

NEW INSIGHTS FROM OLD EGGS – THE SHAPE AND THICKNESS OF GREAT AUK *Pinguinus impennis* EGGS

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Abstract: We compared the shape and eggshell thickness of Great Auk's eggs with those of its closest relatives, the Razorbill, Common Guillemot and Brünnich's Guillemot in order to gain additional insights into the breeding biology of the extinct Great Auk. The egg of the Great Auk was most similar in shape to that of Brünnich's Guillemot. The absolute thickness of the Great Auk's eggshell was greater than that of the Common Guillemot and Razorbill egg, which is as expected given its greater size, but relative shell thickness at the equator and pointed end (compared to the blunt end) was more similar to that of the Common Guillemot. On the basis of these and other results we suggest that Great Auk incubated in an upright posture in open habitat with little or no nest, where its pyriform egg shape provided stability and allowed safe maneuverability duration incubation. On the basis of a recent phylogeny of the Alcidae, we speculate that a single brood patch, a pyriform egg and upright incubation posture as in the Great Auk and the two *Uria* guillemots, is the ancestral state, and that the Razorbill — the Great Auk's closest relative — secondarily evolved two brood patches and an elliptical egg, as adaptations for horizontal incubation which provides flexibility in incubation site selection,

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allowing breeding in enclosed spaces such as crevices, burrows or under boulders, as well as on open ledges.

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The Great Auk *Pinguinus impennis* is extinct. What are thought to have been the last two individuals were killed on the island of Eldey, Iceland in June 1844 (Grieve 1885; Newton 1896; Fuller 1999). Since then attempts have been made to reconstruct aspects of the Great Auk's life history from two main sources: (i) anecdotal accounts of live birds observed at their breeding colonies only by those intent on harvesting the birds and their eggs rather than by scientists, and (ii) the ~80 skins, skeletal material and alcohol-preserved internal organs of two individuals, as well as ~70 eggs, most of which now exist in museum collections (Bengtson 1984; Fuller 1999). This material is all that is available for reconstructing the life of the Great Auk — albeit with the help of new technologies (e.g. Thomas *et al.* 2017).

The Great Auk was a member of the Alcidae (auks), but was unique among contemporaneous alcids in being flightless. The living Alcidae comprise at least 24 species in 10 genera that separate into at least two distinct groups in six tribes. Recent phylogenetic analysis identifies the Great Auk and the Razorbill *Alca torda* as sister species within Tribe Alcini with a common ancestor about 11 million years ago (mya), while the two *Uria* guillemots (Common Guillemot *U. aalge* and Brünnich's Guillemot *U. lomvia*: known as Common Murre and Thick-billed Murre, respectively in North America) are sister species with a common ancestor some 7 mya, with all four species having a common ancestor about 17mya (Smith & Clark 2015).

Much has been written about the Great Auk, but several aspects of its breeding biology and life history remain a mystery (Newton 1896, Bengtson 1984, Harris & Birkhead 1985). However, it is known that the Great Auk was confined to the in the North Atlantic, where like many other seabirds it bred colonially mainly on

offshore islands. Like the Razorbill and the two guillemots the Great Auk produced a single-egg clutch. The two guillemots have, and the Great Auk had a single, centrally-placed brood patch while the Razorbill, despite its single egg clutch, has two lateral brood patches (Bengtson 1984, Harris & Birkhead 1985).

The characteristics of a species' eggs, such as shape and eggshell thickness, can provide an indication of the ecological conditions in which that species lays and incubates its egg(s) (Birkhead *et al.* 2019) and hence provide the opportunity to obtain new insights into the breeding ecology of the Great Auk.

Egg shape may tell us something about the situation in which the Great Auk laid and incubated its egg (see Birkhead 1993, Montevecchi & Kirk 1996). Like the Common Guillemot and Brünnich's Guillemot, the Great Auk's egg has been described as 'pyriform' or pear-shaped, with one very pointed end (Walters 1994). The Razorbill, despite its closer phylogenetic affinity to the Great Auk than the *Uria* guillemots, produces an egg whose shape is much less pointed, and often described as 'elliptical ovate to elongate ovate' (Bent 1919: 203; see also Harris & Birkhead 1985: 174). A pyriform-shaped egg is one that is relatively elongate, relatively asymmetrical and much more pointed at one end than the other (Thomson 1964, Biggins *et al.* 2018). This extreme among avian egg shapes has long been considered difficult to quantify (see Biggins *et al.* 2018). In contrast, the shape of most other birds' eggs can be adequately described by two indices: (i) elongation (length relative to breadth), and (ii) asymmetry (the length from the egg's widest point to the most pointed end, divided by the overall length; called 'Pointedness' in Biggins *et al.* 2018). Variants of these indices in different studies are identified and defined in Biggins *et al.* (2018). The two indices, elongation and asymmetry however, do not adequately capture the shape of pyriform eggs (e.g. see Stoddard *et al.* 2017). To deal with this Biggins *et al.* (2018) used a third index, Polar Asymmetry (see below).

Recent studies of the Common Guillemot egg show that its pyriform shape confers stability and is less likely to be dislodged on a sloping substrate than a more typically shaped avian egg (Birkhead *et al.* 2019). This stability in turn

seems likely to increase the control that incubating birds have over the egg's movement, for example during egg turning and incubation change-overs, and when birds incubate in an upright posture with no nest (Birkhead *et al.* 2018, 2019).

Eggshell thickness may provide information relating to the substrate on which Great Auk eggs were incubated. For example, a comparison between the Common Guillemot and Razorbill (Birkhead *et al.* 2017a) showed that the region below the equator (adjacent to the pointed end of the egg) of the Common Guillemot egg is relatively thicker than that of the Razorbill. This difference may relate to egg size or shape, with the more elongate (and hence weaker) shape of Guillemot eggs requiring reinforcement at the equator (Maurer *et al.* 2012). Guillemots breed at high density and incubate on bare rock where the risk of physical damage to the egg is high and the greater thickness and hence strength of this part of the eggshell may reinforce a region that lies in contact with the substrate and where damage is most likely to occur (Uspenski 1958, Belopol'skii 1961, Birkhead *et al.* 2017a). A comparison of the thickness of the different regions of Great Auk eggs with other alcids may therefore allow us to infer something about the risks of damage and hence its breeding situation.

Recent developments in: (i) accurately quantifying avian egg shape (Biggins *et al.* 2018), (ii) interpreting the adaptive significance of egg shape (Birkhead *et al.* 2018, 2019, Deeming 2018, Stoddard *et al.* 2017), and (iii) micro-CT techniques for visualising and measuring the thickness of avian eggshells (Riley *et al.* 2014, Birkhead *et al.* 2017a, Jackson *et al.* 2018), provide the opportunity to obtain new data from Great Auk eggs. Our overall aim was to compare the shape of, and the variation in shell thickness along the length of Great Auk eggs with those of the Common Guillemot, Brünnich's Guillemot and Razorbill, in the hope of obtaining a better understanding of the Great Auk's breeding biology.

METHODS

Egg shape: We quantified egg shape using the methods described by Biggins *et al.* (2018) that provides three indices of shape: (i) Elongation: the ratio of the length to the width at the widest point, (ii) Asymmetry (Pointedness): the length from the point where the egg is widest to the more distant end divided by the overall length, and (iii) Polar Asymmetry: the ratio of the diameter of the largest circle that will fit within the egg outline and touch the egg at its blunt pole to the diameter of the largest circle within the egg outline and touching the more pointed pole.

Indices of egg shape were obtained from photographs taken under standardised conditions (Birkhead *et al.* 2017a,b) for all eggs except those of the Great Auk, which were obtained from photographs in Tomkinson & Tomkinson (1966), and as described elsewhere (Birkhead *et al.* 2018a) we verified that these photographs were completely appropriate for shape analyses. Eggs of Common Guillemots and Razorbills were either from museum collections and/or collected under licence in the field between 2014 and 2016 (and then placed in a museum collection) and the three scanned Great Auk eggs were from the Natural History Museum, Tring, UK. Sample sizes for egg shape indices were as follows: Razorbill ($n = 101$, comprising 10 and 17 from Skomer Island in 2015 and 2016, respectively, and 74 from museums), Great Auk ($n = 51$ from Tomkinson & Tomkinson 1966), Common Guillemot ($n = 735$, comprising 98, 62 and 54 from Skomer Island in 2014, 2015 and 2016, respectively, and 521 from museums) and Brünnich's Guillemot ($n = 296$ all from museum collections) (see also Birkhead *et al.* 2019 Appendix S1).

Although we previously found a (weak) relationship between egg volume and shape (Birkhead *et al.* 2017), in the present study we did not control for egg volume in our analyses of egg shape primarily because we were interested in using egg shape to infer something about the ecology and breeding site of the Great Auk in terms of the stability of their egg (see below, and online supporting information Appendix S1).

Stability: It has recently been shown that the most likely benefit of a pyriform shape in the Common Guillemot's egg is that it confers stability by maximizing the surface area of the egg in contact with the substrate such that the egg is more easily and more swiftly positioned in a stable stationary position and therefore is inherently less likely to be dislodged on a sloping surface (Birkhead *et al.* 2018). Given the similar pyriform shape of Great Auk eggs to those of the two guillemot species, it is predicted that their shape will also confer some stability. What is not known whether the greater size (and fresh mass estimated to be 327g, *cf* Common Guillemot: ~ 110g; Brünnich's Guillemot ~ 100g; Razorbill ~90g — all values from Harris & Birkhead 1985) of a Great Auk egg influences its stability. To establish the extent to which the shape and mass of the Great Auk's egg confers stability, it is impossible to use real 'live' eggs. We therefore created ten pairs of 3-D printed eggs (using shape measurements based on ten real Great Auk eggs (see online supporting information Appendix S2), one the size and shape of a Great Auk egg and one of exactly the same shape but the size of a Brünnich's Guillemot's egg). To simulate the consistency of fresh eggs, we included an appropriately sized air cell at the blunt pole and then completely filled the remaining space in the egg with albumen from chicken eggs. The mass (mean \pm SD) of the filled eggs was Great Auk: 312.90g \pm 37.70 and Brünnich's Guillemot: 82.00g \pm 5.10. We used Brünnich's Guillemot egg size as a comparison because it had previously been suggested that they were more similar in shape to Great Auk eggs than Common Guillemot eggs (Harris & Birkhead 1985) — as we confirmed (see below). We then subjected each egg to exactly the same tests, using the identical methods that we had used previously in a comparison of the stability of Common Guillemot and Razorbill eggs, establishing the steepest slope an egg would remain stable on, either on a moving (i.e. gradually increasing) slope or a static slope (see Birkhead *et al.* 2017b). (For details see online supporting information Appendix S2).

Eggshell thickness: We used Micro-Computed Tomography (micro-CT) to visualise and quantify the thickness of eggshells in three different regions of the egg: (i) adjacent to the blunt pole, (ii) just below the equator towards the pointed

pole, and (iii) adjacent to the pointed pole. Our measure of eggshell thickness was 'effective eggshell thickness', which is the distance between the point of fusion of the palisade columns to the outer surface of the shell accessory material, and this is likely to be the most important aspect of shell thickness for eggshell strength (Bain 2005, Solomon 2010, Birkhead *et al.* 2017a Fig. 2). Effective shell thickness is positively correlated with both trueshell thickness (i.e. the calcium carbonate shell and any shell accessory material) and total shell thickness (i.e. all shell layers including the organic membranes; see Birkhead *et al.* 2017a). We examined thickness in the three different regions of each species' egg relative to each other (as in Birkhead *et al.* 2017a Fig. 2). Sample sizes were as follows: Razorbill (10, $n = 5$ three replicates per region per egg, $n = 5$ one replicate per region per egg), Great Auk (3, three replicates per region per egg), and Common Guillemot (10, $n = 5$ three replicates per region per egg, $n = 5$ one replicate per region per egg). The data on Common Guillemot and Razorbill eggs are from Birkhead *et al.* (2017a). For these comparisons we did not have access to shell material for Brünnich's Guillemot eggs. CT scanning of the two guillemot and Razorbill egg shells was conducted as described earlier using fragments of shell (Birkhead *et al.* 2017a), but the Great Auk eggs were scanned whole, mounted in protective casings, as described by Russell *et al.* (2018). The sample size for the Great Auk is small because of the time required (and the concomitant cost) to scan entire eggs. The CT scanner and settings used for the Great Auk were as described in the online supporting information Appendix 3.

RESULTS

Shape: All three shape parameters (asymmetry/pointedness, elongation and polar asymmetry) were statistically different across the four auk species in multivariate testing (MANOVA: Wilks' lambda = 0.56, $F_{9, 2864.7} = 84.45$, $P < 0.0001$). Considered separately, the overall differences amongst the four species also differed significantly for each of the three shape indices (ANOVAs asymmetry/pointedness: $F_{3, 1179} = 257.4$, $P < 0.0001$; Elongation: $F_{3, 1179} = 44.81$, $P < 0.0001$; Polar Asymmetry: $F_{3, 1179} = 78.98$, $P < 0.0001$). However, post-hoc Tukey tests highlighted that, whilst all other paired species comparisons showed

significant differences in egg shape, the Great Auk and Brünnich's Guillemot paired species comparisons showed no significant differences between any of the three shape indices (asymmetry/pointedness: $P = 0.924$; elongation: $P = 0.582$; polar asymmetry: $P = 0.408$; see Figs. 1 and online supporting information Appendix S4). These results therefore highlight that Great Auk eggs are most similar to Brünnich's Guillemot eggs in terms of their shape (Fig. 1; online supporting information Appendix S4).

Stability: We found no difference in the maximum slope a model Great Auk egg or a Brünnich's Guillemot's sized egg would remain stable (Fig.2; mean slope angle \pm SD, Great Auk: $20.19^\circ \pm 3.99$ and Brünnich's Guillemot: $22.27^\circ \pm 4.79$; Paired t-test: $t = 1.18$, $df = 9$, $P = 0.269$; see online supporting information Appendix S4), or a static slope of 35° (mean success proportion \pm SD, Great Auk: 0.65 ± 0.37 and Brünnich's Guillemot: 0.66 ± 0.32 ; Paired t-test: $t = 0.17$, $df = 9$, $P = 0.868$; Fig. 2).

Eggshell thickness: Overall, and not surprisingly given its greater egg and body size, the eggshell of the Great Auk egg was absolutely thicker, in terms of effective thickness, than that of the Common Guillemot, which in turn was thicker than that of the Razorbill (Fig. 3, MANOVA: Pillai's trace = 1.04, $F_{6,38} = 6.91$, $P < 0.0001$; separate one-way ANOVAs for each region, blunt end: $F_{2,20} = 56.6$, $P < 0.0001$; equator: $F_{2,20} = 243.7$, $p < 0.0001$; pointed end: $F_{2,20} = 76.1$, $P < 0.0001$; all multiple comparisons between species at each egg region were significant $P < 0.05$). In all three species, the equator was thicker than the blunt end. In both the Great Auk and in the Common Guillemot the two regions sampled below the egg's widest point were relatively thicker than in the Razorbill (Fig. 3). One can also consider these results the other way: that in Great Auk and in the Common Guillemot egg the blunt pole of the egg was relatively thinner than the equator/pointed end than in the Razorbill egg.

DISCUSSION

The Great Auk's egg is more similar in shape to that of the two guillemots, and in particular Brünnich's Guillemot, than to the Razorbill to which it is phylogenetically closest. The eggshell of the Great Auk is absolutely thicker than either the Common Guillemot or Razorbill egg, and although we did not have the material to measure it directly, also thicker than Brünnich's Guillemot egg (see Uspenski 1956: 41) undoubtedly because the greater size of the Great Auk's egg (Ar *et al.* 1974; Rahn & Pagenelli 1989).

Although the sample sizes for the Great Auk were small, our results indicate that the differences in thickness within Great Auk eggs is similar to, but more pronounced than in the Common Guillemot and the Razorbill (Fig. 34) (and also Brünnich's Guillemot — see Uspenski 1956 for measures of total shell-thickness). This may be a consequence of the Great Auk (i) laying an elongate egg which as a result, was weaker along its long axis; (ii) laying an absolutely larger egg; (iii) being up to five times heavier than a guillemot or Razorbill, and hence increasing the weight the egg has to support during incubation, and (iv) potentially incubating its egg on a hard surface and therefore requiring reinforcement in the region where the egg is in contact with the brood patch and substrate (Uspenski 1958, Belopol'skii 1961, Birchard & Deeming 2009, Maurer *et al.* 2012). The relatively thin blunt end of the Great Auk egg may facilitate hatching — assuming the Great Auk is like most other birds, including the guillemots and Razorbill — by pipping at and emerging from the blunt end of the egg (Tschanz 1968), from an egg whose shell is otherwise fairly robust.

The fact that the average shape of the Great Auk egg is virtually identical to that of an average Brünnich's Guillemot's egg suggests that the Great Auk egg would have had similar stability and 'safe manoeuvrability' to that of a Brünnich's Guillemot's egg, and greater stability than a Razorbill's egg, but perhaps less than a Common Guillemot egg, which is often more pyriform (Fig. 1; and Birkhead *et al.* 2018). Our results using 3-D printed eggs strongly suggest that eggs of

identical pyriform shape but different mass have similar stability on sloping surfaces.

We have previously suggested that in the alcids a pyriform shaped egg and a single, centrally-positioned brood patch facilitates an upright or semi-upright incubation posture that may be an adaptation to breeding on bare, open habitat with no nest (Birkhead 1993; Birkhead *et al.* 2019). The Razorbill by contrast has a more rounded, elliptical shaped egg, two lateral brood patches and incubates in a horizontal position. Both guillemot species incubate their egg with the blunt end oriented forwards, lying between (but not on) the legs, resting on the substrate or partially on the foot webs. An upright posture may also facilitate high density breeding in Common Guillemots which breed at higher densities than Brünnich's Guillemots, and incubate in a more upright posture (Spring 1971). There are no descriptions of undisturbed, incubating Great Auks, but their single, central brood patch suggests that like the guillemots *Uria* spp., this species may also have incubated in an upright position (Birkhead 1993).

Five additional factors could potentially explain the evolution of the Great Auk's pyriform egg.

(i) To minimise the likelihood of dirt contamination of the egg's blunt end, as in the Common Guillemot whose pyriform egg lies an angle with its long, straight edge horizontal to, and in direct contact with the substrate such that its blunt end is free from any dirt on the substrate (see Fig. 1 in Birkhead *et al.* 2017a).

(ii) A pyriform shape may confer greater strength and resistance to impacts during incubation (see Birkhead *et al.* 2017a). This idea has proved challenging to test (unpublished results) because of the difficulty of separating the effects of shape from eggshell thickness in conferring strength.

(iii) Johnson (1941) suggested that for Common Guillemots a pyriform egg, together with upright incubation, would result in a greater surface area of the egg in contact with the brood patch and more efficient incubation. Our attempts

to test this using 3D printed eggs matched for mass and the thermal properties of real Common Guillemot eggs, revealed that the brood patch was so efficient at warming eggs of different shapes that the idea that a pyriform egg facilitates more efficient incubation seems unlikely (T. R. Birkhead and J. E. Thompson, unpublished results).

(iv) Birds laying relatively larger eggs are more likely to produce eggs that are more elongate and asymmetrical in shape (Stoddard *et al.* 2017; Deeming 2018). In Stoddard *et al.*'s study (2017, Tables S2-B and S2-C) egg size and female body size accounted for 29-47% of the explained variation in egg shape (ellipticity and asymmetry), with an additional 4 to 5% of the explained variation accounted for by 'flight efficiency'. Birds are able to produce eggs that are relatively much larger (up to 29% of female body mass: Warham 1990) than the neonates of mammals (or the eggs of dinosaurs), because unlike mammals (and dinosaurs) most birds have an open pelvis (Deeming 2018). However, there must be some constraints on avian egg diameter since the way birds produce relatively larger eggs is — apparently — to produce relatively elongate eggs, (although it is not clear why relatively larger eggs tend also to be more asymmetric). We can probably discount the idea that the Great Auk's pyriform egg (which is both relatively elongate and asymmetric) is solely a consequence of its size since, although large in absolute terms, it is relatively the smallest egg among alcids, comprising just 7% of estimated female body mass (compared with 11-12% for the two guillemots and the Razorbill and over 20% in the Ancient Murrelet *Synthliboramphus antiquus* and Guadalupe (Xantus') Murrelet *S. hypoleucus* (Gaston & Jones 1998; Birkhead *et al.* 2018a)). Yet, in auks and penguins absolutely larger eggs tended to be more pyriform so we cannot rule out that the Great Auk's egg is more asymmetric and elongate with high polar asymmetry, because — at least in part — its egg is absolutely large. Since incubation site alone explained 65% of the variation in egg-shape indices across the auks and penguins (Birkhead *et al.*, 2019) it is likely to be relatively more important than egg size in the evolution of egg shape in the Great Auk.

(v) Stoddard *et al.* (2017) and Deeming (2018) reported that some of the variation in avian egg shape is associated with developmental mode (or some correlate of it, such as relative egg size, as discussed above). It is generally assumed that like its closest relatives the Razorbill and the two guillemots, the Great Auk chicks had an ‘intermediate’ mode of development and departed from the colony at about 20% of adult body mass at 17-21 days of age (compared with precocial alcids, like the Ancient Murrelet whose chicks depart after 2 days, or at the other extreme, the semi-precocial Atlantic Puffin *Fratercula arctica* whose chick departs after 40 days) (Gaston & Jones 1998, Houston *et al.* 2010, Birkhead *et al.* 2018a). It seems unlikely that developmental mode explains the pyriform egg of the Great Auk since across species (including auks) precocial and semi-precocial chicks hatch from both pyriform and non-pyriform eggs (Birkhead *et al.* 2018a).

Breeding in the open

Like the two guillemots, Great Auks also bred in the open, and at high density, and as far as is known, with no nest of any kind (Bengtson 1984; Montevecchi & Kirk 1996). The fact that Great Auk eggs exhibit such enormous variation in the pattern, distribution and density of their maculation (see images in Tomkinson & Tomkinson 1966; Fuller 1999), is consistent with the idea that, like the two guillemots, eggs laid in close proximity risked becoming mixed up, and a unique maculation signature may have enabled parents to recognize and retrieve their own egg (see Tschanz 1968).

The best evidence that Great Auks bred at high density is the surveyor William Taverner’s 1718 report from Penguin Islands, Newfoundland: ‘*They [the French inhabitants of Placentia, Newfoundland] told me that a Mann, could not goe ashoar upon those islands, without Bootes, for otherwise they would spoile his Leggs, that they were Intirely covred with those fowles, soe close that a Mann could not put his foot between them*’ (cited in Montevecchi & Kirk 1996).

While Taverner's statement clearly indicates that Great Auks bred at high density, it could be interpreted in two ways, (i) literally, and hence indicating that Great Auks bred in direct bodily contact with one another like Common Guillemots, in which case adjacent eggs might be as little as 30 cm apart, or (ii) as a slight exaggeration, as was common when describing for example, the abundance of seabirds, indicating that Great Auks bred close together but not in bodily contact. Given that Great Auks were flightless, they had to walk to reach their individual breeding sites, which would have meant finding a way between other breeding individuals, and hence that some spacing existed between breeding pairs.

Common Guillemots benefit from breeding at high density since this allows them to protect their eggs and chicks from predators such as gulls and corvids (Birkhead 1977). It may not have been necessary for Great Auks to breed in direct contact with conspecifics to protect their eggs and chicks from predators, for two reasons. The Great Auks' large body size (~70 cm tall; Bengtson 1984: estimated mass 5000g, Bédard 1969), compared to guillemots *Uria* spp. (~30 cm tall and ~1000g body mass), means that Great Auks were probably better able to defend their eggs and chicks from aerial predators, in part because they were stronger and could potentially inflict greater damage on these predators (maximum body mass for Great Black-backed Gull *Larus marinus* is 2300g) than can the two guillemots *Uria* or the Razorbill, and predators may therefore have been more reluctant to risk injury. In addition, when gulls or corvids take guillemot or Razorbill eggs from the incubating parent birds they do so warily and by rapid snatching (to avoid being injured by the parent), grasping the egg at its maximum diameter in their bill. The Great Auk's larger egg (mean maximum width ~75 mm) would have been relatively difficult for gulls and ravens to grasp such that their actively incubated eggs were probably less vulnerable to gull and corvid predation than those of guillemots *Uria* spp. and the Razorbill (see online supporting information Fig. S5).

One puzzle remains. It is generally accepted that the Great Auk's closest relative is the Razorbill. Indeed, the two species are very similar in their physical conformation (even though the Great Auk is considerably larger), and phylogenetic analyses place the two as sister species (Smith & Clarke 2015). It is somewhat surprising therefore that the Great Auk exhibits several traits — including its egg shape — that are more similar to the two *Uria* guillemots than the Razorbill. A possible explanation for this relates to the brood patch. Superimposing the number of brood patches (one or two) onto Smith & Clarke's (2015) phylogeny suggests that a single brood patch, a pyriform egg and upright incubation posture (as in the Great Auk and *Uria* guillemots) is the ancestral state and that the Razorbill secondarily evolved two brood patches and a more elliptically shaped egg, presumably as adaptations for horizontal incubation. This in turn allows the Razorbill greater flexibility in incubation site selection allowing them to breed in relatively small enclosed spaces including crevices, under boulders and in burrows, as well as out in the open on ledges. Other alcids (auklets and puffins) that lay a single egg and incubate in a crevice or burrow have two lateral brood patches (Gaston & Jones 1998: 26). Laterally located brood patches may be more efficient for horizontal incubation posture, and also allows the incubating alcid to position its single egg on either side of its body and hence also to adjust its own orientation within its breeding site.

In summary, on the basis of the shape of its egg and eggshell thickness we suggest that the Great Auk incubated in an upright posture, probably on bare rock surfaces, where its pyriform-shaped egg provided stability during incubation and its relatively thick shell at the equator and pointed end provided protection from mechanical damage.

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FIGURES

Fig 1

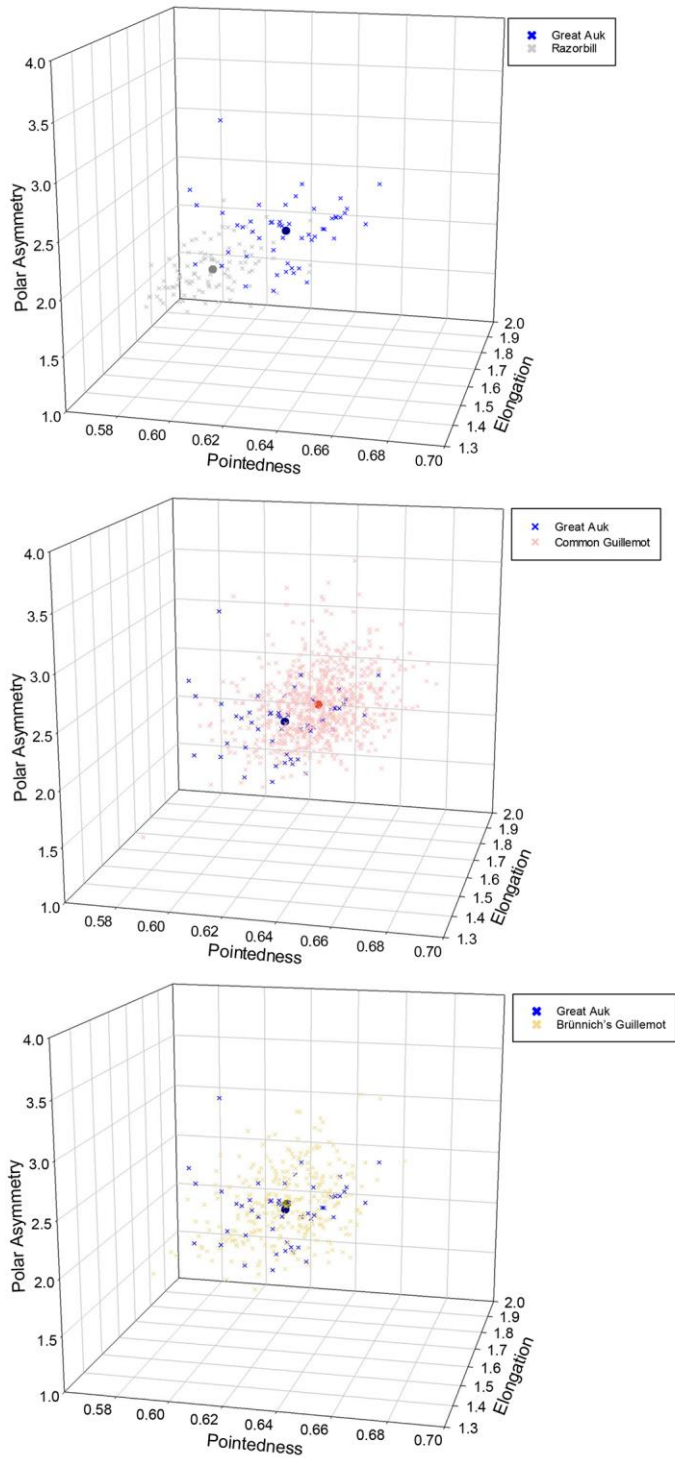


Fig 2

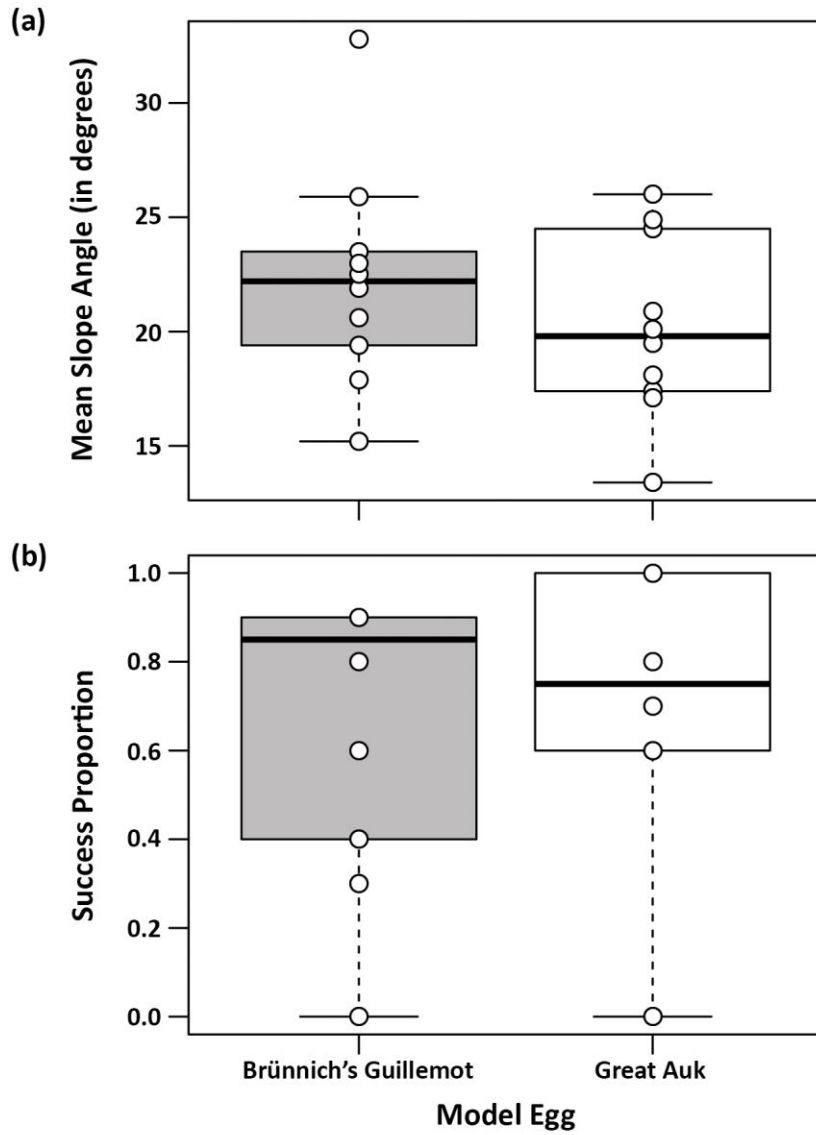
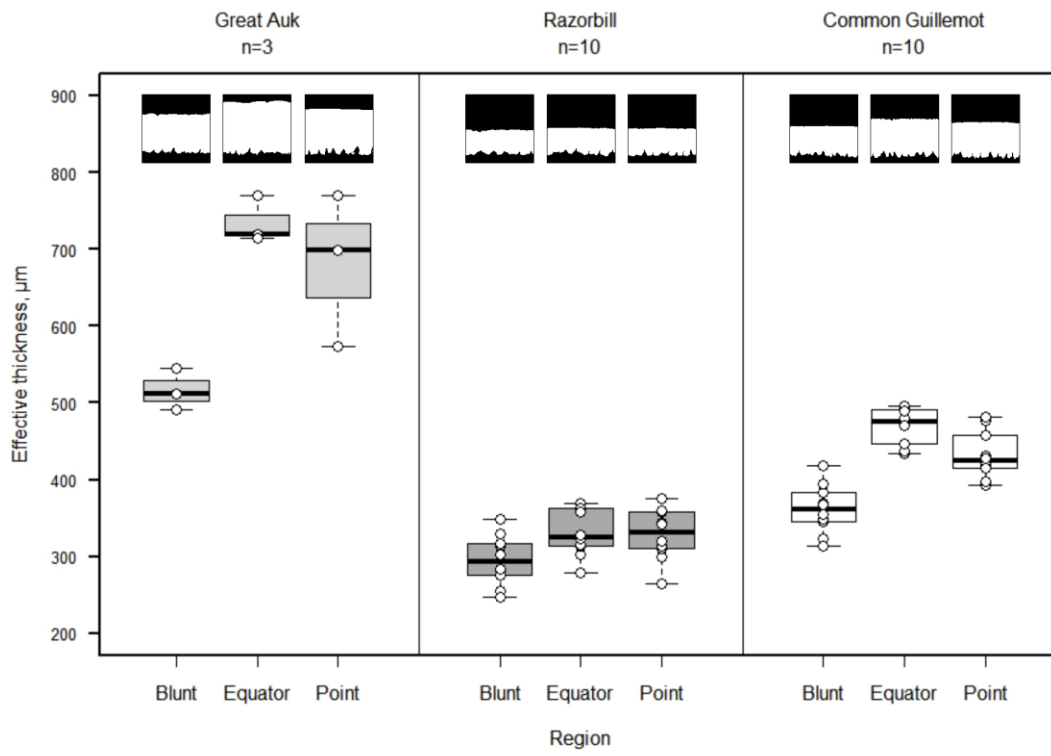


Fig 3



SUPPORTING INFORMATION

Additional Supporting Information can be found in the online version of this article:

Appendix S1. Methods: Adjusting Egg Shape for Egg Size

Appendix S2. The effect of egg size on egg stability, when shape indices are similar, using 3-D printed model eggs: a comparison of Great Auk and Brünnich's Guillemot sized eggs.

Appendix S3. Statistical analyses of shape, effective eggshell thickness, pore density and distribution and egg surface topography across species and egg regions.

Appendix S4. Details of egg size and the statistical analyses of shape

Appendix S5. Figure S5. Assessing the capabilities of typical auk egg predators to grasp a Great Auk egg in their beaks

FIGURES

Fig. 1. 3-D plots of three egg shape indices (Elongation, Pointedness and Polar Asymmetry derived see Biggins et al. (2018), separately comparing the Great Auk, to Razorbill, Common Guillemot and Brünnich's Guillemot.

Fig. 2. Comparisons between a typical Brünnich's Guillemot-sized and Great Auk-sized 3D-printed model eggs of identical shape for (a) mean slope angle reached in the moving slope experiment, and (b) the success proportion obtained in the static slope experiment. Comparisons were based on 10 pairs of eggs. The purpose of these tests was to assess the stability of eggs of identical shape but different sizes. These tests should not be compared to similar stability tests performed in Birkhead, Thompson and Montgomerie (2018) where real eggs were tested. Boxes are the interquartile range, black line within the box is the median and the whiskers show the highest and lowest values (excluding outlier data points). Black circles with no fill are the individual data points. The differences between the two egg sizes for each experiment are not statistically significant (see text). See online Supporting Information Appendix 2.

Fig. 3. Effective eggshell thickness for three different regions (blunt end, equator and pointed end) of Great Auk, Razorbill and Common Guillemot eggs. Differences between regions are significant in all three species (see online Supporting Information Appendix 3 for statistical comparisons). Examples of variation in shell thickness along a single egg (selected to closely represent the median) for each species are shown above the box plot, each square is 1mm long (see Fig A3.1 for details).