict (2) that egg soiling and spottiness should make eggs less detectable by predators. Finally, we expect (3) that variability in egg coloration should be high among clutches (i.e. high within-clutch repeatability) if eggs convey a clutch signature. Testing these predictions is a crucial initial step in the questioning of the relative importance and potential incompatibility of predation

and sexual selection in driving eggshell colour evolution in kittiwakes.

## MATERIAL AND METHODS

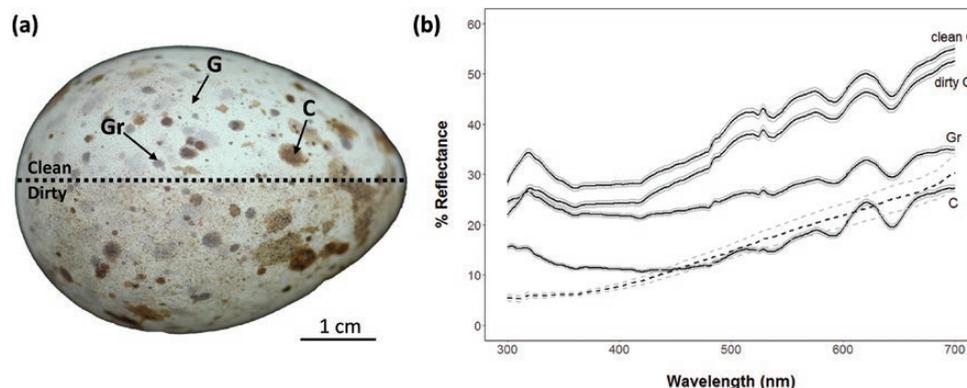
### STUDY SITE AND ETHICS

This study was conducted in June 2006 on Hornøya, an island of northern Norway (70°22'N, 31°10'E) on the black-legged kittiwake as a part of a long-term study ([Boulinier \*et al.\*, 2008](#)). All work was carried out in accordance with standard animal care protocols and approved by the Ethical Committee of the French Polar Institute. Permits to manipulate nest contents of kittiwakes and conduct the experiment were granted by the Norwegian Animal Research Authority and the Regional Ethical Committee of the French Polar Institute for programme IPEV No. 333.

### EGG COLORATION MEASUREMENTS

We measured the coloration of the entire clutch of 51 randomly selected nests (11 nests with 1 egg, 38 with 2, and 2 with 3;  $N = 93$  eggs) from 9 cliffs in the population using objective reflectance spectrometry (300–700 nm) with an Ocean Optics USB 4000 spectrometer, a PX-2 xenon lamp (Florida, USA) and a 200- $\mu$ m fiberoptic probe. All measurements were taken outdoors and perpendicular to the eggshell surface using the probe mount with a black rubber cap to exclude ambient light and which ensured that the probe was at a constant distance of 2 mm from the egg surface but protected from the ambient light. At that distance, the light spot was 2.2 mm in diameter, which was suited to measure egg speckling. Eggshell appearance is comprised by its ground coloration (G), as well as grey (Gr) and chestnut (C) spots ([Fig. 1](#)). We measured ground coloration before and after gently cleaning the eggshells with tap water. However, we only measured eggshell spots from cleaned eggs because dirty spots were difficult to assign to one colour type ([Fig. 1](#)). For each parameter, we took four measurements randomly at different points of the eggshell surface, calculated repeatability estimates  $R \pm SE$  ([Becker, 1984](#); [Lessells & Boag, 1987](#)) and found that these were repeatable (dirty G:  $0.65 \pm 0.04 < R \pm SE < 0.68 \pm 0.04$ ,  $8 < F_{92,277} < 9$ ; clean G:  $0.83 \pm 0.02 < R \pm SE < 0.88 \pm 0.02$ ,  $21 < F_{92,279} < 30$ ; clean Gr:  $0.44 \pm 0.06 < R \pm SE < 0.47 \pm 0.05$ ,  $4 < F_{92,282} < 5$ ; clean C:  $0.47 \pm 0.05 < R \pm SE < 0.56 \pm 0.05$ ,  $5 < F_{92,277} < 6$ ; all  $P < 0.0001$ ). We averaged the four replicated spectra per parameter and thus obtained four averaged spectra per egg for subsequent analyses.

To quantify the amount of surface each colour type covered (G, Gr and C), we took one photo per egg (see [Fig. 1a](#) for an example) with a digital camera



**Figure 1.** (a) Photograph of a kittiwake egg with and without soiling (upper and lower part of the egg, respectively). (b) Mean weighed reflectance spectra ( $\pm 1$  SE, grey lines) of 93 kittiwake eggs (solid lines) and 5 nests (dotted line). G, Gr and C indicate the egg Ground colour, Grey spots and Chestnut spots, respectively.

(Nikon D70S), a macro lens (AF-S VR105 F/2.8), and a ring flash (macro Nikon SB-29s) with the following settings (Mode A, Aperture;  $f/3.2-8$ , mostly  $f/4$ ;  $1/40$  s– $1/320$  s, mostly  $1/250$  s). We then analysed the photos ( $3008 \times 2000$  pixels; .jpeg) using Image J (Rasband, 1997–2016). We previously validated the high repeatability of this method (Holveck *et al.*, 2012). Ground coloration, grey and chestnut spots, respectively, accounted on average for  $75.9 \pm 7.53\%$  (SD),  $16.9 \pm 7.07\%$  and  $7.2 \pm 4.62\%$  of eggshell surface.

#### NEST COLORATION MEASUREMENTS

Detectability of an object primarily depends on its contrast against its visual surrounding. We thus quantified the visual contrast of eggs against the nest background. As we were interested in how eggshell coloration affected detectability and given that the mud out of which kittiwake nests are made give them a typical brownish background colour (Coulson, 2011; Burger *et al.*, 2016), we used the same average nest spectrum for all eggs. Using the aforementioned spectrometric device, we measured nest coloration from a subset of five nests in the study population, with four to five measurements per nest. We computed one average nest coloration spectrum that we used in the analyses.

#### VISUAL CONTRASTS

We considered three types of contrasts for long viewing distance. (1) We assessed the single contribution of the eggshell ground coloration to egg detectability. Indeed, eggs seen from a distance may simply be perceived as a whitish-bluish patch against the nest background (Marshall *et al.*, 2003). We thus quantified the contrast between eggshell ground coloration and average nest coloration. (2) We assessed the visual relevance of eggshell soiling in comparing clean eggshell

ground coloration to dirty one, both contrasted against the average nest coloration. As soiling may increase with time (Mayani-Parás *et al.*, 2015), we recorded the time elapsed since the laying date until the spectral measurement date. (3) On clean eggs, we assessed the simultaneous contribution of eggshell ground coloration and spots to egg detectability. We thus computed an average reflectance spectrum per egg by weighting raw spectra  $R$  (ground coloration, grey spots, chestnut spots) by the proportion of surface ( $\alpha$ ) they covered on the egg, as follows:  $R_{\text{spotted egg}} = \alpha_{\text{eggshell ground coloration}} R_{\text{eggshell ground coloration}} + \alpha_{\text{grey spots}} R_{\text{grey spots}} + \alpha_{\text{chestnut spots}} R_{\text{chestnut spots}}$  (see Endler, 1990). We then compared the contrasts against average nest coloration of this ('real') spectrum to the ('hypothetical') spectrum of the same egg without spots, for which the ground coloration occupied the entire egg surface, namely  $R_{\text{unspotted egg}} = R_{\text{eggshell ground coloration}}$  [i.e. same as (1) above]. We established all three types of visual contrast for each egg and for both raven and kittiwake visual systems.

#### AVIAN VISION MODELLING

We set out to determine the visual contrasts between eggs and nest background as seen by kittiwakes and predators. We quantified the colour contrast with Vorobyev & Osorio's discriminability model (Vorobyev & Osorio, 1998) in its log form (Osorio *et al.*, 2004). The original model has been validated for bird vision in bright light conditions (Vorobyev & Osorio, 1998), and its log formulation, which accurately reflects photon capture (Endler & Mielke, 2005), has been found to accurately predict bird behaviour (Avilés *et al.*, 2010). As kittiwakes nest in open cups in cliffs, birds experience bright light conditions when seeing eggs. The model is thus fully justified. In addition to the colour contrast, we also quantified the brightness contrast using the same approach and following calculations presented in Loyau *et al.* (2007).

The model quantifies the contrast between two objects illuminated by a particular ambient light and seen by a perceiver with a particular spectral sensitivity. The contrast is quantified in just noticeable differences (JNDs), relative to a discrimination threshold (usually taken as 1 JND). Contrast values below 1 JND indicate that the two objects are indistinguishable in coloration; values above 1 JND indicate that objects can be distinguished based on their coloration. As values increase above the threshold, the two objects become easier to discriminate (Schaefer, Schaefer & Vorobyev, 2007; Cassey *et al.*, 2008b; Avilés *et al.*, 2010).

In all calculations, we used the midday open area D65 standard illuminant (CIE) to model the ambient light prevailing at kittiwake nests. We assumed detectability was limited by neural noise only, as recommended when implementing the model for bright light conditions. To compute neural noise, we used the average values for photoreceptor (UVS/VS:SWS:MWS:LWS) relative densities on the retina often taken to model bird vision, that is 1:1.9:2.2:2.1 for the VS model and 1:1.92:2.68:2.7 for the UVS model (Håstad, Victorsson & Ödeen, 2005b). Regarding spectral sensitivity, we considered that both bird species detected colours with their four classes of single cones, and brightness with their double cones, as shown before (Campenhausen & Kirschfeld, 1998).

Physiological data were not available for the spectral sensitivity of the common raven. As shown by Hart (2001), birds can have two different types of spectral sensitivity in the short-wavelength domain, namely either an UV-sensitive (UVS) or a violet-sensitive (VS) vision. Species such as Corvids have a VS vision, with VS photoreceptors maximally sensitive above 400 nm, at 406–408 nm (Hart, 2001). In the absence of physiological data for the study species, it is reasonable to assume similarity to another species with VS vision with a peak located in the same range of wavelengths. Hence, to model the vision of the common raven, we chose the wedge-tail shearwater (*Puffinus pacificus*) in which visual sensitivity, characterized in spectrometry, peaks at 406 nm (Hart, 2004).

Likewise, physiological data were not available for kittiwake vision. Kittiwakes have a UVS vision (Håstad *et al.*, 2005a). As shown by Hart (2004), all species with UVS system have similar vision, most of them with a sensitivity peaking at around 370 nm. Hence, we chose the blue tit (*Cyanistes caeruleus*) to model kittiwake vision. Blue tits have their visual system well characterized, and they are commonly taken as a good representative of UVS vision (Håstad *et al.*, 2005b; Avilés *et al.*, 2010). We performed all colour analyses and visual modelling with Avicol v5 (Gomez, 2006).

## STATISTICAL ANALYSES

### *Colour and brightness contrasts*

We analysed the variations of colour and brightness contrasts using linear mixed models (lmer package in R) with a normal error structure. In all models, we used 'egg identity' nested within 'nest', itself nested within 'cliff' as random term. As recommended by Bolker *et al.* (2009), mixed models are well suited to take into account random effects, that is when there are repeated observations at different levels (here at cliff or nest levels), often in unbalanced designs (different numbers of nests from different cliffs). We used a maximum likelihood approach and minimization of the second-order Akaike's information criteria (AICc), which includes a correction term for small sample sizes in comparison to the number of estimated parameters. We thus selected the best statistical models according to the parsimony principle, considering that two models differing by less than two AICc units are statistically indistinguishable, as currently accepted (Burnham & Anderson, 2002). We rescaled and centred the continuous explanatory variables on the mean, thus generating standardized *z*-scores, to lessen the correlation between the interactions and their component variables. We computed coefficients and standard errors using a restricted maximum likelihood approach and tested factor significance with *t*-tests, that is the ratios between the fixed effect estimates and their approximate standard errors; we also provide the denominator degrees of freedom and the associated *P*-value from a *t* distribution (Bolker *et al.*, 2009).

First, we tested the interactive effects of the 'visual system' (kittiwake or raven), the 'soiling status' (clean or dirty) and the 'time' (time elapsed since the laying date) on the contrast of egg coloration against average nest coloration. Second, we tested the interactive effects of the 'visual system', the 'spottiness' (coloration with or without spots) and the 'surface' (proportion of unspotted surface on each egg) on the contrast of clean egg coloration against average nest coloration.

### *Differential response of receptors*

Following the above-described statistical procedure, we tested which differential response of each of the four receptors (UVS/VS, SWS, MWS or LWS) best explained the difference in colour contrast of eggs against the nest background ( $\Delta S$ ) between the visual systems as follows:  $(\Delta S_{\text{kittiwake}} - \Delta S_{\text{raven}}) \sim (\Delta f_{\text{UVS kittiwake}} - \Delta f_{\text{VS raven}}) + (\Delta f_{\text{SWS kittiwake}} - \Delta f_{\text{SWS raven}}) + (\Delta f_{\text{MWS kittiwake}} - \Delta f_{\text{MWS raven}}) + (\Delta f_{\text{LWS kittiwake}} - \Delta f_{\text{LWS raven}})$  with 'nest' nested within 'cliff' as random term.  $\Delta f$  is the log of the ratio (i.e. the difference of the logs) of the receptor responses to the nest background and to the eggshell colour (Vorobyev & Osorio, 1998).

### Egg variability in coloration

We tested whether soiling affected among-egg variability in visual contrasts (1) by correlating, within eggs, dirty and clean eggshell ground coloration, both contrasted against average nest coloration, with Pearson correlations, and (2) with Bartlett tests of homogeneity of variances.

### Clutch signature

To assess if eggs could convey a clutch signature, we tested whether among-clutch variation of eggshell coloration (i.e. spotted surface and visual contrasts) exceeded within-clutch variation with repeatability estimates  $R \pm SE$  (Becker, 1984; Lessells & Boag, 1987).

We performed all statistics with R 3.3.2 (R Core Team, 2016). Data are available as an online appendix (Table S1).

## RESULTS

### COLOUR CONTRASTS

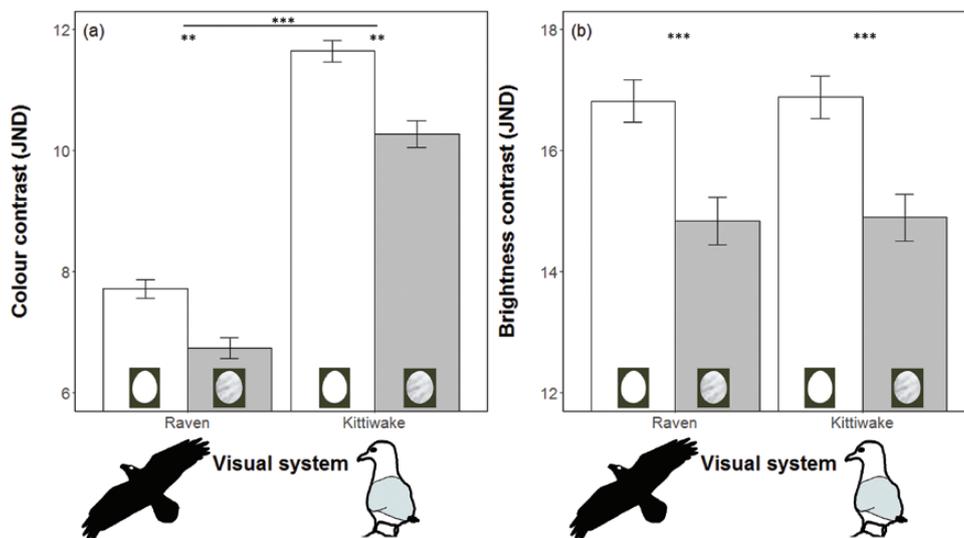
The colour contrast of eggshell ground coloration against the nest was higher for kittiwakes than for their egg predator (visual system effect, estimate  $\pm 1 SE = 3.93 \pm 0.11$ , d.f. = 275,  $t = 34.7$ ,  $P < 0.001$ ; Fig. 2a). Compared to clean eggshell ground coloration, dirty eggshell ground coloration contrasted less with the nest environment, and this decrease was greater for kittiwakes than for their predators (visual system by soiling status interaction, est. =  $-0.40 \pm 0.16$ , d.f. = 275,  $t = -2.48$ ,  $P = 0.014$ ). Still, dirty eggs remained much

more visible (i.e. 3.53 JNDs higher; Fig. 2a) for kittiwakes than for ravens. For both visual systems, the reduction in detectability provided by soiling increased linearly with time elapsed since the laying date, while the detectability of clean eggs did not decrease through time (soiling status by time interaction, est. =  $-0.27 \pm 0.08$ , d.f. = 275,  $t = -2.48$ ,  $P = 0.001$ ).

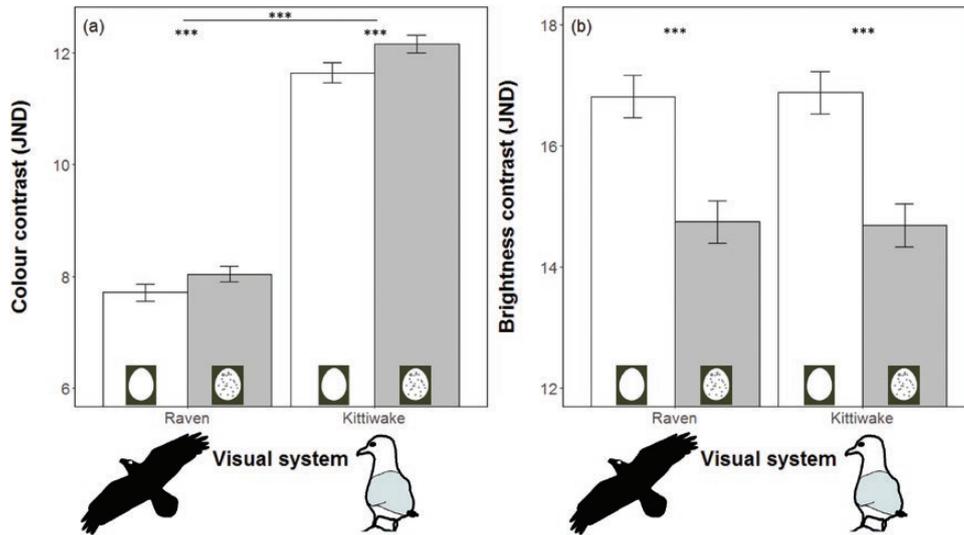
As previously, kittiwake clean eggs (with or without spots) had a higher colour contrast against nest environment for conspecifics than for the predator (visual system effect, est. =  $3.93 \pm 0.05$ , d.f. = 275,  $t = 83.15$ ,  $P < 0.0001$ ; Fig. 3a). Compared to a (hypothetical) purely whitish-bluish egg, a (real) spotted egg provided more colour contrast against the nest (spottiness effect, est. =  $0.33 \pm 0.05$ , d.f. = 275,  $t = 6.93$ ,  $P < 0.0001$ ; Fig. 3a). The gain in contrast was higher for kittiwakes than for the predator (visual system by spottiness interaction, est. =  $0.19 \pm 0.07$ , d.f. = 275,  $t = 2.79$ ,  $P = 0.006$ ), but it was only 0.5 JND on average (Fig. 3a), leading us to anticipate a reduced or null effect on perception. For both visual systems (visual system by spottiness interaction term not retained in the best model), eggs with spots covering a larger surface increased colour contrast more strongly (spottiness by surface interaction, est. =  $-0.19 \pm 0.03$ , d.f. = 275,  $t = -5.82$ ,  $P < 0.0001$ ).

### BRIGHTNESS CONTRASTS

The brightness contrast of eggshell ground coloration against the nest was similar for kittiwakes and ravens (visual system term not retained in the best model; Fig. 2b). Soiling significantly decreased brightness contrast (soiling status effect, est. =  $-1.98 \pm 0.14$ , d.f. = 278,



**Figure 2.** Colour (a) and brightness (b) contrasts between eggshell ground coloration and nest for the visual systems of kittiwakes and ravens (mean  $\pm 1 SE$ ). Empty and grey bars represent, respectively, contrasts in absence and presence of soiling as schematized within bars ( $N = 93$  eggs). \*\*\* $P < 0.001$ , \*\* $P < 0.01$ . Of note, the y-scales are different in (a) and (b) to allow visualizing interactions.



**Figure 3.** Colour (a) and brightness (b) contrasts between clean eggshells and nest for the visual systems of kittiwakes and ravens (mean  $\pm$  1 SE). Empty and grey bars represent, respectively, contrasts for the egg 'without spots' (ground coloration covering the whole surface, i.e. same as empty bars in Fig. 2) and for the speckled egg as schematized within bars ( $N = 93$  eggs). \*\*\* $P < 0.001$ , \*\* $P < 0.01$ . Of note, the  $y$ -scales are different in (a) and (b) to allow visualizing interactions.

$t = -13.95$ ,  $P < 0.001$ ), but contrary to colour contrast, the effect was similar for both visual systems (visual system by soiling status interaction term not retained in the best model) and independent of time elapsed since the laying date (neither soiling status nor its interaction with time was retained in the best model).

As above, kittiwake eggs (with or without spots) had a similar brightness contrast against nest environment for conspecifics and the predator (visual system term not retained in the best model, and not significant in the second best model, est. =  $0.07 \pm 0.05$ , d.f. = 275,  $t = 1.33$ ,  $P = 0.2$ ,  $\Delta_{AICc} = 1.05$ ; Fig. 3b). Conversely to colour contrast, a (real) spotted egg showed less brightness contrast against the nest than a (hypothetical) purely whitish-bluish egg (spottiness effect, est. =  $-2.13 \pm 0.04$ , d.f. = 277,  $t = -59.41$ ,  $P < 0.0001$ ; Fig. 3b). This decrease in detectability provided by spotted eggs was more pronounced when spots covered a larger proportion of egg surface (spottiness by surface interaction, est. =  $0.75 \pm 0.04$ , d.f. = 277,  $t = 21.04$ ,  $P < 0.0001$ ), but was similar for both visual systems (visual system by spottiness interaction term not retained in the best model, and not significant in the second best model: est. =  $-0.13 \pm 0.07$ , d.f. = 275,  $t = -1.77$ ,  $P = 0.08$ ; Fig. 3b).

#### DIFFERENTIAL RESPONSE OF RECEPTORS

As predicted, the differential response of UVS/VS and SWS receptors accounted for most of the differential visibility of clean eggshell ground coloration against the nest background between the visual systems ( $\Delta f_{UVS \text{ kittiwake}} - \Delta f_{VS \text{ raven}}$ : est. =  $15.8 \pm 0.18$ , d.f. = 38,  $t = 90.0$ ,

$P < 0.001$ ;  $\Delta f_{SWS \text{ kittiwake}} - \Delta f_{SWS \text{ raven}}$ : est. =  $10.2 \pm 0.29$ , d.f. = 38,  $t = 34.8$ ,  $P < 0.001$ ;  $\Delta f_{MWS \text{ kittiwake}} - \Delta f_{MWS \text{ raven}}$ : est. =  $32.9 \pm 13.68$ , d.f. = 38,  $t = 2.4$ ,  $P = 0.02$ ;  $\Delta f_{LWS \text{ kittiwake}} - \Delta f_{LWS \text{ raven}}$ : est. =  $-16.8 \pm 6.41$ , d.f. = 38,  $t = -2.6$ ,  $P = 0.01$ ; results are qualitatively similar for clean spotted eggs).

#### EGG VARIABILITY IN COLORATION

Both colour and brightness contrasts were highly correlated within eggs in presence and absence of soiling for both visual systems (all Pearson  $0.75 < r_{91} < 0.78$ ,  $P < 0.0001$ ). Among-egg variability in both colour and brightness contrasts was not affected by soiling in the eye of kittiwakes or their egg predators ( $73.5 < \text{Bartlett's } K^2 < 87.1$ , d.f. = 92, all  $P > 0.62$ ).

#### CLUTCH SIGNATURE

We found a significant within-clutch repeatability for the spotted surface relative to eggshell ground coloration ( $F_{42,50} = 2.23$ ,  $P = 0.004$ , repeatability estimates  $R \pm \text{SE} = 0.40 \pm 0.12$ ) and for all visual contrasts against nest environment in both visual systems, namely the colour contrasts of either (real) spotted or (hypothetical) purely whitish-bluish eggs ( $2.11 \leq F_{42,50} \leq 2.48$ ,  $0.002 \leq P \leq 0.007$ ,  $0.38 \pm 0.13 \leq R \pm \text{SE} \leq 0.45 \pm 0.12$ ), the brightness contrasts of either real or hypothetical eggs ( $3.11 \leq F_{42,50} \leq 3.40$ , all  $P \leq 0.0001$ ,  $0.54 \pm 0.11 \leq R \pm \text{SE} \leq 0.57 \pm 0.10$ ) and, to a lower extent, the visual contrasts of soiled eggshell ground coloration (colour:  $1.76 \leq F_{42,50} \leq 1.91$ ,  $0.016 \leq P \leq 0.031$ ,  $0.30 \pm 0.14 \leq R \pm \text{SE} \leq 0.33 \pm 0.14$ ; brightness: both  $F_{42,50} = 2.1$ ,  $P = 0.009$ ,

$R \pm SE = 0.37 \pm 0.13$ ). It suggests that both eggshell speckling and coloration may convey a clutch signature.

## DISCUSSION

Eggs are detectable against nest background by both predators and conspecifics, as visual contrasts always exceed bird discrimination threshold value. Eggs appear similar in brightness for both visual systems. Conversely, eggs generate higher colour contrasts for kittiwake conspecifics than for their egg predator, the common raven, no matter if ground coloration is considered alone or with spots. Interestingly, spots increase colour detectability but decrease brightness detectability. Spots may provide an additional (but likely limited) detectability to kittiwakes when they cover a larger surface. Therefore, given that detectability increases with contrast value (Cassey *et al.*, 2008b; Avilés *et al.*, 2010), kittiwake speckled eggs appear more conspicuous to kittiwakes than to common ravens.

Spots slightly increase the colour contrast between the eggs and the nest, but they decrease the brightness contrast for both visual systems, and more strongly when they cover a larger surface on the eggshell. The latter could impede egg detectability from a distance as brightness cues are crucial for animals to detect distant objects (Giurfa *et al.*, 1997; Osorio, Mikló & Gonda, 1999), either static or in movement relative to the perceiver (Schaefer & Neumeyer, 1996; Srinivasan, Poteser & Kral, 1999). Nevertheless, some eggs are likely more detectable than others, and thus potentially suffer more from predation, as we found that egg colour detectability increases as spots cover a larger surface on eggshell and eggs vary in their level of spottness among clutches (i.e. clutch signature). Likewise, previous studies in birds have shown that the differential in contrast shown by their potential prey (contrast scored or measured in JNDs well above the discrimination threshold) generates a significant differential in the minimal detectability distance and capture probability (Montgomerie *et al.*, 2001; Schaefer *et al.*, 2006). Thus, although the contrasts reported here are well above the discrimination threshold, the differential in contrast between kittiwake eggs and the nest may substantially affect the distance at which some eggs are detected, which is biologically relevant as ravens patrol in the air at a distance from the cliffs on which kittiwakes nest.

Soiling deposition on eggshell significantly decreases egg detectability through both brightness and colour contrasts and for both kittiwakes and ravens. Egg colour detectability decreases with time owing to soiling, suggesting that eggs get progressively dirtier. This effect is not explained by the progressive fading of egg

colour through time as reported in other bird species (Hanley *et al.*, 2016; Morales, Torres & Velando, 2010b; Moreno, Lobato & Morales, 2011) as we found that the colour detectability of clean eggs does not change with the time elapsed between egg colour measurements and laying date. Soiling deposition on kittiwake eggs likely provides an advantageous concealment against predators by reducing their detectability, as recently shown in the blue-footed booby *Sula nebouxi* (Mayani-Parás *et al.*, 2015). Future studies are now required to experimentally assess the effectiveness of egg soiling and specking in decreasing predation risks in kittiwakes and to evaluate the potential role that disruptive coloration (not studied here) or background matching (not thoroughly studied here as it would have required measuring precisely the coloration of each nest) plays in their egg camouflage (Stoddard *et al.*, 2016; Troscianko *et al.*, 2016a). These mechanisms, in addition to the colour contrasts between the eggs and the nest, could further lower the detectability to the predator or even make the eggs totally undetectable.

The occurrence of a clutch signature suggests kittiwakes may easily recognize their eggs. It (1) may allow them to identify their clutch in the colony when returning to the cliff and (2) may concur to explain why clutch parasitism appears inexistent in kittiwakes (Yom-Tov, 2001; Helfenstein *et al.*, 2004; Coulson, 2011). Individual clutch signature suggests that kittiwakes may utilize egg coloration as a signal of female quality and thus may explain its possible evolution through sexual selection.

A preventive character of soiling against predation does not preclude a role for sexual selection in the coloration of kittiwake eggs. First, soiled eggs are detectable against the nest background. Second, soiled eggs, although less detectable than clean eggs, nevertheless remain more visible for kittiwakes than for their egg predator. Third, egg variability in coloration is maintained after soiling. Variation in coloration among eggs within or among nests in the population is thus maintained (including the clutch signature), or in other words, soiling does not homogenize colour differences among nests. Fourth, eggs only become progressively dirtier (Mayani-Parás *et al.*, 2015); given the high reproductive synchronization in kittiwake colonies (Danchin, 1988), the time during which eggs remain clean soon after laying may be sufficient for males to adjust their reproductive decisions accordingly. Therefore, soiling does not prevent kittiwake conspecifics to use egg coloration as a potential sexual signal.

Kittiwake conspecifics may potentially use the chromatic cues provided by eggs, as shown for spotless starlings (Avilés *et al.*, 2011). They may also assess the visual contrasts of spots against eggshell

ground coloration (Holveck *et al.*, 2010) or spot distribution on eggshell (Sanz & García-Navas, 2009; Holveck *et al.*, 2012; de Coster, de Neve & Lens, 2013) as a source of fine-scale information perceived only at short viewing distance, aspects not studied here. We found that egg ground coloration and speckled eggs are more contrasted in colour to kittiwakes than to ravens, are mostly differentially visible in the UV and short-wavelength range, show a reflectance peak in the UV (Fig. 1) and deliver a clutch signature. These elements altogether enhance the possibility for kittiwakes to drive egg colour evolution through sexual selection via potentially private channels of communication, for example using spot pattern signals or the previously suggested UV signals (Guilford & Harvey, 1998; Håstad *et al.*, 2005b; but see Renoult, Courtiol & Schaefer, 2013). In kittiwakes, males vary in their incubation and feeding effort (Coulson & Johnson, 1993; Leclaire *et al.*, 2010) and divorce is not rare (Hatch *et al.*, 1993). Experimental testing is thus now needed to assess the effective use of such putative colour signals by males for their investment during incubation, feeding or divorce decision afterwards.

The potential effect of sexual selection on the evolution of eggshell coloration represents a highly debated question (Reynolds *et al.*, 2009; Cherry & Gosler, 2010). Numerous empirical or vision modelling studies support a role of sexual selection in egg colour evolution (Moreno *et al.*, 2006a, b, 2008; Morales *et al.*, 2008; Soler *et al.*, 2008; Holveck *et al.*, 2010; Avilés *et al.*, 2011; English & Montgomerie, 2011; Walters, Olszewski & Sobol, 2014), with some exceptions (Krist & Grim, 2007; Cassey *et al.*, 2008a; Hanley & Doucet, 2009; Johnsen, Vesterkjaer & Slagsvold, 2011; Stoddard *et al.*, 2012). Models of visual perception were considered only recently for the study of the effect of predation on egg coloration (e.g. in a comparative context: Cassey *et al.*, 2010) and yielded good experimental support for the survival advantage of egg camouflage (e.g. in a natural context: Troscianko *et al.*, 2016b; Wilson-Aggarwal *et al.*, 2016). Our results suggest that predation, sexual selection, and clutch, nest or egg recognition may act concomitantly on eggshell coloration evolution in kittiwakes. They do not exclude other potential, but not studied here, mechanical or physiological functions of eggshell colour (reviewed in Kilner, 2006; Reynolds *et al.*, 2009; Cherry & Gosler, 2010; Cassey *et al.*, 2011; Maurer *et al.*, 2011) possibly involved in trade-offs with a signaling function (Gómez *et al.*, 2016). They highlight the benefits of considering simultaneously multiple perceivers to identify the selective forces acting on the – still largely enigmatic – evolution of egg coloration. In addition, our results showing visual consequences of soiling deposition and speckling encourage further empirical work to test whether this process may be

incidental or the product of selection and how egg speckling may help discrimination and/or crypsis.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher’s website:

**Table S1.** Colour and brightness contrasts between eggshells and nest for the visual systems of kittiwakes and ravens, for clean (clean white) or soiled (soiled white) eggs ‘without spots’ and for clean speckled eggs (clean white and spots), together with the percentage of unspotted surface on each measured egg, the delay between egg laying date and spectral measure and the origin (nest and cliff ID) and identity of all kittiwake eggs.