The pyriform egg of the Common Murre (Uria aalge) is more stable on sloping surfaces

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RESEARCH ARTICLE

The pyriform egg of the Common Murre (*Uria aalge*) is more stable on sloping surfaces

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ABSTRACT

The adaptive significance of avian egg shape is a long-standing problem in biology. For many years, it was widely believed that the pyriform shape of the Common Murre (*Uria aalge*) egg allowed it to either "spin like a top" or "roll in an arc," thereby reducing its risk of rolling off the breeding ledge. There is no evidence in support of either mechanism. Two recent alternative hypotheses suggest that a pyriform egg confers mechanical strength and minimizes the risk of dirt contamination of the blunt end. We present a new hypothesis: that the Common Murre egg's pyriform shape confers stability on the breeding ledge, thus reducing the chance that it will begin to roll. We tested this hypothesis by measuring the stability of Common Murre and Razorbill (*Alca torda*) eggs of different shapes on slopes of 20°, 30°, and 40° above the horizontal. Common Murre eggs were more stable, and easier to stabilize, than the more elliptical Razorbill eggs. Within Common Murre eggs, more pyriform eggs were more stable. From a fitness perspective, the stability of the Common Murre egg on a slope seems likely to confer an advantage and thus may be a strong force of natural selection favoring the pyriform shape.

Keywords: egg shape, pyriform, Razorbill, sloping surfaces, stability

El huevo piriforme de *Uria aalge* es más estable en superficies inclinadas

RESUMEN

El significado adaptativo de la forma del huevo de las aves es un problema de larga data en biología. Por largo tiempo, se creyó ampliamente que la forma piriforme del huevo de *Uria aalge* le permitía ya sea 'girar como una tapa' o 'rodar en un arco', reduciendo de este modo el riesgo de salirse del lecho de cría. No hay evidencia que apoye ninguno de estos mecanismos. Dos hipótesis alternativas recientes sugieren que un huevo piriforme brinda robustez mecánica y minimiza el riesgo de contaminación con suciedad del extremo romo. Aquí, presentamos y evaluamos una nueva hipótesis: que la forma piriforme del huevo de *U. aalge* brinda estabilidad en el lecho de cría, por ende reduciendo la probabilidad de comenzar a rodar. Evaluamos esta hipótesis midiendo la estabilidad de los huevos de diferentes formas de *U. aalge* y *Alca torda* en pendientes de 20°, 30° y 40° por sobre la horizontal. Los huevos de *U. aalge* fueron más estables y más fáciles de estabilizar que los huevos más elípticos de *A. torda*, y entre los huevos de *U. aalge*, los huevos más piriformes fueron los más estables. Desde una perspectiva de la adecuación biológica, la estabilidad en pendiente del huevo de *U. aalge* parece conferir una ventaja y por ende ser una potente fuerza de selección natural a favor de la forma piriforme.

Palabras clave: *Alca torda*, estabilidad, forma del huevo, piriforme, superficies inclinadas

INTRODUCTION

The shapes of birds' eggs vary considerably among the 10,000 extant and recently extinct species, from almost spherical to ovate to bi-conical to pyriform (i.e. pear-like or pointed), and one of the most extreme is the pyriform egg of the Common Murre (*Uria aalge*; Birkhead 2017, Birkhead et al. 2017a, 2017b, Stoddard et al. 2017). The adaptive significance of this shape, and indeed of the shapes of all other birds' eggs, is unclear. In a wide-ranging comparative study of avian egg shape, Stoddard et al. (2017) suggested that "flight efficiency" and thus adaptations for flight have been "critical drivers of egg shape variation in birds," with species best adapted for high-powered flight producing more elongated, more asymmetric eggs. However, only 4% of the variation in egg shape across the ~1,400 species studied by Stoddard et al. (2017) is explained by the hand-wing index (their measure of "flight efficiency") analyzed in that study. An alternative hypothesis is that egg shape evolves in response to adult posture during incubation and the type of substrate on which eggs are incubated.

Until recently, it was widely believed that the adaptive significance of the Common Murre's pyriform egg shape had been established. The most popular idea was that, when knocked by a bird or blown by the wind, the pyriform egg would spin on its axis (Hewitson 1831, Morris 1856, Thomson 1923). However, as early as 1903, this effect was shown to be an artifact of testing empty museum eggshells; real eggs are too heavy to spin in this way without unreasonable force (Wade 1903). A second idea, proposed initially by Belopol'skii (1957; see also Tschanz et al. 1969), was that its pyriform shape allowed the Common Murre's egg to roll in an arc and, hence, be less likely to roll off the breeding ledge. This idea was (and still is) widely reported in the ornithological literature (Drent 1975, Gill 2007, Lovette and Fitzpatrick 2016) and the popular press. But extensive testing by Ingold (1980) provided little conclusive support for this hypothesis (see also Birkhead 2017, Birkhead et al. 2017a, 2017b).

In an earlier paper (Birkhead et al. 2017b), we suggested that the pyriform shape might (1) reduce the chance of shell breakage by dissipating the forces of any impact—like an adult landing or stepping on the egg—across a wider surface of the shell; or (2) help to keep the blunt pole of the egg (where the embryo's head and the air cell are located) relatively free from debris and fecal contamination, allowing the embryo to respire more efficiently, because that region of the egg has a relatively high density of pores. Empirical observations confirm that, among naturally incubated Common Murre eggs, fecal contamination of the eggshell is less likely at the blunt end of the egg (Birkhead et al. 2017b).

Here, we present and test a new hypothesis: that the Common Murre's pyriform egg is more stable on a sloping ledge, and easier for the parent to manipulate, than a more elliptical egg. Common Murres breed at high densities (typically 20 pairs m^{-2}, but up to 70 pairs m^{-2}) and thus gain protection from aerial predators such as gulls and corvids (Birkhead 1977). High-density breeding can be achieved only by birds being extremely flexible with regard to their individual breeding site (an area typically 10 cm in diameter), and this often means that Common Murres breed on sloping ledges. In studies of both Common Murres and Thick-billed Murres (*U. lomvia*), around half of all breeding sites were classified as sloping (Gaston and Nettleship 1981, Birkhead and Nettleship 1987). In neither of these studies was the angle of the slopes measured directly; instead it was judged by eye, from a distance (through a telescope or binoculars) without disturbing the birds. In Birkhead and Nettleship (1987), "sloping" was classified as >15° above the horizontal.

Several other details are relevant here. Both Common and Thick-billed murres typically breed with no nest and with neighboring birds often in direct physical contact. Like the extinct Great Auk (*Pinguinus impennis*), which also produced a single pyriform egg (Bengtson 1984), both murres have a single, centrally located brood patch (Belopol'skii 1957, Bengtson 1984) and incubate in a semi-upright position, usually with their egg held between (but not on) the legs or feet, with the blunt end of the egg facing outward. In 44 of 56 (79%) incubating Common Murres on Skomer Island, Wales, UK, where at least one foot could be clearly seen, the egg was not resting on the webs. In the remaining 12 birds, the egg rested to some extent on the inner web. In no case was the egg resting fully on the web(s) (T. R. Birkhead et al. personal observation).

Murres almost never leave their egg unattended (Tschanz 1990, T. R. Birkhead et al. personal observation). When breeding on a sloping site, they almost always incubate facing upslope (Figure 1), with the blunt end of the egg oriented upslope. Among 116 sites on Skomer where there was a perceptible slope, the egg was oriented with its blunt end upslope in 109 cases (94%). This is likely an underestimate, given that eggs in other positions were easier to see (T. R. Birkhead et al. personal observation).

By contrast, the Razorbill (*Alca torda*), a close relative of the murres, breeds at lower densities and often on the same cliff ledges as murres, but not in contact with, or even very close to, other Razorbills or murres. Razorbills very rarely breed on sloping sites and they incubate in a horizontal posture, with the egg positioned under one wing, often resting on a bed of pebbles (Tschanz 1990, T. R. Birkhead et al. personal observation). They lay a single elliptical-ovate egg, but they have 2 brood patches—one on either side of their midline (Belopol'skii 1957). When breeding in crevices, Razorbills routinely leave their egg unattended, which would not be possible without the risk of the egg rolling out of place if they used sloping ledges (Tschanz 1990).

A murre egg is most vulnerable to rolling—especially on a sloping site—during the exchange of incubation duties, which takes place once or twice every 24 hr (e.g., Verspoor et al. 1987). At the end of each incubation bout, the incubating bird gently eases itself off its egg, leaving the egg at the site, even if the site is sloping. During the exchange, the egg is allowed to rest—albeit briefly—on the substrate with little or no assistance or support from either parent. This is not an issue for pairs breeding on horizontal sites (or for Razorbills), but it requires careful maneuvering and manipulation of the egg by murres breeding on sloping sites. These differences between the Razorbill and Common and Thick-billed murres suggest that the murres' pyriform egg shape may be an adaptation to breeding on sloping ledges.

METHODS

This study was conducted on Skomer Island in May–June 2017. Eggs were weighed (±0.01 g), and their maximum
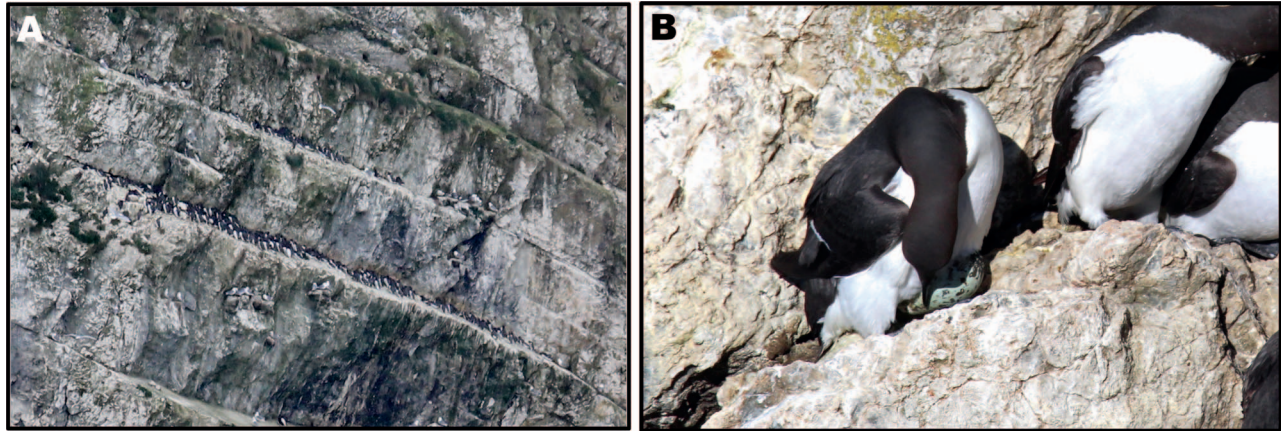
FIGURE 1. Common Murre breeding sites. (**A**) Part of the colony on a steep (30°) slope on Bempton Cliffs, Yorkshire, UK, showing that the majority of incubating birds are oriented with heads directed upslope. (**B**) An adult Common Murre on Skomer Island, Wales, UK, incubating its single egg, with the blunt end oriented away from the bird and upslope. Photo credit: T. R. Birkhead

length and breadth were measured (±0.1 mm) using vernier calipers. Each egg was scored as clean or dirty, with a dirty egg defined as one with enough dirt on it to obscure the smoothness of the outline.

We calculated the shape of each egg from photographs taken under standardized conditions. We have shown elsewhere (Biggins et al. 2018) that the shapes of birds' eggs, including the pyriform shape of Common Murre eggs, can be accurately quantified by 3 shape indices, described by Preston (1968, 1969), that we refer to as (1) pointedness, (2) elongation, and (3) polar asymmetry. Pointedness is the proportion of overall egg length that lies between the egg's widest point and its more pointed end. Elongation is the ratio of maximum length to maximum breadth. Polar asymmetry is determined by measuring the diameter of a circle at each end of the egg, such that each circle is the largest one that touches the respective pole of the egg but remains inside the outline of the eggshell. Polar asymmetry is the ratio of those diameters (large end: pointed end). Eggs with a relatively small pointed end have higher polar asymmetry values (Biggins et al. 2018).

Egg Stability Experiments
We tested the ability of recently laid eggs of different shapes to remain stable on 2 sloping surfaces, one moving and one static, in 2 experiments.

Experiment 1: Moving slope. One of us (J.E.T.) placed individual eggs on a horizontal platform covered with a 10 × 10 cm sheet of sandpaper on a motor-controlled slope such that the blunt end of the egg faced upslope (as it would during natural incubation). Slowly raising the slope of this surface at $4.5°\ s^{-1}$, we recorded the angle above the horizontal at which the egg began to roll away from its original position. Tests were conducted with 38 Common

Murre eggs ($n = 30$ clean, $n = 8$ dirty) and 10 Razorbill eggs.

We used a P120-grit aluminum oxide sandpaper substrate to simulate the friction that Common Murre eggs might experience on natural rocky breeding sites. P120 is the ISO/FEPA grit designation with an average particle diameter of 125 μm of abrading materials embedded in the sandpaper. We did not use smooth, uniform substrates because Common Murre breeding sites are rarely, if ever, like that. Instead, we used sandpaper (rather than rock) as a rough surface and humans (rather than Common Murres) as manipulators to standardize our experiments, recognizing that the actual surfaces that Common Murres breed on are more complex and irregular and that Common Murres would likely have considerably more difficulty stabilizing eggs than humans do. Thus, our experiments were not designed to perfectly mimic the natural situation, which would be extremely difficult. Our substrate (sandpaper) was rough but constant, and the egg manipulators (humans) were adept. Thus, the effects of slope on egg stability that we report are likely to be much stronger in nature, where substrates (rock) are more variable and the manipulators (Common Murres) much less likely to be able to stabilize the eggs.

Experiment 2: Static slope. Using information from experiment 1—which showed that almost all eggs were stable when the slope was <20° but that only a few were stable when the slope was increased to 40°—we created 3 slopes (20°, 30°, and 40°) using the same sandpaper substrate as above. J.E.T. attempted to position each egg stably on each slope within 10 s. Ten trials were conducted for each egg ($n = 59$ Common Murre, $n = 10$ Razorbill), and the number of successful attempts was recorded. Thirty-nine of the Common Murre eggs were clean and 20 were dirty. For the shape parameters of the eggs used in
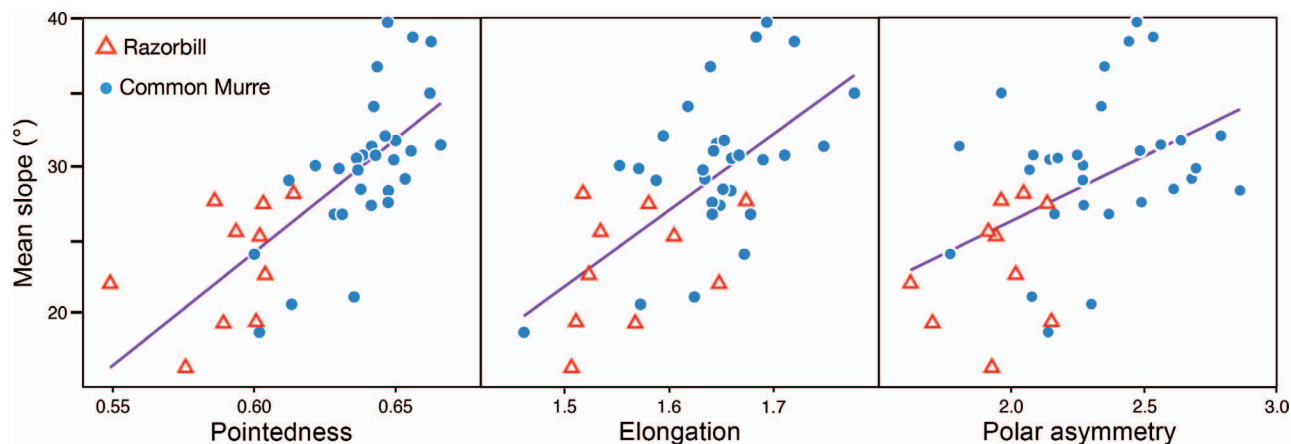
FIGURE 2. Stability of clean Razorbill ($n = 10$) and Common Murre ($n = 30$) eggs in relation to egg shape parameters, showing the mean slope at which each egg began to roll. Each point is the average of 5 measurements for each egg on a surface that slowly increased in slope. The regression is drawn through all the data because the species were not significantly different (see Appendix Table 6). These graphs do not control for the other variables in the best-fitting models (Table 1).

this experiment, see Appendix Figure 6 and Appendix Table 3.

Because the single observer in this experiment was not blind to the hypotheses being tested and thus was potentially biased, we repeated the experimental protocol using that single observer and 12 naive observers on a subset of the original eggs ($n = 2$ Razorbill, $n = 10$ Common Murre). There was no significant effect of potential bias on the success rates of stabilizing eggs of either species (generalized linear mixed models with binomial link, $P > 0.60$; see Appendix Table 4).

Slopes of Natural Breeding Sites
We measured the slope of the substrate on which 39 Common Murres and 23 Razorbills incubated on Skomer. To do this, we used a digital spirit level (Digi-Pas DWL-80E 0.1° resolution, 10 cm) attached to a 3D-printed Common Murre egg of average shape made of rigid nylon, such that when the egg had its maximum shell area (see Birkhead et al. 2017b) in contact with the substrate, the spirit level read zero.

Statistical Analyses
All analyses were performed using R 3.5.0 (R Core Team 2018). The full models we tested included egg mass and egg density (mass per unit volume) because both these variables might influence egg stability independent of egg shape. We reasoned that a heavier egg might make an egg more stable by increasing the friction against the substrate. We used density as a proxy for stage of incubation because Belopol'skii (1957) showed that the egg's center of gravity changes as incubation proceeds and that the mass of the egg of each species decreases by ~15% during the incubation period (Birkhead and Nettleship 1984).

We used Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham et al. 2011) to rank all models in each set and considered all models within 2 AIC_c of the best-fitting model to be statistically equivalent, given the data. All continuous variables were standardized (mean = 0, SD = 1) so that the magnitudes of the estimates (std beta) could be directly compared. We report the best-fitting models below (for a summary of the top and averaged models in each set, see the Appendix).

RESULTS

Experiment 1: Increasing Slope Angle
On average, clean Common Murre eggs began to roll (i.e. become unstable) on higher slopes (30.0°, 95% confidence interval [CI]: 28.8–31.1) than clean Razorbill eggs 23.4° (95% CI: 21.7–25.0), a difference of 6.6° (linear model, $t = 5.9$, $P < 0.001$). However, despite this difference, the *relationships* between the mean slope at which a clean egg began to roll and each of the egg shape parameters were all positive (Figure 2) and did not differ significantly between the 2 species (Appendix Table 5). To establish whether the slope at which eggs began to roll was dependent on the mass and shape of eggs, we controlled for these 2 factors; as expected, the slopes at which clean Razorbill eggs (marginal mean = 27.7°, 95% CI: 23.1–32.2, $n = 10$) and Common Murre eggs (28.8°, 95% CI: 27.3–30.4, $n = 30$) began to roll did not differ significantly (Appendix Table 5), which confirms that the difference in the instability of eggs between these 2 species is due to their different size and shape.

Because 8 of the Common Murre eggs were dirty, we analyzed the species separately so that we could assess the effect of dirtiness on stability in that species. In the best-
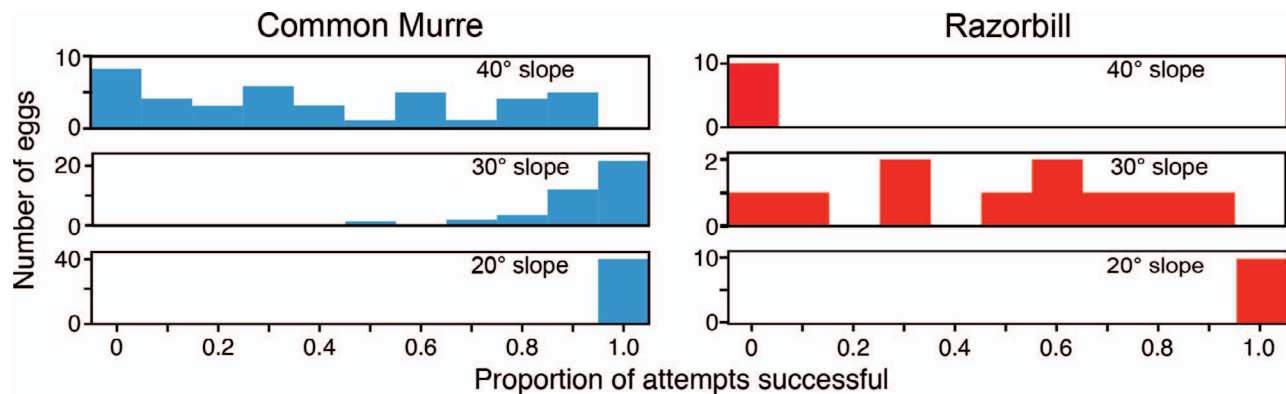
FIGURE 3. Stability of the clean eggs from 39 Common Murres and 10 Razorbills each tested on slopes of 20°, 30°, and 40° above the horizontal by a single observer. For each egg, the order of slopes on which it was tested was randomized, and each egg was tested 10 times on each slope to see whether it could be made stable within 10 s.

fitting models, pointedness was a significant predictor of the angle at which the egg began to roll in both Razorbills and Common Murres when the slope angle was gradually increased (Table 1). For Razorbills but not Common Murres, this model also included elongation, whereas for Common Murres the model also included egg density but that effect was not significant (Table 1). For both species, pointedness had the largest effect (std beta) on the angle that resulted in instability (Table 1). These best-fitting models predict 19–27% of the variation in the angle at which an egg began to roll (Table 1). Statistically equivalent models (top models, with $AIC_c < 2$) added egg density as a predictor for Razorbill eggs, and elongation, polar asymmetry, and dirtiness as predictors for Common Murre eggs (see Appendix Table 7). Thus, egg shape influenced the stability of eggs of both species as the slope increased, with pointedness having the largest effect.

Experiment 2: Static Slope at Different Angles

It was possible to balance all 49 clean eggs of both species stably in every trial on 20° slopes, but none of the Razorbill eggs could be stabilized on the 40° slope (Figure 3). Thus, we focus our analyses on the results from experiments on 30° and 40° slopes, where there was variation in the ability to stabilize.

At both 30° and 40° slopes, Common Murre eggs were more likely to be stabilized than Razorbill eggs (Figure 3). For both species, the best-fitting models to predict stability contained elongation as a positive predictor (Table 2 and Figure 4). For Common Murre eggs on 40° slopes and Razorbill eggs on 30° slopes, pointedness was also included in the best-fitting models and had a larger effect (std beta) than elongation on the success of stabilizing. Also, for Common Murres, dirty eggs were easier to stabilize than clean ones on both 30° and 40° slopes (Table 2 and Figure 4). On the 40° slope, the ability to stabilize Common Murre eggs also increased significantly with egg density

(Table 2 and Figure 4), presumably reflecting the increase in surface contact with the substrate as incubation advances. Statistically equivalent models (with $AIC_c < 2$) for Common Murres added polar asymmetry as predictors on both 30° and 40° slopes, and both pointedness and egg density on 30° slopes (see Appendix Table 8).

We conclude from these analyses that egg shape influenced the stability of Common Murre and Razorbill eggs on sloped sites, with pointedness and elongation having the largest effects. In general, variation in polar asymmetry had little effect on the stability of eggs of either species, but dirty and more dense Common Murre eggs were easier to stabilize than clean ones on the steepest slope.

Slopes of Natural Breeding Sites

The slopes of Common Murre and Razorbill breeding sites on Skomer were clearly different, Common Murre sites

TABLE 1. Generalized linear mixed models to predict the angle at which an egg ($n = 10$ Razorbill, $n = 38$ Common Murre) began to roll as the slope of a rough surface was increased (std beta = magnitude of difference, CI = confidence interval). Predictors tested in the full model: egg shape parameters—pointedness (PT), elongation (EL), and polar asymmetry (PA)—as well as egg density (DE) and dirtiness (DT, Common Murres only). Best-fitting models are reported here (for top and averaged models, see Appendix Table 7). Each egg was measured on each slope, so egg identity was entered as a random effect in every model. Coefficients of multiple determination (R^2) calculated by the method of Nakagawa et al. (2017), which estimate the variance explained by both fixed and random effects.

Species	Predictor	Std beta (95% CI)	F (P)	R^2
Razorbill	PT	3.10 (1.25 to 4.95)	9.17 (0.02)	0.27
	EL	3.01 (1.16 to 4.86)	8.67 (0.02)	
Common Murre	PT	3.00 (1.84 to 4.28)	23.7 (<0.001)	0.19
	DE	−0.80 (−1.79 to 0.19)	1.59 (0.11)	

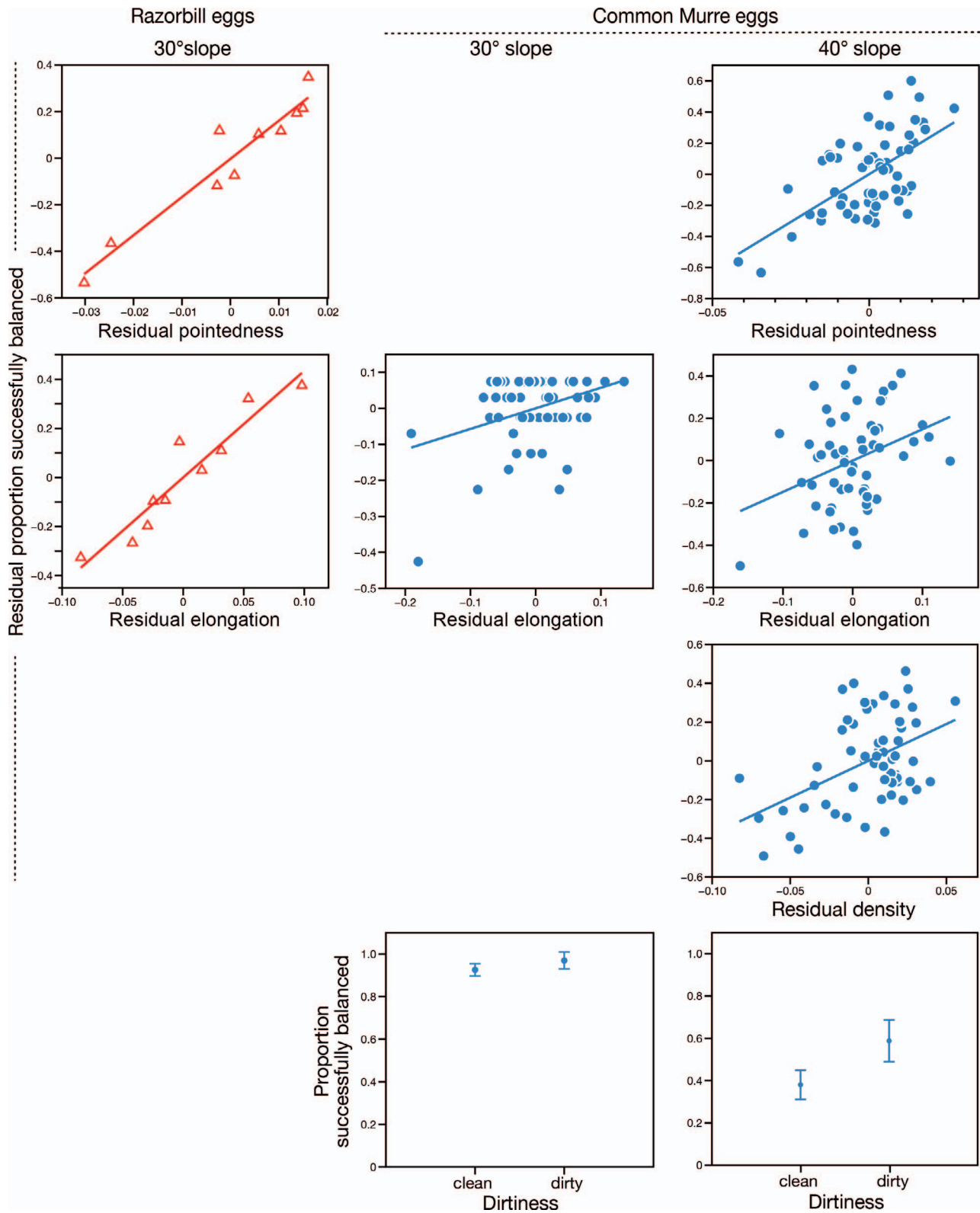**FIGURE 4.** Partial regression plots of fixed effects for egg shape indices that significantly predict the success of stabilizing 10 Razorbill and 59 Common Murre eggs on different slopes (see Table 2). Plots for Common Murres also show the effects of dirtiness plotted as marginal means ($\pm$ 95% confidence interval). These plots are from models whose predictors were not scaled, so that the magnitude of variation could be illustrated.
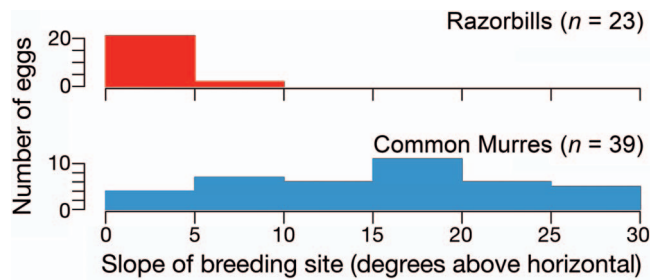
FIGURE 5. Slopes of ledges measured at breeding sites for 23 Razorbill and 39 Common Murre eggs on Skomer Island, Wales, UK.

being more sloping (median = 16.9°, range: 3.2–29.0°) than Razorbill sites (median = 1.3°, range: 0.3–6.9°; Mann-Whitney U-test, $W = 878.5$, $P < 0.001$), and the slopes of Common Murre sites were much more variable (Figure 5).

DISCUSSION

Our experiments demonstrate unequivocally that more pyriform (i.e. more pointed) eggs are more stable on sloping surfaces. We also show that, of our 3 egg shape indices, stability is primarily a consequence of pointedness and elongation. Given that pointedness also predicts the proportion of egg surface area in contact with the substrate (Birkhead et al. 2017b), the greater stability of pyriform eggs could be due in part to the friction resulting from the greater "contact area" that the narrow part of a pyriform egg has with the substrate.

It also seems likely that Common Murre eggs' center of gravity contributes to their stability, given that egg density positively affected stability on 40° slopes. Belopol'skii (1957) demonstrated that the angle at which a murre egg rests on the substrate changes through the course of incubation as the air cell (at the blunt pole) increases in size and the center of gravity shifts toward the pointed end of the egg. The result of this is that as incubation proceeds, the contact between the egg shell and the substrate increases. Belopols'kii (1957), who first proposed the rolling-in-an-arc explanation for the murre egg's pyriform shape, also noticed that the change in the center of gravity resulted in the egg rolling in a smaller arc and hence, he suggested, being less likely to fall from a ledge. However, we now know from Ingold's (1980) extensive experiments that neither the pyriform egg shape nor the shift in the center of gravity reduces the likelihood of the egg rolling off a ledge (see also Birkhead et al. 2017a, 2017b). Belopol'skii (1957) also interpreted the shift in the center of gravity as a murre-specific adaptation, although it is now known that the same change occurs in all birds' eggs during the course of incubation.

TABLE 2. Generalized linear models with binomial error to predict the number of trials out of 10 in which a Razorbill or Common Murre egg could be stabilized within 10 s by a single observer (std beta = magnitude of difference, CI = confidence interval). Best-fitting models are reported here (for top and averaged models, see Appendix Table 8); for Razorbills, there was only one top model. Each egg (n = 39 Common Murre, n = 10 Razorbill) was measured on each slope, so egg identity was entered as a random effect in every model. Predictors are the egg shape parameters pointedness (PT), elongation (EL), and polar asymmetry (PA), as well as egg density (DE). The coefficients of multiple determination (R^2) reported here estimate the proportion of variance explained by each model, following Nakagawa et al. (2017).

Slope, species	Predictor	Std beta (95% CI)	z (P)	R^2
30°, Razorbill	PT	1.64 (0.98–2.47)	4.40 (<0.001)	0.90
	EL	1.41 (0.76–2.19)	3.93 (<0.001)	
30°, Common Murre	DT	1.02 (0.18–2.03)	2.20 (0.03)	0.10
	EL	0.57 (0.25–0.89)	3.55 (<0.001)	
40°, Common Murre	DT	1.32 (0.83–1.82)	5.25 (<0.001)	0.70
	DE	0.75 (0.50–1.01)	5.78 (<0.001)	
	PT	1.17 (0.89–1.46)	8.10 (<0.001)	
	EL	0.52 (0.29–0.77)	4.23 (<0.001)	

Despite the apparent ubiquity and persistence of the spinning-like-a-top and rolling-in-an-arc "explanations" for the murre egg's pyriform shape, some previous authors have alluded to the stability conferred by this shape. For example, while not explicitly identifying the stability-on-a-slope hypothesis we present here, Pennant (1768:404) wrote: "What is also matter of great amazement, they [murres] fix their egg on the smooth rock, with so exact a balance, as to secure it from rolling off." Similarly, Macgillivray (1852:321) stated: "A very little inequality suffices to steady an egg [of a murre], and it is further prevented from rolling over by its pyriform shape."

Many Common Murres breed on approximately horizontal substrates, for obvious reasons, but as our data show, they are more likely than Razorbills to breed on sloping sites. In our study, the strongest stability effects were observed on slopes of 40°, yet our human subjects were undoubtedly much more dexterous and proficient using their hand to position an egg stably on a slope than a Common Murre would be using its beak, breast, legs, and wings. Our data indicate that few Common Murres breeding on Skomer use such steeply sloping sites, but our sampling was necessarily biased in this respect, precisely because our gaining access to such sites would probably result in the loss of eggs as the incubating bird left and, hence, the loss of our ability to identify them as breeding sites. On the other hand, visual inspection of sites without disturbing the birds (as in Gaston and Nettleship 1981, Birkhead and Nettleship 1987) does not indicate that breeding sites of 40° are common (Figure 1). Nonetheless,

we suggest that the effect we have detected provides a meaningful index of the stability of an egg on sloping surfaces and the ability of the parent to manipulate and orient the egg for incubation on a sloping surface. The ability to keep an egg stable, especially during changeovers, provides Common Murres a flexibility in their choice of breeding site that allows them to achieve the high breeding densities necessary to provide protection from egg and chick predators like gulls.

We have shown elsewhere (Birkhead et al. 2017a) that egg shape in murres (of both species) is variable (but consistent within females), but no more so than in many other bird species that lay more-elliptical eggs. Nonetheless, the variation in murre egg shape raises the question of whether the birds "know" their own egg shape and select their breeding site accordingly.

The eggs of Great Auks and Thick-billed Murres are almost identical in shape but are slightly less pyriform than those of Common Murres (T. R. Birkhead et al. personal observation). How are these differences related to breeding on sloping sites? Thick-billed Murres are less "constrained" to breed at densities as high as those of Common Murres because they do not breed on broad ledges surrounded by conspecifics. Instead, Thick-billed Murres tend to breed predominantly on narrow ledges with no more than 1 or 2 neighbors (Birkhead and Nettleship 1987). This implies that they may have more flexibility regarding the type of site they use and may therefore not need to produce such a stable (pyriform) egg. A similar argument may apply to Great Auks, which also bred at high density (Montevecchi and Kirk 1996), but whether they bred as densely as Common Murres is not known. However, Great Auks' larger size would have provided better protection from predatory gulls and corvids, and it may therefore not have been as critical that they bred as densely as Common Murres. This, in turn, may have allowed them greater flexibility in their choice of breeding site.

In conclusion, the Common Murre's pyriform egg is both more stable and easier to stabilize on sloping surfaces than the more elliptical egg of the Razorbill. Among the Common Murre eggs that we tested, more pyriform eggs were also more stable. How do we rank this "stability hypothesis" with our 2 other hypotheses (Birkhead et al. 2017b), (1) minimizing egg shell breakage and (2) minimizing contamination at the blunt end? While not dismissing those 2 hypotheses (in part because they still require rigorous testing), we consider that the stability hypothesis provides a compelling additional reason why pyriform eggs might be favored by selection.

Because of the long and convoluted history of murre egg-shape explanations (see Birkhead 2017), there is a risk that our results will be misquoted or misinterpreted. To be clear, we do not dispute that the risk of the Common Murre's egg being lost from the breeding site is likely an important selection pressure on egg shape. Two mechanisms have previously been proposed to minimize the risk of murre eggs being lost from the breeding site—spinning like-a-top and rolling-in-an-arc—but neither is supported by the evidence. The spinning-like-a-top idea was based on the false assumption that the egg would spin on its axis when knocked or when blown by wind. The rolling-in-an-arc mechanism has been extensively tested but found not to be correct; in rolling tests, Ingold (1980) showed that a pyriform egg is no less likely to roll off a ledge than a Razorbill's more elliptical egg. Our new hypothesis—that pyriform eggs are more stable and easier to stabilize on a sloping surface—is supported by our experimental evidence. Increased stability would reduce the chance that an egg might roll away from the incubation site and off the ledge during incubation exchanges or when the adults flush in panic from the ledge when disturbed by a predator. Thus, we argue that the pyriform shape protects the Common Murre's egg by reducing the chance that it will roll, and not because it influences the rolling trajectory. Ease of stabilizing would also make incubation transfers between the parents safer and more efficient and would help the parents retrieve a slightly displaced egg.

ACKNOWLEDGMENTS

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APPENDIX

Here, we provide further details on the models and analyses reported in the text. The Statistical Supplement referred to below is archived in the Dryad Data Repository at doi: 10.5061/dryad.gb90p1c (Birkhead et al. 2018).

Statistical Analyses

In all models, continuous predictors were standardized so that the magnitudes of the estimates (std beta) can be directly compared, and the effect of each predictor is positive unless otherwise noted. Averaged models are calculated as the conditional average, as recommended by Dormann et al. (2018) when evaluating the effects of specific predictors, rather than using the model for prediction. We tested the significance of predictors in the linear mixed models using the Satterthwaite approximation (see Luke 2017).

Because sample sizes were relatively small, we limited the number of potential predictors in statistical models reported here and in the text. In the Statistical Supplement, we show more complex, but overparameterized, models that reach the same conclusions, as well as details of models presented here and tests of assumptions. Those more complex models suggest that interactions between egg parameters might also influence egg stability. While our results reported in this article show clearly that egg shape, density, and dirtiness influence the stability of Common Murre and Razorbill eggs on sloping surfaces, further research with larger sample sizes are needed to

determine the effects of each egg shape parameter and their interactions.

Comparing Naive Observers to a Potentially Biased Observer

To evaluate the potential bias of the single observer who conducted experiment 2, we employed 12 observers (6 female and 6 male), naive to the purpose of the experiment, who were informed only that this was a test of their dexterity. Instead of using all eggs from experiment 2, we used a subset of those eggs consisting of 10 Common Murre eggs that spanned, as uniformly as possible, the range of egg shapes studied in that experiment, and 2 Razorbill eggs near the middle of the distribution of egg shapes from that species (Appendix Table 3 and Appendix Figure 6).

APPENDIX TABLE 3. Mean values of egg traits (with ranges in parentheses) for Razorbill and Common Murre eggs used in experiment 2 and in the procedure to determine whether the single observer in that experiment might have been biased. Egg mass and density both decreased slightly over the course of the experiment, so the descriptive statistics shown here are calculated from mean values per egg.

| Egg trait | Experiment 2, single potentially biased observer | | | Experiment 2, comparing observers | |
| | Razorbill | Common Murre | | Razorbill | Common Murre |
		Clean eggs	Dirty eggs		
Sample size	10	39	20	2	10
Mass (g)	81.9 (67.7–91.1)	106.2 (91.6–116.9)	103.5 (91.6–119.7)	76.7 (73.9–79.6)	103.6 (93.2–111.8)
Density (g mL^{-1})	1.04 (1.00–1.08)	1.08 (1.00–1.11)	1.06 (0.99–1.11)	1.03 (1.02–1.04)	1.07 (1.06–1.08)
Pointedness	0.59 (0.55–0.61)	0.64 (0.60–0.67)	0.64 (0.61–0.67)	0.58 (0.55–0.61)	0.64 (0.60–0.67)
Elongation	1.57 (1.51–1.67)	1.64 (1.46–1.78)	1.64 (1.45–1.73)	1.58 (1.52–1.65)	1.65 (1.46–1.78)
Polar asymmetry	1.94 (1.6–2.15)	2.35 (1.77–3.06)	2.35 (1.90–2.93)	1.83 (1.62–2.05)	2.19 (1.77–2.64)

APPENDIX TABLE 4. Generalized linear mixed models with binomial error to predict the success of balancing 2 Razorbill or 10 Common Murre eggs on different slopes (20°, 30°, and 40° above horizontal) by different kinds of participants in the study: one potentially biased observer vs. 12 students blind to the hypothesis being tested. Participant identities, egg identities, and slopes were entered as random factors in each model to control for multiple measurements.

Species	Predictor	z (P)
Razorbill	Participant	0.64 (0.532)
Common Murre	Participant	0.74 (0.46)

APPENDIX TABLE 5. Linear models to predict the mean slope angle at which a clean egg ($n = 30$ Common Murre, $n = 10$ Razorbill) began to roll as the slope of a rough sandpaper surface was increased. Means were calculated for 5 measurements of each egg (CI = confidence interval). Separate models compared the 2 species for the different egg parameters without controlling for other variables in the models. Interaction terms between species and egg shape parameters were not significant ($P > 0.20$) and were removed from each model shown here.

Model	Response	Predictor	Estimate (95% CI)	t (P)	R^2
1	Mean slope angle	Pointedness	154.5 (109.3–199.7)	6.88 (<0.001)	0.51
2	Mean slope angle	Elongation	43.4 (24.9–62.0)	4.71 (<0.001)	0.33
3	Mean slope angle	Polar asymmetry	7.5 (2.7–12.3)	3.16 (0.003)	0.18

APPENDIX TABLE 6. Best-fitting generalized linear mixed model to predict the angle at which a clean egg began to roll as the slope of a rough sandpaper surface was increased (CI = confidence interval). This model compares species (clean eggs only: $n = 30$ Common Murre, $n = 10$ Razorbill) while controlling for egg mass, pointedness, and elongation, with egg identity as a random effect to control for multiple measurements of each egg. For all top models, see Statistical Supplement.

Predictors	Estimate (95% CI)	F (P)
Species	1.16 (−4.09 to 6.40)	0.17 (0.6)
Egg mass (g)	−1.32 (−3.05 to 0.41)	2.08 (0.16)
Pointedness	3.45 (1.86 to 5.05)	16.80 (0.0002)
Elongation	1.56 (0.40 to 2.72)	6.46 (0.01)

APPENDIX TABLE 7. Generalized linear mixed models for each species to predict the angle at which an egg ($n = 38$ Common Murre, $n = 10$ Razorbill) began to roll as the slope of a rough sandpaper surface was increased. Predictors tested in the full models were egg shape parameters—pointedness (PT), elongation (EL), and polar asymmetry (PA)—as well as egg density (DE, as a proxy for stage of incubation) and dirtiness (DT, scored as either clean [$n = 30$] or dirty [$n = 8$], for Common Murres only). Egg identity was included as a random effect to control for multiple measurements of each egg. (A) All top models ($\Delta AIC_c < 2$). (B) Averaged models calculated from those top models (std beta = magnitude of difference, CI = confidence interval, RVI = relative variable importance).

(A)

Species	Predictors	ΔAIC_c	Weight
Razorbill	PT, EL	0	0.57
	DE, PT, EL	1.52	0.27
Common Murre	−DE, PT	0	0.17
	PT	0.47	0.14
	−DE, PT, EL	0.49	0.14
	EL, PT	0.82	0.11
	−DE, PT, −PA	1.77	0.07
	DT, PT	1.94	0.07
	DT, DE, PT	1.97	0.06

(B)

Species	Predictor	Std beta (95% CI)	z (P)	RVI
Razorbill	EL	2.99 (1.29 to 4.69)	3.44 (<0.001)	1.0
	PT	3.17 (1.44 to 4.89)	3.60 (<0.001)	1.0
	DE	0.80 (−0.87 to 1.39)	1.03 (0.30)	0.32
Common Murre	PT	2.90 (1.57 to 4.23)	4.27 (<0.001)	1.0
	DE	−0.79 (−1.78 to 0.19)	1.57 (0.11)	0.58
	EL	0.90 (−0.45 to 2.24)	1.31 (0.19)	0.33
	DT	0.91 (−2.12 to 3.93)	0.59 (0.56)	0.17
	PA	−0.39 (−1.67 to 0.89)	0.60 (0.55)	0.09

APPENDIX TABLE 8. Generalized linear mixed models with binomial error to predict the number of trials out of 10 in which an egg could be stabilized within 10 s by a single observer. Each egg ($n = 59$ Common Murre, $n = 10$ Razorbill) was measured on each slope. Predictors tested in the full model: egg shape parameters—pointedness (PT), elongation (EL), and polar asymmetry (PA)—as well as dirtiness (DT, scored as either clean or dirty), egg density (DE, for Common Murres only), and egg mass (MA). Egg identity was included as a random effect to control for multiple measurements of each egg. (A) All top models ($\Delta AIC_c < 2$) as determined using an information-theoretic approach to model evaluation. (B) Averaged models calculated from those top models (std beta = magnitude of difference, CI = confidence interval, RVI = relative variable importance).

(A)

Slope, species	Predictors	ΔAIC_c	Weight
30°, Razorbill	PT, EL	0	1
30°, Common Murre	DT, EL	0	0.10
	DT, −DE, EL	0.01	0.10
	DT, EL, PT	0.66	0.07
	−DE, EL	0.72	0.07
	DT, −DE, EL, PT	0.74	0.07
	−DE, EL, PT	0.81	0.06
	−DE, PT, −PA	1.27	0.05
	DT, −DE, PT, −PA	1.61	0.04
	−DE, EL, PT, −PA	1.82	0.04
40°, Common Murre	DT, DE, EL, PT	0	0.55
	DT, DE, EL, PT, −PA	1.29	0.29

(B)

Slope, species	Predictor	Std beta (95% CI)	z (P)	RVI
30°, Common Murre	EL	0.44 (0.04 to 0.85)	2.16 (0.03)	0.85
	DE	−0.40 (−0.88 to 0.07)	1.66 (0.10)	0.68
	DT	0.86 (−0.12 to 1.85)	1.71 (0.09)	0.65
	PT	0.39 (−0.10 to 0.88)	1.55 (0.12)	0.59
	PA	−0.29 (−0.71 to 0.12)	1.38 (0.17)	0.27
40°, Common Murre	DT	1.31 (0.81 to 1.81)	5.11 (<0.001)	1
	DE	0.76 (0.50 to 1.02)	5.68 (<0.001)	1
	EL	0.50 (0.25 to 0.76)	3.84 (0.001)	1
	PT	1.19 (0.89 to 1.50)	7.61 (<0.001)	1
	PA	−0.12 (−0.35 to 0.10)	1.07 (0.29)	0.34
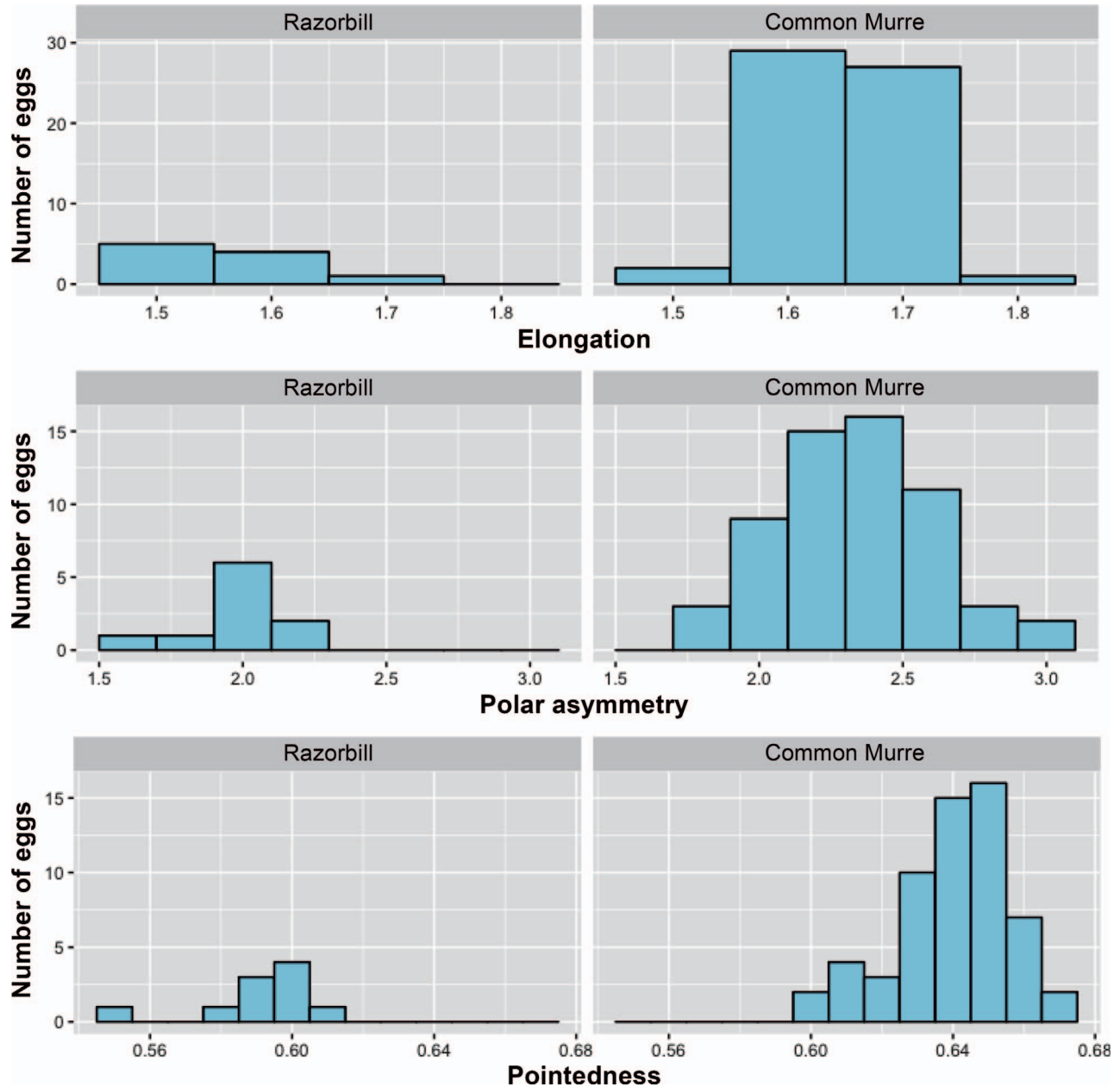
APPENDIX FIGURE 6. Frequency distribution of egg shape parameters for the 59 Common Murre ($n = 39$ clean, $n = 20$ dirty) and 10 clean Razorbill eggs used in experiment 2.