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The point of a Guillemot's egg

TIMOTHY R. BIRKHEAD^{1*}, JAMIE E. THOMPSON¹, DUNCAN JACKSON¹ AND JOHN D. BIGGINS²

¹*Department of Animal & Plant Sciences, University of Sheffield, Sheffield, S10 2TN, UK*

²*School of Mathematics and Statistics, University of Sheffield, Sheffield S3 7RH, UK*

*Corresponding author.

Email: t.r.birkhead@sheffield.ac.uk

The adaptive significance of avian egg shape in birds is poorly known. The pyriform (pear-like) shape of the Common Guillemot's egg has long been considered to be an adaptation to prevent eggs rolling off the bare cliff ledges on which this species breed. Rolling was thought to be prevented by either the egg: (i) spinning like a top — which is not the case, or (ii) rolling-in-an-arc, which it does, although it has little influence on whether an egg will fall from a ledge. Accordingly, we sought alternative hypotheses for the pyriform shape of the Common Guillemot egg. This species breeds in extremely dense colonies, which makes their eggs vulnerable to: (i) mechanical damage from conspecifics, and (ii) contamination by debris — mainly faeces and soil. We present evidence consistent with both hypotheses. First, the pyriform shape of Common Guillemot eggs means that a higher proportion of the eggshell lies in contact with the substrate and this may minimise the effect of impacts. Resistance to impacts may be further enhanced because their eggshells are especially thick where they contact the substrate. Second, Common Guillemot eggs are often heavily contaminated with faecal material and other debris during incubation. Most contamination is on the pointed end of the egg where the egg is in contact with the substrate; the pyriform shape thus keeps the blunt end — which has the highest porosity — of the Common Guillemot egg relatively free of contamination, which in turn may facilitate both gas exchange during incubation,

and the hatching process because the blunt end of the egg is where the chick emerges.

Key words egg shape, eggshell thickness, faecal contamination, pyriform, Razorbill *Alca torda*, stress concentration, Common Murre

The shape of birds' eggs varies considerably, from near-spherical, to oval, elongate, bi-conical and pyriform (Thompson 1964). With few exceptions (e.g. in waders, Andersson 1978), the adaptive significance of avian egg shape is poorly understood. However, the pyriform (pear-shaped) egg of the Common Guillemot *Uria aalge* (hereafter Guillemot) and Brünnich's Guillemot *Uria lomvia* has long been considered an adaptation to minimise rolling off the narrow, rocky cliff ledges on which these species breed without constructing a nest (MacGillivray 1852; Belopol'skii 1957; Gill 2007).

The first explanation for the Guillemot's pyriform egg shape was that it allowed the egg to spin like a top (on its side) when knocked or blown by the wind (Hewitson 1831). However, the ability of Guillemot eggs to spin was based on empty, museum eggshells and is biologically meaningless, and it was later shown that intact Guillemot eggs containing yolk and/or an embryo did not move in this way when knocked. Instead, they tended to roll in an arc (Belopol'skii 1957; Ingold 1980; reviewed in Birkhead 2016). In contrast, the 'elliptical ovate' (i.e. much less pointed) egg of the Razorbill *Alca torda*, rolls in a much wider arc (Kaftanovski 1941; Belopol'skii 1957; Ingold 1980).

Tschanz *et al.* (1969) provided what appeared to be clear-cut evidence that the more pyriform the shape of Guillemot eggs, the tighter the rolling arc, and the greater the protection it provided against falling off a ledge. However, Tschanz *et al.*'s (1969) results were derived from model eggs made of plaster that do not behave in the same way as real eggs (Ingold 1980). Comparing real Guillemot and Razorbill eggs on natural substrates, Ingold (1980) found little difference in their rolling arc, suggesting that the pyriform shape of the Guillemot's egg

provided little or no protection from rolling. Even so, and slightly confusingly, having found that mass as well as shape affected an egg's rolling trajectory, Ingold (1980) concluded that a pyriform shape must still be advantageous for Guillemot eggs, because if they were the same shape as Razorbill eggs (which are smaller and therefore lighter in mass), they would be more likely to roll off the ledge.

The evidence that the Guillemot's pyriform egg shape is an adaptation to facilitate rolling-in-an-arc and minimise the risk of rolling off the ledge is very limited. Moreover, there are several reasons for questioning the assumptions of the rolling-in-an-arc hypothesis: (i) Guillemots often breed on ledges much narrower than the arc described by a rolling egg (Harris & Birkhead 1985; Birkhead & Nettleship 1987); (ii) since Guillemots typically incubate facing the cliff wall with the pointed end of their egg directed towards the cliff edge (Tschanz 1968; pers. obs.), a dislodged egg would roll *outwards* towards the cliff edge and thus be more likely to fall; (iii) Guillemot eggs vary considerably in shape (Tschanz *et al.* 1969; Birkhead *et al.* 2017), suggesting that there is little stabilizing selection on egg shape; (iv) Brünnich's Guillemots produce less pyriform shaped eggs than Common Guillemots (Belopol'skii 1957; Birkhead & Harris 1985), despite their breeding on narrower ledges (Birkhead & Nettleship 1987). Ingold (1980) explained this apparent anomaly by invoking the interaction between shape and mass and suggesting that because the eggs of Brünnich's Guillemots were smaller and lighter in mass, they would therefore roll in a smaller arc and thus be less vulnerable to falling than Common Guillemot eggs.

The eggs of both guillemot species are subject to two selection pressures that have not previously been considered: (i) the risk of physical damage from conspecifics, and (ii) contamination by debris.

(i) Physical damage: Guillemots typically breed in direct bodily contact with conspecifics at high densities (regularly at around 20 pairs per square metre, but up to 70 pairs per square metre; see Birkhead 1993) on both broad and narrow

ledges (Birkhead 1977). Incubating birds are frequently jostled by their neighbours during fights and it is not uncommon for birds returning from the sea to land heavily (body mass ~ 1 kg) directly on top of incubating conspecifics.

It has been argued that all else being equal, a spherical egg will have the greatest resilience to impacts (Smart 1969; Bain 1991). However, no bird lays a completely spherical egg. Moreover, with a spherical egg the effects of any impact, from above, for example, would be concentrated onto a very small region of the shell where the egg is in contact with the substrate. In engineering terms, this point is referred to as the 'stress concentration' (Pilkey & Pilkey 2008) and is the place on the shell where it is most likely to break. With a pyriform egg, it seems likely that a greater proportion of the shell lies in contact with the substrate, meaning that the stress of any impact will be spread over a greater surface area, thereby conferring greater eggshell strength.

(ii) Contamination by debris: Guillemots defecate without regard to their neighbours so that the rocky substrate on which they breed is usually covered with faecal material. Along with already present soil, faecal material can contaminate the eggs, especially in wet weather. Brünnich's Guillemots breed under similar crowded and 'dirty' conditions, albeit on narrower cliff ledges at lower density (Gaston & Nettleship 1980; Birkhead & Nettleship 1987). Contamination of the eggshell by faeces and other debris can potentially compromise gas exchange and facilitate microbial infection, both of which can be fatal to avian embryos (Board 1982; Verbeek 1984).

Our aim here is to offer two new hypotheses for the pyriform shape of Guillemot eggs. (1) The pyriform egg shape confers physical strength that enables Guillemot eggs to withstand impacts resulting from the vigorous 'rough and tumble' of a dense breeding colony. (2) The pyriform egg shape reduces the consequences of debris contamination of the egg surface. We provide data relevant to each hypothesis, and some suggestions for further study.

METHODS

To obtain measurements of eggshell characteristics we used Guillemot eggs from our field site, Skomer Island, Wales, UK (under licence). We made some comparisons between the eggshells of Guillemots and Razorbills, the latter also from Skomer and collected under licence; all from 2014, 2015 and 2016. The Razorbill is closely related to the Guillemot and also breeds colonially on sea cliffs (and often in close proximity to Guillemots), but as isolated pairs and often in rocky cavities where there is little risk of their egg falling (Smith & Clarke 2014; Harris & Birkhead 1985). Ingold's (1980) investigation of the adaptive significance of Guillemot egg shape was based partly on comparisons with Razorbill eggs, which is why we have included data for that species here.

Contact of the eggshell with the substrate

We calculated the 'contact index' (defined below) for Guillemot and Razorbill eggs to quantify the extent to which the eggshell is in contact with the substrate and the extent to which the pyriform shape of the Guillemot egg results in a higher value. A greater area in contact with the substrate would reduce the stress per unit area should there be an impact, particularly from above, and thus reduce the probability of breakage. To obtain a sufficiently large sample of eggs of both Guillemot ($n = 83$) and Razorbill ($n = 79$) from the same colony, we used eggshells from Bempton, Yorkshire, UK in the Natural History Museum, Tring for this part of the study.

Typically, an egg's centre of gravity moves towards the pointed end of the egg as incubation proceeds and the air cell increases in size, which changes the egg area in contact with the substrate over incubation (Belopol'skii 1957). Because Guillemots incubate in a semi-upright posture, the weight of the bird's body essentially causes the egg to adopt the maximum contact with the substrate (Tschanz 1990; pers. obs.). To account for this, we used the following method to obtain an objective index of the maximum proportion of the egg in contact with the substrate during incubation. Using the outline from an egg silhouette image obtained by photographing each egg against a lightbox, we mathematically

captured the shape of an egg from which we could derive the other parameters including the two-dimensional area of the silhouette and the egg surface area, using the methods described by Preston (1953) and Todd & Smart (1984). The formula for the shape was then used to locate the place on the eggshell surface where the profile was flattest. Although the actual profile is a smooth curve with only a tiny point of contact, in reality, imperfections in the egg surface and irregularities in the substrate will spread this contact. We calculated the area in the plane that is tangent at this point and within 0.2 mm of the egg surface on the assumption that a 0.2 mm tolerance reflects both the flexing of the shell and these imperfections and irregularities. That area in contact with the substrate was then expressed as a percentage of the area of the egg silhouette, so that egg size is not a factor, to give the 'contact index'. We also explored the consequences of tolerances of 0.1 mm and 0.5 mm to account for the unevenness of the substrate. See supplementary material for further methodological details.

Measuring eggshell thickness

Eggshell strength is determined in part by thickness (Romanoff & Romanoff 1949), and since the two *Uria* species have thicker eggshells than those of any other bird laying similar sized eggs (Schoenwetter 1960-1992; see also Pirie-Hay & Bond 2014), it follows that their eggshells are particularly strong. Our aim was to compare shell thickness in different regions of the eggshell, to establish whether the shell was thickest in the region where it is in contact with the substrate. Different studies have measured eggshell thickness in different ways, but most have assessed the entire thickness of the shell, with or without the shell membrane. According to Bain (2005), however, the measure of thickness that best reflects eggshell strength is the distance between the point of fusion of the palisade columns to the outer edge of the shell accessory material; a measure referred to as 'effective thickness' (see Fig. S2; Table S1).

Eggshell thickness measures were obtained from ten Guillemot eggs collected on Skomer Island in 2014 ($n = 5$), 2015 ($n = 3$) and 2016 ($n = 2$). For each egg, ten measures were taken from the blunt pole, the equator (maximum diameter) and

near (but not at) the pointed end of the egg (see Results for details on sampling location) using Micro-CT scanning. From these ten measures, we calculated mean values for several different measures of thickness for each eggshell fragment, obtained as follows.

Fresh eggs were drained of their contents, washed in distilled water and allowed to dry. To obtain shell fragments for measuring, a hand-held rotary saw (DREMEL Multi, Mod. 395 Type 5 Code 83; DREMEL USA) was used to cut a ~ 1 cm² pieces from each of three regions of the egg. Eggshell fragments were scanned in a Bruker Skyscan 1172 using the following settings; scanner set at 100 kV electron acceleration energy and 90 uA current with the sample 48.7 mm from the X-ray source with a 1.0 mm Aluminium filter, with the sample 283.349 mm away from the camera. Camera resolution was set at 1048 x 2000 pixels, with a pixel size of 4 μ m. We used the same setting for each scan, collecting a total of 1048 projection images using a rotation step size of 0.4° and a detector exposure of 1475 ms integrated over three averaged images resulting in a total scan time of fifty minutes. Two eggshell fragments were scanned during each session. Projection images were then reconstructed in NRecon software (version 1.6.10.1) before image analysis was performed in CT analyser (Ctan, version 1.14.41), CTVox (version 3.0; software provided by Bruker) and ImageJ (version 1.49p). Reconstruction parameters were: dynamic image range; minimum attenuation coefficient = 0, maximum = 0.08, level 2 Gaussian smoothing, ring artefact correction = 12, beam hardening correction of 20% and auto misalignment compensation, images saved as 8-bit bitmaps. Shell thickness was measured in CTan software using the line measurement tool at ten haphazardly selected locations within each shell fragment.

To test for differences in eggshell thickness between the three regions of the Guillemot eggshell we ran a one-way ANOVA, using repeated measures analysis to control for multiple measures from the same egg. To test for differences in the relative variation in effective eggshell thickness between Guillemot and Razorbill eggs (whose eggs are slightly smaller: Harris & Birkhead 1985), we calculated

the ratios between eggshell thickness in different regions of the eggs (blunt/equator, blunt/point and equator/point) of both species.

Measuring debris contamination on the egg surface

We recorded the extent of debris (i.e. mainly faeces and soil) contamination of 59 Guillemot and 40 Razorbill eggs on Skomer Island, Wales in 2016. To standardize the time period available to accumulate debris, we photographed eggs on a single occasion 22-25 days after each species' median laying date (9 May for Guillemots and 12 May for Razorbills, respectively; pers. obs.). The eggs of both species were all on the same (mixed) colony where the two species were breeding as close as 15 cm to each other.

Using a life-size image of each egg we superimposed a grid, that consisted of 5 mm x 5 mm squares, and recorded: (i) whether each egg had any opaque debris (that is, debris that obscured the ground colour or maculation), to provide an estimate of the proportion of 'dirty' eggs. We also recorded, (ii) whether each square contained any debris, to provide an estimate of the extent (expressed as a percentage) of the total area of the blunt end (i.e. lying above the maximum egg diameter) and the pointed end (below the maximum egg diameter) of each egg covered by debris. To check for repeatability (Lessells & Boag 1987; Nakagawa & Schielzeth 2010), twenty Guillemot and Razorbill egg images were scored independently by five different individuals and showed that repeatability was high (blunt end: $F_{19,80} = 62.3$, $r = 0.92$, $P < 0.0001$; pointed end: $F_{19,80} = 43.8$, $r = 0.89$, $P < 0.0001$).

Measuring eggshell porosity

The efficacy of gas exchange between the embryo and outside world is determined by the number and dimensions of the eggshell pores (Ar & Rahn 1985). However, gas exchange is likely to be compromised if eggshell pores are blocked with debris (Board 1982).

The limiting dimension for the diffusion of gases is the minimum cross sectional pore area, that is, the narrowest part of the pore (Tøien *et al.* 1988). Using ~ 1 cm² fragments of eggshell from three different regions of each egg (as above), we calculated eggshell porosity (that is, total pore area in mm²) by multiplying the average minimum cross sectional area of pores by the pore density (n , per mm²), to give the total functional pore area in 1 mm² of eggshell (Ar & Rahn, 1985). Our method was similar to that of Riley *et al.* (2014), who also used micro-CT to identify and measure the narrowest cross sectional pore areas directly. Fragment area and minimum cross sectional pore area were both measured in ImageJ. Pores were measured by re-slicing the reconstructed image stack and taking measurements from orthogonal views; working through 4 μ m image slices one at a time from the shell's outer surface to the inner surface until the minimum cross sectional area of the pore was measured. Ten pores per fragment were haphazardly selected for measurements. Image stacks were then loaded into CTVox to produce 3D volumetric reconstructions of the eggshell fragment and the number of pores was counted and then divided by fragment area (mm²) to obtain pore density.

We determined the repeatability of porosity and shell thickness measures within each region of an egg, using three fragments from each region of five Guillemot and five Razorbill eggs (Lessells & Boag, 1987; Nakagawa & Schielzeth, 2010). Repeatability was very high for effective shell thickness for both species ($r = 0.97$, for both species) and reasonably high for porosity (Guillemot: $r = 0.74$, Razorbill: $r = 0.58$) (Table S2).

To test for differences in porosity between the three regions of the Guillemot eggshell, we ran a one-way ANOVA on log transformed data, with the repeated measures analysis to control for multiple measures for each egg. Log transformation was necessary to make the Guillemot egg data fulfil the assumptions of the analysis. This was not necessary for the Razorbill egg data.

All data were analysed using the base package R (R Development Core Team 2012). Where two-sample t-tests were used, Welch's correction was applied to

account for unequal samples sizes and variances and thus provide degrees of freedom that are lower than would otherwise be expected for given samples sizes. Means are expressed \pm sd.

RESULTS

Contact of the eggshell with the substrate

The Guillemot's pyriform-shaped egg is characterised by a relatively long, straight surface below the equator towards the point, compared with that of the elliptical-ovate egg of a Razorbill (Fig. 1). The contact index of Guillemot eggs, assuming a tolerance of 0.2 mm, was significantly greater (mean = 2.14 ± 0.32 , $n = 83$) than that of Razorbill eggs (mean = 1.81 ± 0.14 , $n = 79$) (Welch two-sample t-test: $t = 8.48$, $df = 111$, $P < 0.001$; Fig. 1). We obtained very similar results with tolerances of 0.1 mm and 0.5 mm, both of which were highly correlated with the 0.2 mm tolerance measures (Spearman's correlation: $r_s > 0.997$ in both cases). For 83 Guillemot eggs, this contact index is strongly and positively correlated (Spearman's correlation: $r_s = 0.83$, $n = 83$, $P < 0.001$; results not shown) with the degree of pointedness (i.e. the proportion of overall egg length between the egg's widest point and the more pointed end of the egg). These results are consistent with our hypothesis that the pyriform shape of the Guillemot's egg results in a relatively larger proportion of the egg's surface in contact with the substrate that could reduce the stress per unit area during impacts.

Eggshell thickness

Guillemot eggshells were thinnest (i.e. total eggshell thickness including the shell membranes) at the blunt end ($536 \mu\text{m} \pm 23.8$) and thickest at the equator ($651 \mu\text{m} \pm 28.2$) and pointed end ($639 \mu\text{m} \pm 39.5$). This difference in thickness between the blunt end and the other regions was significant ($F_{2,18} = 44.1$, $P < 0.001$; Tukey multiple comparison test: $P < 0.05$). Pirie-Hay and Bond (2014) obtained a similar result with Common Guillemot eggs, as did Uspenski (1958) for Brännich's Guillemot eggs. In terms of effective eggshell thickness (see

Methods), the equator was significantly thickest ($471 \mu\text{m} \pm 23.8$), followed closely by the pointed end ($432 \mu\text{m} \pm 30.6$) and the blunt end of eggs was thinnest ($362 \mu\text{m} \pm 32$) ($F_{2,18} = 41.0$, $P < 0.001$; Tukey multiple comparison test: $P < 0.05$). However, effective thickness ratios between different regions of the egg showed that the pattern in shell thickness differs between Guillemot and Razorbill eggs, primarily in the magnitude of difference between the blunt and equator region, but also in the magnitude of difference between the equator and pointed region (Fig. 2).

Debris contamination on the egg surface

Guillemot eggs were significantly more likely to have *any* visible faecal material and/or soil – measured as opaque contamination – on their surface (56/59, 97%) than Razorbill eggs (17/40, 43%) (chi-squared test: $\chi^2 = 31.2$, $df = 1$, $P < 0.001$; see also Fig. 3). In the Guillemot eggs, debris contamination was more frequent on the pointed end of the egg than the blunt end (paired t-test: $t = 7.75$, $df = 58$, $P < 0.001$), but this was not the case with the Razorbill eggs (paired t-test: $t = 0.01$, $df = 39$, $P = 0.992$) (Fig. 4).

Eggshell porosity

The blunt end of Guillemot eggshells was significantly more porous than other egg regions (one-way ANOVA with repeated measures: $F_{2,8} = 13.5$, $P < 0.001$; Tukey multiple comparison test: $P < 0.05$; Fig. 5). Specifically, the blunt end of a Guillemot egg ($3.21 \times 10^{-4} \text{ mm}^2 \pm 1.58 \times 10^{-4}$) was significantly more porous than both the equator ($1.24 \times 10^{-4} \text{ mm}^2 \pm 7.25 \times 10^{-5}$) and the pointed region ($9.68 \times 10^{-5} \text{ mm}^2 \pm 4.57 \times 10^{-5}$). Although the pattern was similar in Razorbill eggs, it was much less pronounced and not statistically significant (one-way ANOVA with repeated measures: $F_{2,8} = 3.13$, $P = 0.0684$; Fig. 5).

DISCUSSION

Contrary to popular belief, there is almost no evidence that the pyriform shape of Guillemot eggs, and their resulting tendency to roll in an arc, is an adaptation to reduce the risk of falling off cliff ledges. We offer two new hypotheses to account for the pyriform shape of Guillemot eggs: that it provides resistance against impacts and protection from faecal, and other, contamination.

We obtained several results consistent with our first hypothesis that the Guillemot's pyriform egg shape confers strength and resistance against impacts.

The pyriform shape of the Guillemot's egg results in a greater proportion of the egg surface area in contact with the substrate than in the closely related Razorbill, which has less pear-shaped eggs. We propose that a large proportion of the egg in contact with the substrate minimises the 'stress concentration', that is, it disperses the consequences of any impact, which in turn reduces the likelihood of breakage resulting from an impact, particularly from above (Pilkey & Pilkey 2008). We suggest that the pyriform shape means that Guillemot eggs are relatively crush-proof in the region where impact is most likely.

As noted by several other authors, the eggshells of the Common Guillemot and Brünnich's Guillemot are, for their size, thicker than almost any other bird (Schoenwetter 1960-1992; Pirie-Hay & Bond 2014). We found Guillemot eggshells to be thickest at the equator and the pointed pole (as did Maurer *et al.* 2012), essentially the area that lies in contact with the substrate during incubation. Indeed, as Maurer *et al.* (2012) found, although the blunt pole is thinner than the equator in the eggs of many of the 230 bird species they examined, that difference was most extreme in the Guillemot (also see Fig. 2). Our data show that the greater thickness at the equator is primarily due to an increase in effective shell thickness, rather than an increase in membrane or mammillary layer thickness (Fig. S3). This is also the case for the thickness at the pointed end, although an increase in membrane thickness contributes to the total thickness in this region. Since greater shell thickness within a Guillemot egg is due to an increase in effective shell thickness, it is likely that the eggshell strength at the equator and pointed end is enhanced compared to the blunt pole.

The blunt pole is less vulnerable to impact and, by being thinner, may enable the chick to emerge more easily from the shell. If it is true that a spherical egg has the greatest resistance to crushing (Smart 1969; Bain 1991), the enhanced shell strength at the equator and pointed end may be necessary to reinforce a potentially weak egg shape resulting from the Guillemot egg's elongation and deviation from a sphere (Maurer *et al.* 2012).

In reality, the minimisation of the stress concentration by maximising contact with the substrate, together with the increased shell thickness in the region of the eggshell where impact is most likely, must work together to create the Guillemot's robust eggshell, but it will require detailed experiments to establish the relative importance of these two features.

We also obtained evidence consistent with our second hypothesis, that a pyriform shape provides some protection from debris contamination. In other species, debris contamination of eggshells can be fatal for the embryo, either because the pores in the eggshell become blocked and compromise gas exchange, or because of microbial infection (Verbeek 1984). The pyriform shape of the Guillemot egg means that the blunt end of the egg is raised above the substrate surface and less likely to be covered in faecal material and/or soil than the pointed end. This may also explain the striking increase in porosity at the blunt end of the egg, which is also the end at which the chick's head is located in the later stages of incubation and from which the chick emerges from the shell (Tschanz 1968).

In a previous study, Zimmermann *et al.* (2007) found no differences in pore density or pore size between the same three regions of Guillemot and Razorbill eggs as examined here. It seems likely that this discrepancy between their result and ours is a consequence of the methods used to assess porosity. Zimmerman *et al.* (2007) measured the area at the pore orifice on the inner surface of the shell, which we found to be on average $545 \mu\text{m}^2 \pm 424$ greater than the minimum pore area measured using micro-CT. Although these two measures are weakly and positively correlated, the scatter is considerable (Fig. S4).

We have not, as yet, tested either hypothesis directly and two remaining questions are: (i) whether an elliptical-ovate egg (like that of a Razorbill) of the same thickness as a Guillemot egg, would confer the same degree of protection from impacts, and (ii) whether the elliptical-ovate Razorbill egg subject to the same degree of faecal exposure as Guillemot eggs would suffer greater contamination of their blunt end and, as a result, reduced hatching success.

There are several reasons why the view that the pyriform shape of a Guillemot's egg is an adaptation to prevent rolling has been so pervasive. First, the idea is intuitively appealing, in part because single factor explanations are often preferred. Second, the rolling-in-an-arc idea gained traction initially because rolling was seen as a major mortality factor. However, this was a consequence of researchers such as Belopol'skii (1957) and Tuck (1961) using crude study methods (including walking on to the breeding ledges and firing guns at colonies), causing massive disturbance. Third, the experimental results of Tschanz *et al.* (1969) helped perpetuate the rolling-in-an-arc idea, even after Tschanz's student and colleague, Ingold (1980) showed that those experiments were flawed. Finally, it is interesting that, in an overview, Tschanz (1990) agreed with Ingold that Guillemot egg shape 'confers no greater advantage than a Razorbill egg on a Guillemot ledge [in preventing egg loss via rolling], but brooding behaviour does'.

Under normal circumstances, undisturbed guillemots of both *Uria* species very rarely leave their egg unattended and the risk of rolling is minimal, except during incubation changeovers, or sometimes during bouts of intraspecific aggression (e.g. Birkhead 1977; Gaston & Nettleship 1981; Harris & Wanless 1988). During incubation exchanges Guillemots minimise the risk of egg rolling by careful manipulation of the egg with their beak, retaining or sometimes transferring the egg between the tarsi, but also using their drooped wings to prevent the egg from rolling (Tschanz 1990; pers. obs.). In addition, incubating Guillemots routinely accumulate small stones under and around the egg, which although dismissed as 'vestigial nest-building' (Tuck 1961), almost certainly provide

additional stability to the egg. In many instances, because Guillemots breed in such close proximity, an egg that rolls away from an incubating bird will, when the colony is undisturbed, roll only as far as an immediate neighbour and be duly recovered. However, in the presence of predators such as Bald Eagles *Haliaeetus leucocephalus*, Red Foxes *Vulpes vulpes*, Arctic Foxes *V. lagopus*, Polar Bears *Ursus maritimus*, or humans, all of which can kill an adult Guillemot, it is hardly surprising that adult Guillemots (which are long-lived) look after their own safety and abandon their eggs (e.g. see Birkhead & Nettleship 1995): under such circumstances no egg rolling adaptation can ensure the safety of an egg.

In summary, in light of the failure of the rolling-in-an-arc hypothesis to account for the pyriform shape of Guillemot eggs. We offer two new hypotheses for that pyriform shape: strength and protection from debris contamination. We are not making a case for either one, and there may well be others (see Ingold 1980; Tschanz 1990). Indeed, it seems likely that the Guillemot's pyriform egg is a compromise between a number of different selection pressures.

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Additional Supporting Information may be found in the online version of this article.

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FIGURES FOR THE FOLLOWING ACCEPTED MANUSCRIPT:

The point of a Guillemot's egg

TIMOTHY R. BIRKHEAD^{1*}, JAMIE E. THOMPSON¹, DUNCAN JACKSON¹ AND JOHN D. BIGGINS²

¹Department of Animal & Plant Sciences, University of Sheffield, Sheffield, S10 2TN, UK

²School of Mathematics and Statistics, University of Sheffield, Sheffield S3 7RH, UK

*Corresponding author.

Email: t.r.birkhead@sheffield.ac.uk

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Main manuscript figures

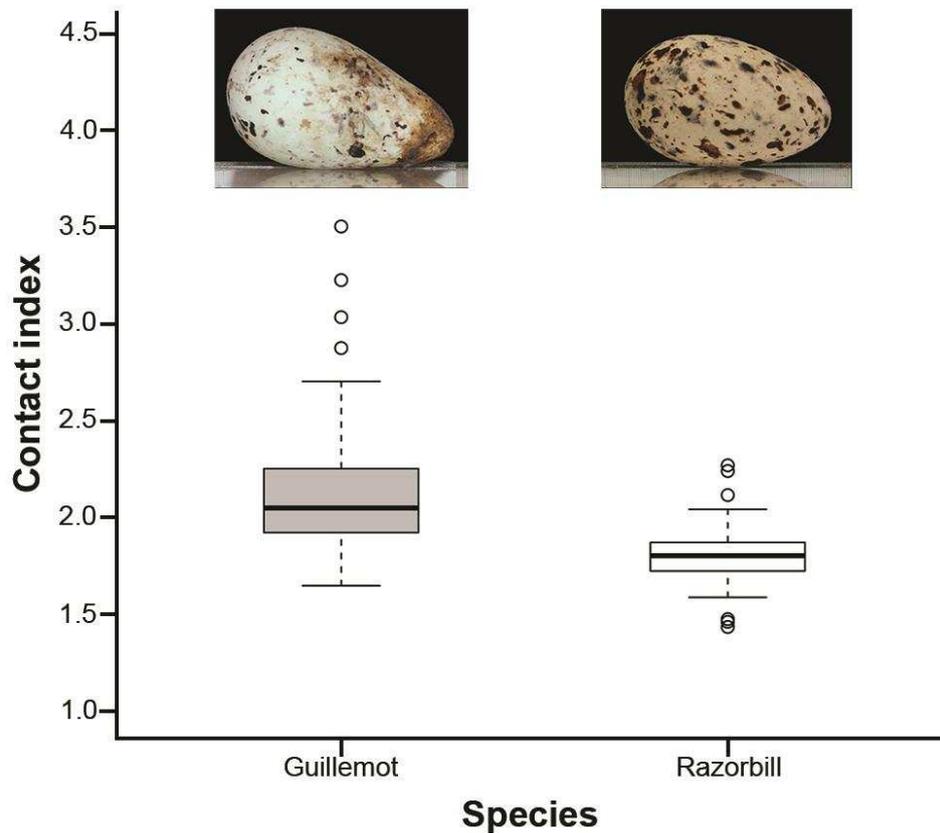


Figure 1. Contact index in Guillemot ($n = 83$) and Razorbill eggs ($n = 79$): museum specimens collected from Bempton Cliffs, Yorkshire, England. Upper images show profiles of an intact and partly incubated Guillemot egg (left) and Razorbill egg (right), to illustrate the difference in the percentage of eggshell in contact with the substrate. Boxes are the interquartile range, black line within the box is the median, the whiskers show the highest and lowest values and open circles indicate potential outliers. The contact index of Guillemot eggs is significantly greater than that of Razorbill eggs ($P < 0.001$): see text for details.

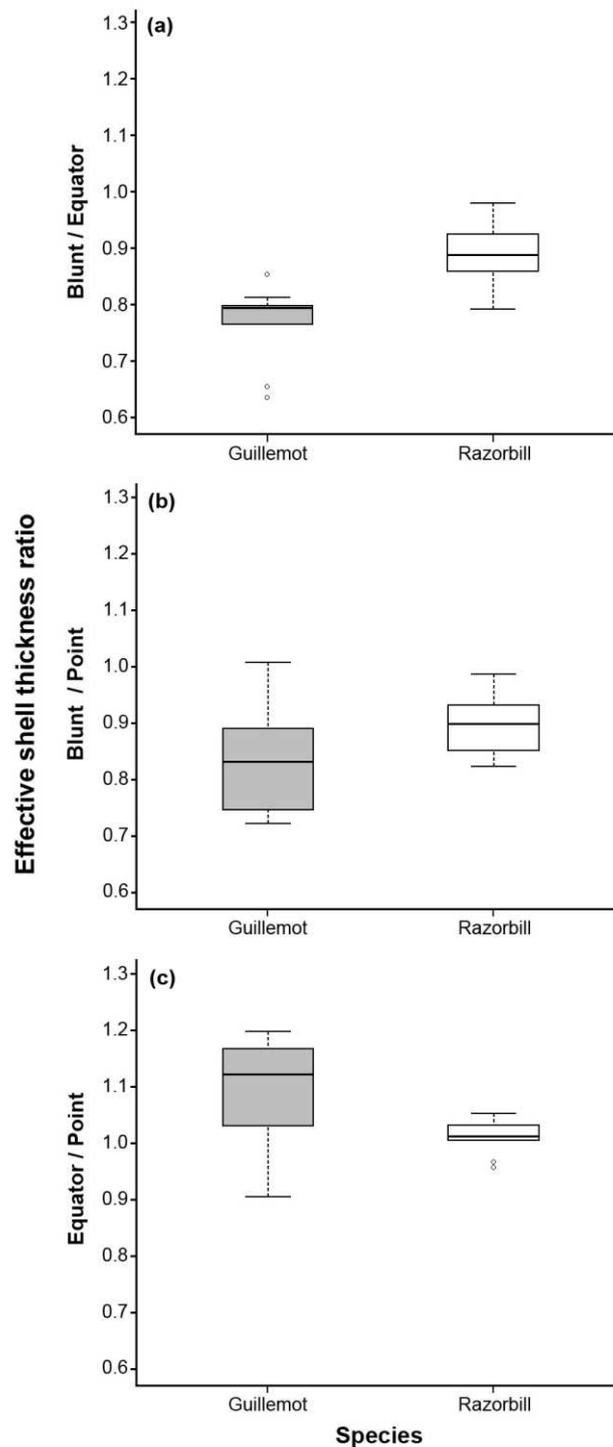


Figure 2. Effective shell thickness ratios between different regions of Guillemot and Razorbill eggs: (a) blunt/equator, (b) blunt/point, (c) equator/point. The Guillemot eggshell blunt/equator ratio (Welch two-sample t-test; $t = 4.38$, $df = 17$, $P < 0.001$) and equator/point ratio (Welch two-sample t-test; $t = 2.74$, $df = 11$, $P = 0.02$) are significantly different from that of Razorbill eggshells. There is no significant difference in blunt/point ratio between the two species (Welch two-sample t-test; $t = 1.79$, $df = 15$, $P = 0.09$). A total of twenty ratios was analysed from ten Guillemot and ten Razorbill eggs.

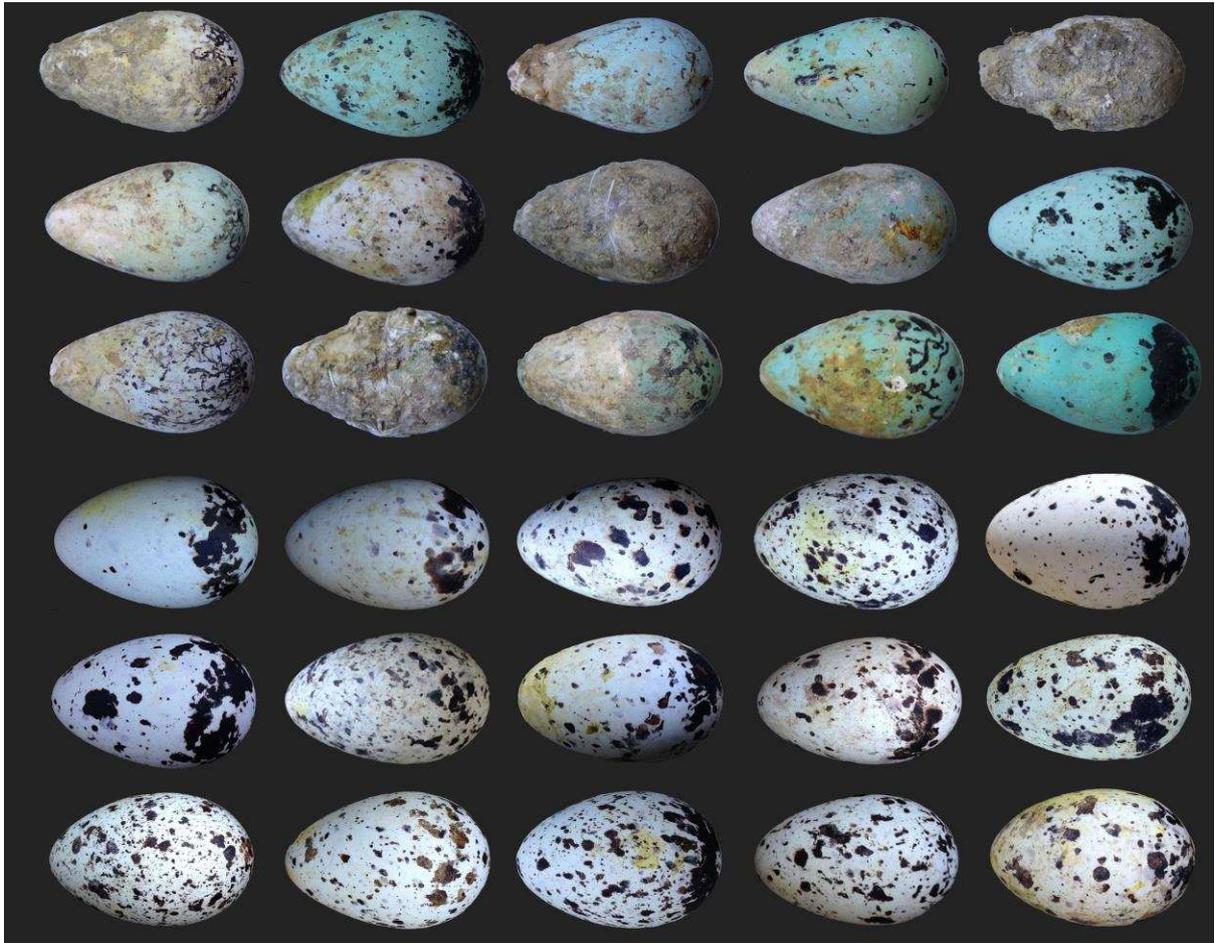


Figure 3. Examples of naturally incubated Guillemot (top three rows) and Razorbill (bottom three rows) eggs ($n = 15$ each), located haphazardly and photographed on the same ledge at approximately the same stage of incubation on Skomer Island, Wales (see text) to illustrate the extent of debris (both faecal and soil) contamination. The Guillemot eggs are more likely to be encrusted with faecal material and dirt, especially towards the pointed end of the egg. Some Razorbill eggs are contaminated with yellow material that we presume is a thin layer of faecal material, but not especially at the pointed and none are encrusted in the same way as Guillemot eggs.

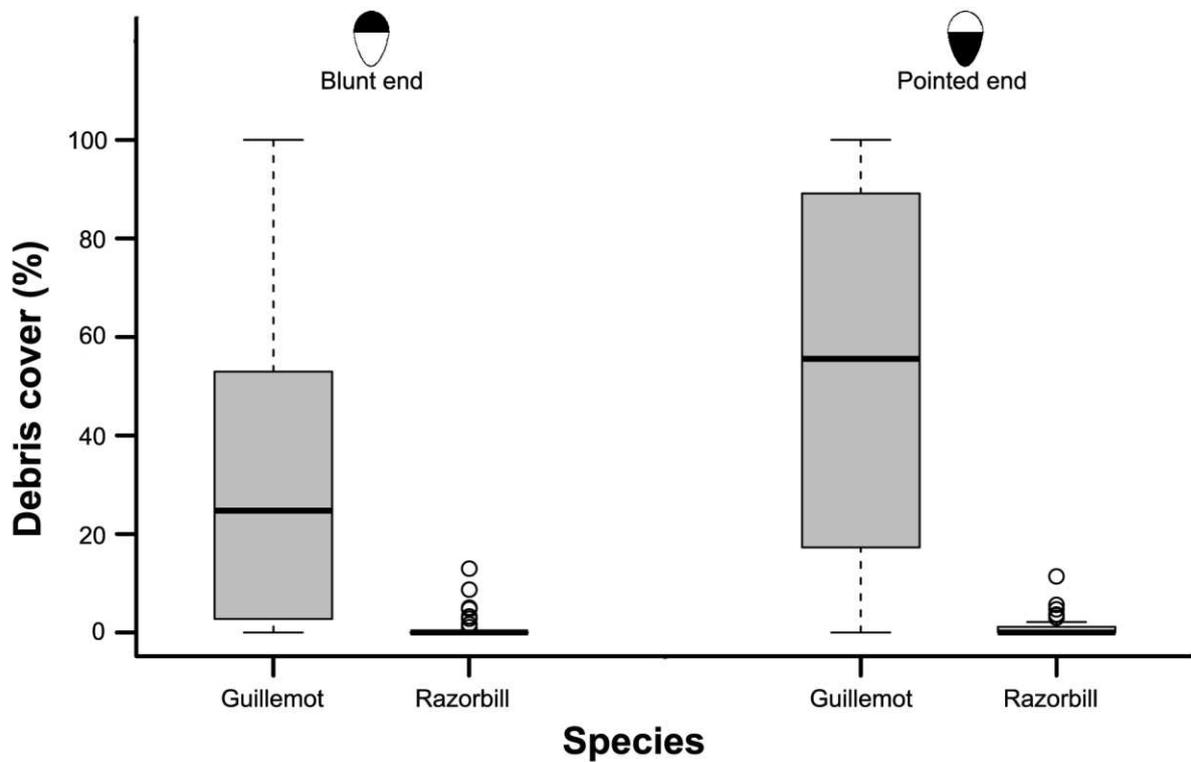


Figure 4. Extent of debris contamination on the eggs of Guillemots ($n = 59$) and Razorbills ($n = 40$) photographed part-way through incubation on Skomer Island, Wales (see Fig. 3). Contamination is significantly greater on Guillemot eggs, on both the blunt and pointed ends, than the contamination on Razorbill eggs. Boxes are the interquartile range, black line within the box is the median, the whiskers show the highest and lowest values and open circles indicate potential outliers.

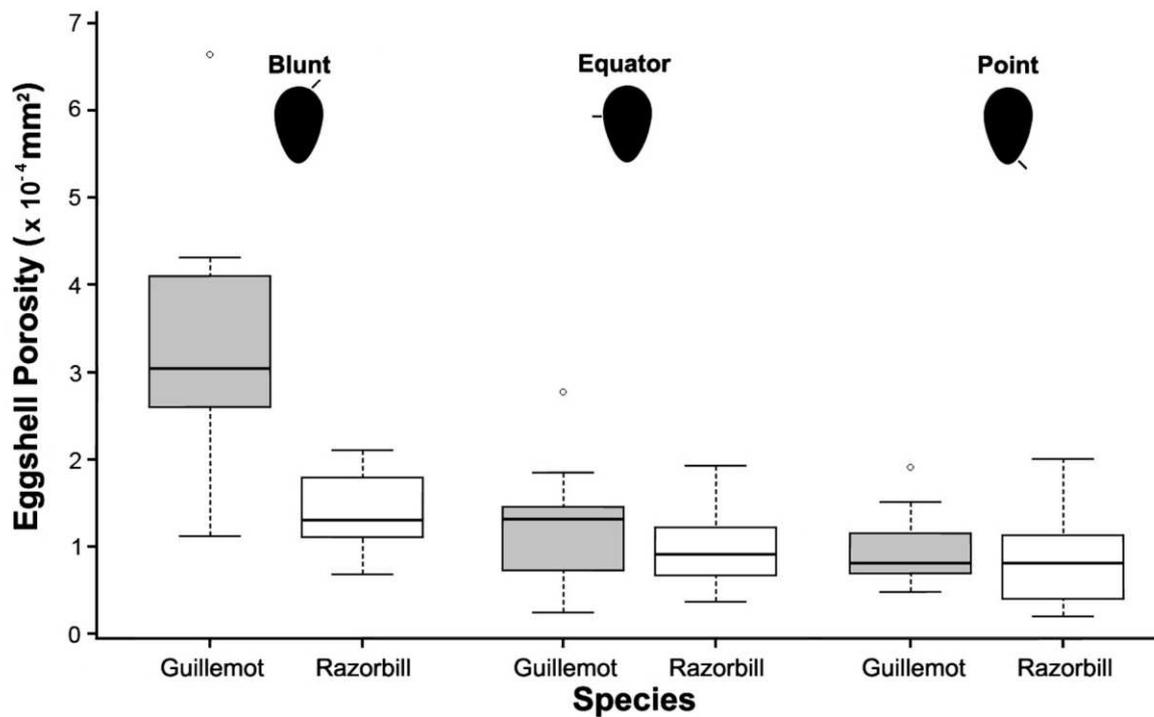


Figure 5. Porosity (total minimum pore area per mm²) of Guillemot and Razorbill eggshells. The blunt end of Guillemot eggshells was significantly more porous than other egg regions ($P < 0.05$); Razorbill eggs were equally porous in all regions ($P > 0.05$). Boxes are the interquartile range, black line within the box is the median, the whiskers show the highest and lowest values and open circles indicate potential outliers. Ten Guillemot eggs and ten Razorbill eggs were analysed and a mean value for each eggshell region (blunt, equator and point) calculated, providing a total of 60 measurements.

SUPPLEMENTARY MATERIAL FOR THE FOLLOWING ACCEPTED MANUSCRIPT:

The point of a Guillemot's egg

TIMOTHY R. BIRKHEAD^{1*}, JAMIE E. THOMPSON¹, DUNCAN JACKSON¹ AND JOHN D. BIGGINS²

¹*Department of Animal & Plant Sciences, University of Sheffield, Sheffield, S10 2TN, UK*

²*School of Mathematics and Statistics, University of Sheffield, Sheffield S3 7RH, UK*

*Corresponding author.

Email: t.r.birkhead@sheffield.ac.uk

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SUPPLEMENTARY MATERIAL

Method for calculating the 'contact index'

We used the mathematically captured shape of the egg's silhouette to give an egg profile, and assumed circular cross sections orthogonal to this to give the egg's overall (three-dimensional) shape. We identified the point on the profile where it was flattest (see main manuscript text), and superimposed a plane that is tangent at this point. Using the (three-dimensional) shape, the points in this plane are within 0.2 mm of the egg are identified (Fig. S1a & b). This is an area in the tangent plane, not an area on the surface of the egg: it is the area of a slice the plane takes out of the egg when it is displaced 0.2 mm into the egg. To account for egg size, this area ('1' in Fig. S1c), was expressed as a proportion of the total two-dimensional area of the egg silhouette, which is the maximum area a plane could slice through, to obtain the contact index. The 0.2 mm "tolerance" accounts for both small deformation of the eggshell, and also small irregularities in the eggshell and substrate surfaces. Using tolerances (see text) of 0.1 mm and 0.5 mm provided results that were highly correlated with those for 0.2 mm.

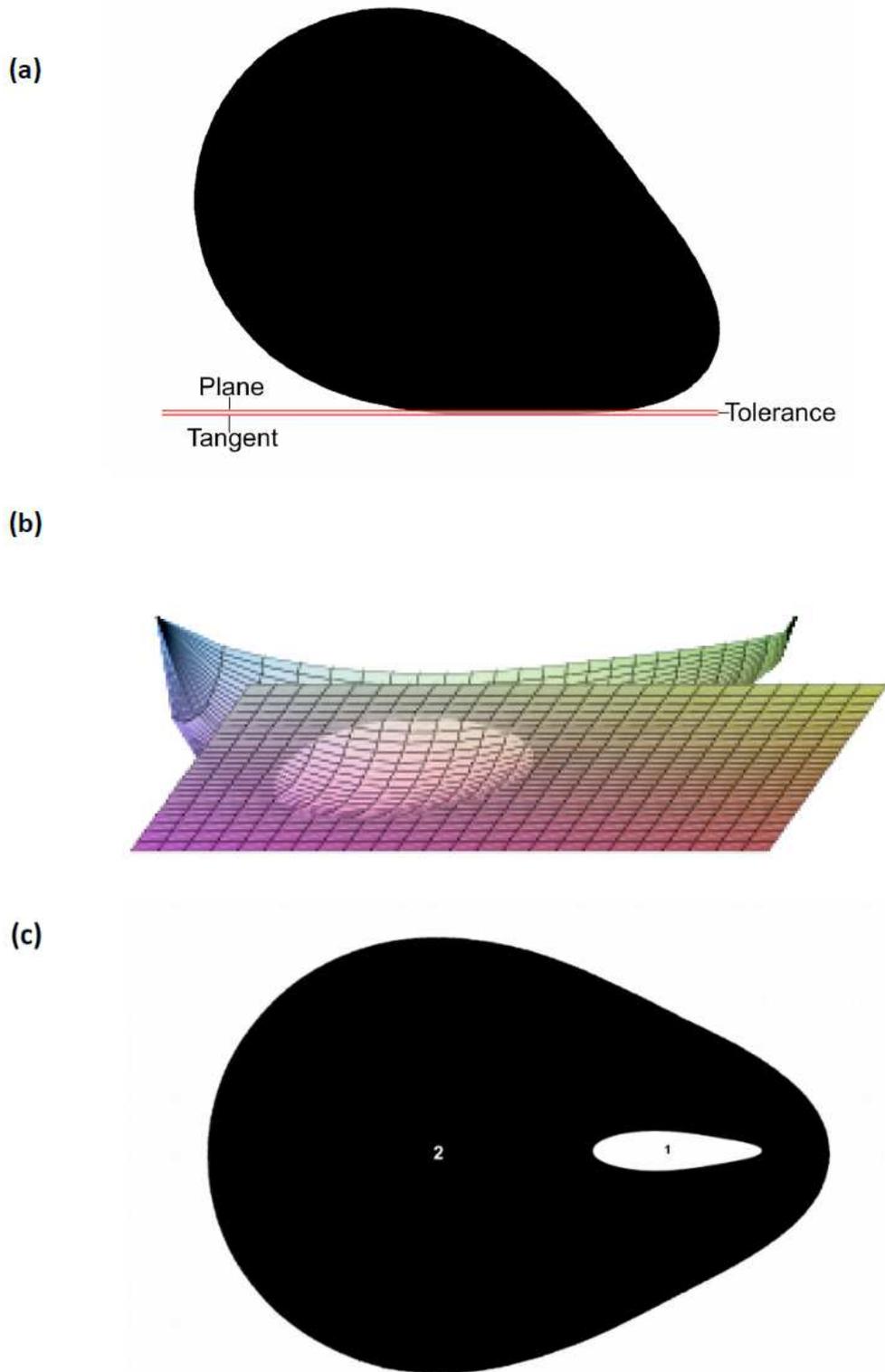


Figure S1. Images illustrating how the contact index was calculated.

(a) Two-dimensional egg silhouette showing the tangent, tolerance and plane.

(b) A three-dimensional model of an egg with a plane cutting through it. The two-dimensional area the plane creates by slicing through the egg is equivalent to our calculated area, not the three-dimensional surface area of the protruding bit of shell.

(c) Two-dimensional egg silhouette showing our calculated area ('1') and the two-dimensional area of the egg silhouette ('2' + '1').

Table S1. Correlation coefficients between different measures of eggshell thickness. Correlation coefficients were calculated using Spearman’s rank correlation on 60 measures from twenty eggs — ten Guillemot and ten Razorbill eggs, for which a mean value for each eggshell region (blunt end, equator, and pointed end) was used.

	Shell thickness parameter ¹				
	Total	True shell	Effective	Mammillary	Membrane
Total ²	-	0.98	0.96	0.65	0.78
True shell ³	0.98	-	0.98	0.68	0.69
Effective	0.96	0.98	-	0.54	0.65
Mammillary	0.65	0.68	0.54	-	0.48
Membrane	0.78	0.69	0.65	0.48	-

¹ see Figure S2 for visualisation and descriptions of the eggshell thickness parameters discussed in the main manuscript.

²Total shell thickness.

³True shell thickness is the distance from the tip of the mammillary bodies to the outer surface of the shell, i.e. the calcium carbonate components of the shell, not the shell membranes. This is equivalent to the sum of effective shell thickness and mammillary layer thickness; see Figure S2.

$P < 0.001$ for all correlations.

Table S2. Repeatability values for eggshell thickness and porosity measures calculated according to the methods in Lessells & Boag (1987) and Nakagwa & Schielzeth (2010). Three mean shell thickness values and three porosity measures were obtained for each region of five Guillemot and five Razorbill eggs, leading to a total of 90 data points per parameter. Analyses were performed on square root transformed data.

Sample	Total shell thickness ¹		Effective shell thickness ¹		Mammillary layer thickness ¹		Membrane thickness ¹		Porosity ¹	
	<i>r</i>	<i>F</i>	<i>r</i>	<i>F</i>	<i>r</i>	<i>F</i>	<i>r</i>	<i>F</i>	<i>r</i>	<i>F</i>
Guillemot ²	0.98	191	0.97	107	0.54	4.59	0.87	20.9	0.74	9.40
Razorbill ²	0.96	82.6	0.97	112	0.63	6.12	0.58	5.23	0.58	5.13
All ³	0.99	426	0.99	271	0.73	8.92	0.87	20.1	0.72	8.63

¹ see Figure S2 for visualisation and definition of shell thickness parameters.

² degrees of freedom for all *F* values (14,30)

³ degrees of freedom for all *F* values (29,60)

P < 0.001 for all *F* values

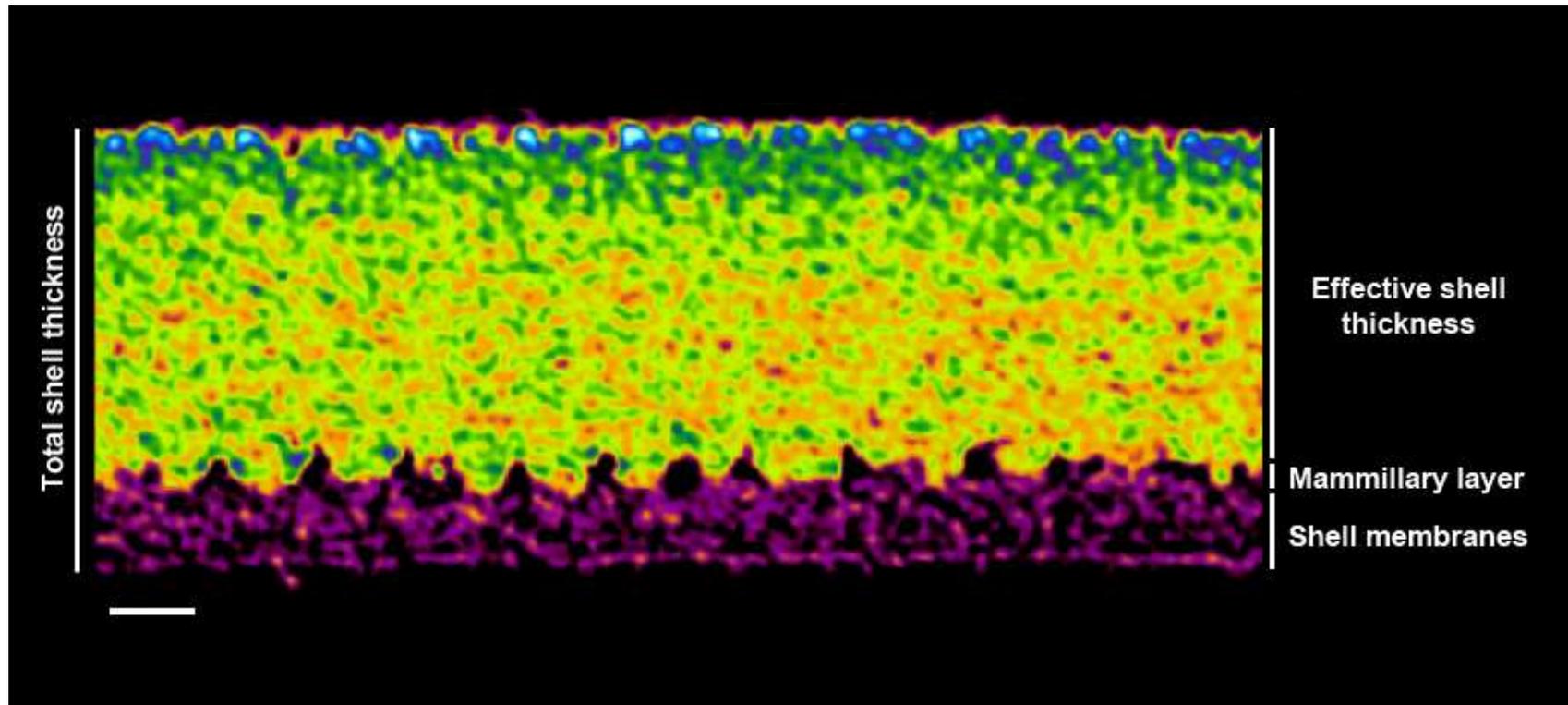


Figure S2. Cross sectional image of a piece of Guillemot eggshell showing the different shell thickness measures, taken using X-ray micro computed tomography. Effective shell thickness is the distance from the point of fusion of the palisade columns to the outer edge of the shell accessory material (see Bain 2005); mammillary layer thickness is the distance from the end of a mammillary body to the point of fusion of the palisade columns, and total shell thickness is the distance from the inner side of the shell membrane to the outer edge of the shell accessory material. Images were false coloured according to grey value to allow better visualisation of the different layers of the eggshell. Scale bar = 100 μm .

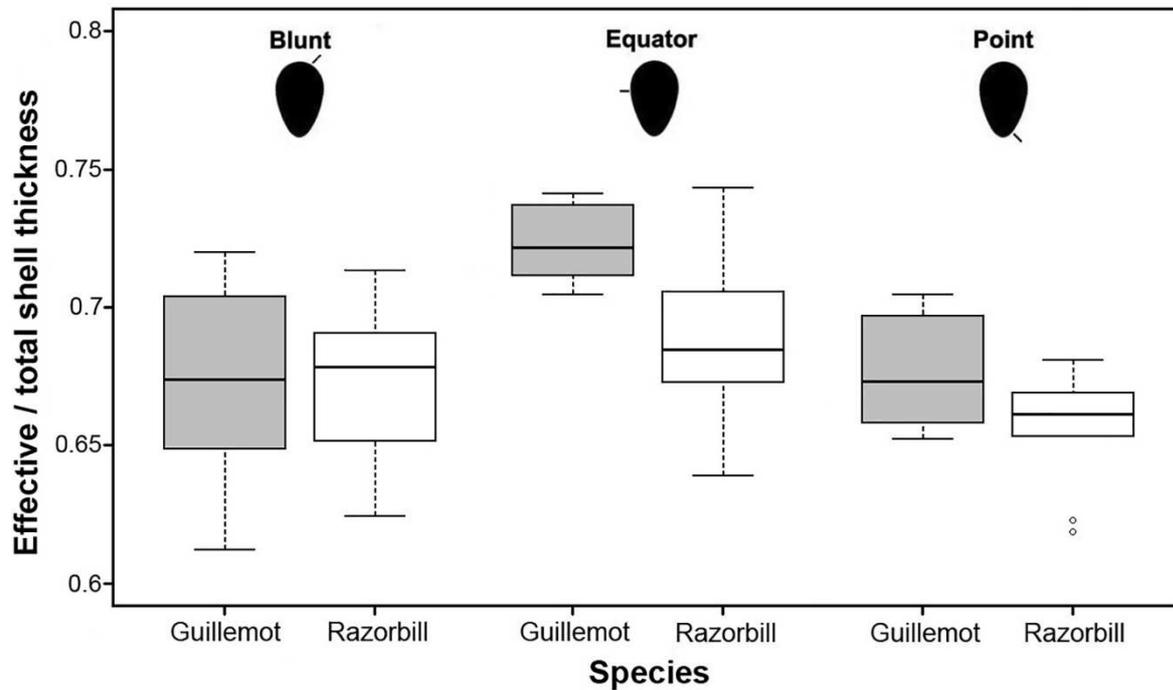


Figure S3. Differences in effective shell thickness/total shell thickness ratios between the three regions of Guillemot and Razorbill eggs. A greater proportion of total shell thickness can be attributed to effective shell thickness at the equator of Guillemot eggs compared to the pointed or blunt end (one-way ANOVA with repeated measures performed on Arcsine square root transformed data: $F_{2,18} = 16.7$, $P < 0.001$; Tukey multiple comparison test $P < 0.05$). Additionally, there are no significant differences in mammillary layer thickness (blunt: $78.3 \mu\text{m} \pm 13.7$, equator: $83.1 \mu\text{m} \pm 6.21$, point: $90.4 \mu\text{m} \pm 7.09$) (one-way ANOVA with repeated measures: $F_{2,18} = 3.15$, $P > 0.05$) and the shell membrane is significantly thicker at the pointed end ($131 \mu\text{m} \pm 15.9$) of the Guillemot egg than at either the equator ($114 \mu\text{m} \pm 10.6$) or blunt end ($110 \mu\text{m} \pm 10.8$) (one-way ANOVA with repeated measure: $F_{2,18} = 12.5$, $P < 0.001$). The increased total eggshell thickness at the equator can therefore be primarily attributed to an increase in effective shell thickness and not an increase in thickness of all the shell layers. Razorbill eggs show a different pattern: a lower proportion of total shell thickness is attributed to effective shell thickness at the pointed end compared to the equator (one-way ANOVA with repeated measures performed on Arcsine square root transformed data: $F_{2,18} = 6.80$, $P < 0.01$) (Tukey multiple comparison test $P < 0.05$). No other differences in effective/ total shell thickness between regions are significant (Tukey multiple comparison test $P > 0.05$), despite the blunt end ($438 \mu\text{m} \pm 37.1$) of Razorbill eggs being significantly thinner than the equator ($483 \mu\text{m} \pm 37.6$) or pointed end ($501 \mu\text{m} \pm 47.3$) (one-way ANOVA with repeated measures: $F_{2,18} = 19.9$, $P < 0.001$; Tukey multiple comparison test $P < 0.05$), indicating that differences in total shell thickness in Razorbill eggs are driven by differences in the thickness of all shell layers and not primarily by changes in the effective thickness layer, as is the case in Guillemot eggs. Ten Guillemot and ten Razorbill eggs were analysed and an average value for each eggshell region was used in analysis, leading to a total of 60 data points.

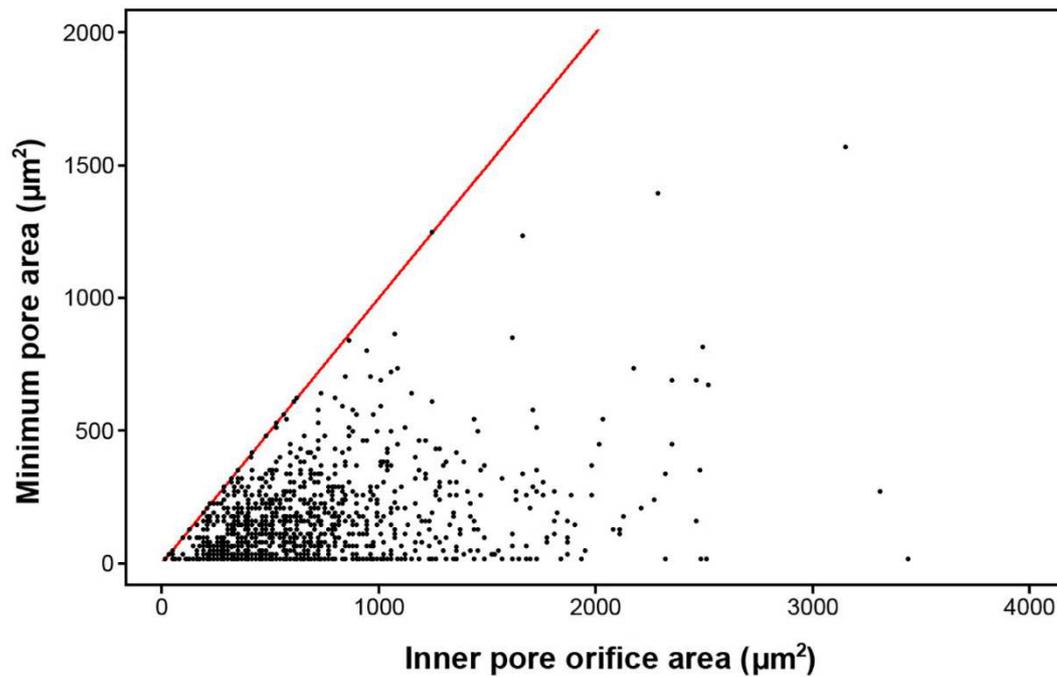


Figure S4. Relationship between minimum cross sectional pore area and inner pore orifice area. Inner pore orifice measures are weakly positively correlated with minimum pore area measures (Spearman's rank correlation, overall dataset: $r_s = 0.287$, $n = 1195$, $P < 0.0001$; Guillemots: $r_s = 0.297$, $n = 595$, $P < 0.0001$; Razorbills: $r_s = 0.246$, $n = 600$, $P < 0.0001$). The red line shows the 1:1 relationship between measures. Most measures lie below this 1:1 line, indicating that inner pore orifice measures are generally larger than minimum pore area measures; for this data, on average, $545 \mu\text{m}^2 \pm 424$ larger. Inner pore orifice measures are therefore not a useful measure of the narrowest part of a pore channel. Ten pores were measured per region (blunt, equator, point) of five Guillemot and five Razorbill eggs and thirty pores per region were measured for another five Guillemot and five Razorbill eggs. Some regions of Guillemot eggs had fewer than 10 pores per region, leading to a total 595 Guillemot pore measurements.