Abnormal eggs of the Common Guillemot *Uria aalge*: the role of stress

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Abstract

This study documents several types of abnormal eggs of the Common Guillemot *Uria aalge* collected from Bempton Cliffs, Yorkshire, UK, during the 1900s and currently housed in the Natural History Museum at Tring, Hertfordshire, UK. These eggs are abnormal in terms of size, shape, colour and surface topography. We suggest that the incidence of these abnormal eggs was relatively high because the manner in which they were collected — repeated visits to the breeding colony — caused considerable disturbance and stress that in turn disrupted the normal process of egg formation. We discuss the possibility of using abnormalities in avian eggs as a measurement of environmental stress.

Introduction

"There has always been considerable popular interest in abnormal eggs. In the past, the mystery of their origin evoked a folklore of fantastic explanations, but superstition has now been largely dispelled by the findings of science" (Romanoff & Romanoff 1949).

From at least the 1500s onwards, people descended the 60–120 m vertical chalk cliffs at Bempton on the Flamborough Headland, Yorkshire (54°8'N 0°9'W) to obtain eggs of the Common Guillemot *Uria aalge* (hereafter 'Guillemot') and other seabirds. Initially, these eggs were taken for human consumption, but from the mid-late 1800s and early 1900s they were also taken to be sold to egg collectors.

The eggs were taken by 'climmers' (climbers) who were labourers from farms adjacent to the cliffs (Vaughan 1998). Harvesting was systematic with each gang of climmers visiting their own stretch of cliff every three days (weather permitting) between May and June. Several tens of thousands of eggs were taken each year, until 1954 when egg collecting became illegal (Vaughan 1998; Birkhead 2016).

As a result of this vast harvest of Guillemot eggs, almost every natural history museum in the UK, and many elsewhere, contains one or more Guillemot eggs from Bempton. The Natural History Museum at Tring, Hertfordshire, holds around 6,000 Guillemot eggs, many of which are from the collection of F. G. Lupton (1881–1970), who obtained eggs from Bempton in the 1920s and 1930s. Lupton specialised in collecting (i) 'sets' of eggs from what were assumed to be the same females within and between breeding seasons, (ii) unusually coloured and patterned eggs (e.g. red eggs; Birkhead & Montgomerie 2018), and (iii) eggs of abnormal size, surface texture and shape (Birkhead 2016).

Abnormal eggs of the domestic fowl *Gallus gallus domesticus* have been recorded from the earliest times (Tiedemann 1814), and Romanoff & Romanoff (1949) classified these in terms of their internal and external appearance. Eggs with abnormal external appearance were of unusual (i) size (larger or smaller than average), (ii) shape (bent, elongate, twisted), (iii) surface texture, often with additional calcareous deposits, or wrinkled, and (iv) pigmentation, including 'banded eggs' with a band of pale pigmentation around the egg's short axis. The shape category also includes stalked eggs, truncated eggs and those with additional shell or tissue attachments, and two eggs bound together, usually by a narrow waist, that occasionally occur in domestic fowl (see illustrations in Romanoff & Romanoff 1949).

Among non-domesticated birds, the most frequently encountered type of abnormal egg is the runt or dwarf egg (Koenig 1980a, b; Mulvihill 1987; Crick 1995; see also Romanoff & Romanoff 1949), arbitrarily defined by Koenig (1980a) as having less than 75% of the volume of 'normal' eggs. Other types of abnormality are rare and rarely encountered in sufficient numbers for systematic study. Among the Guillemot eggs collected from Bempton Cliffs during the 1900s there are several abnormal eggs.

The aim of this study is to document the different types of abnormality in the eggs of the Guillemot and to speculate about their causes and possible value in monitoring stress in populations of other wild bird species.

Methods

We examined the Guillemot eggs in the Natural History Museum at Tring, a large proportion of which had been purchased from the climmers by F. G. Lupton during 1920–30 (Birkhead 2016). Lupton's collection also contains some abnormal eggs dated between 1887–1920, some of which he probably exchanged or purchased from other collectors. There is, for example, one egg with an unusual surface (Figures 2 and 3) dated 1903 with the name 'E. W. Wade', who was an active collector at Bempton at this time (Birkhead & Thompson 2019). We are unable to quantify the frequency of abnormal egg types, in part because it is not known how many normal eggs were taken each year. Instead, we simply present the different types of abnormalities accumulated by Lupton. As Hughes *et al*. (1986) point out for domestic fowl, categorising abnormal eggs can be difficult because the variation in different traits is continuous. However, in the Guillemot eggs in the present study, the abnormalities are discrete, primarily those of unusual size, shape and surface texture. Our focus here is on gross abnormalities as recognised by Lupton, and not eggs that have been altered or damaged while in a collection, such as those damaged by so-called 'Byne's disease' — a destructive reaction between acids in the drawers and/or cotton wool on which eggs are stored, and the calcium of the eggshell (Byne 1899).

For convenience here, we categorise abnormalities according to their size, pigment and shape, but our observations show that abnormal Guillemot eggs often exhibit several abnormalities simultaneously (for example, some (broken) Guillemot eggs of abnormal size and or shape at Tring appeared also to have extremely thin shells).

Results

(i) Under- and over-sized eggs

Guillemot eggs vary in size and shape, but no more so than the eggs of other species (Birkhead *et al*. 2017; T. R. Birkhead, J. E. Thompson & R. Montgomerie, unpubl.). Dwarf and over-sized (double-yolked) eggs are compared with normal Guillemot eggs in Figure 1. Quantifying the shape of these three categories of eggs using the methods described by Biggins *et al*. (2018), revealed that dwarf eggs were less elongated (length/breadth), less 'pointed' (or longitudinally asymmetric) and had lower polar asymmetry (size asymmetry of the large versus small end) than normal eggs, which in turn had lower values of all three shape parameters than double-yolked eggs (Figure 2). Thus, dwarf eggs appear more elliptical, and double-yolked eggs are more stretched out than normal eggs.

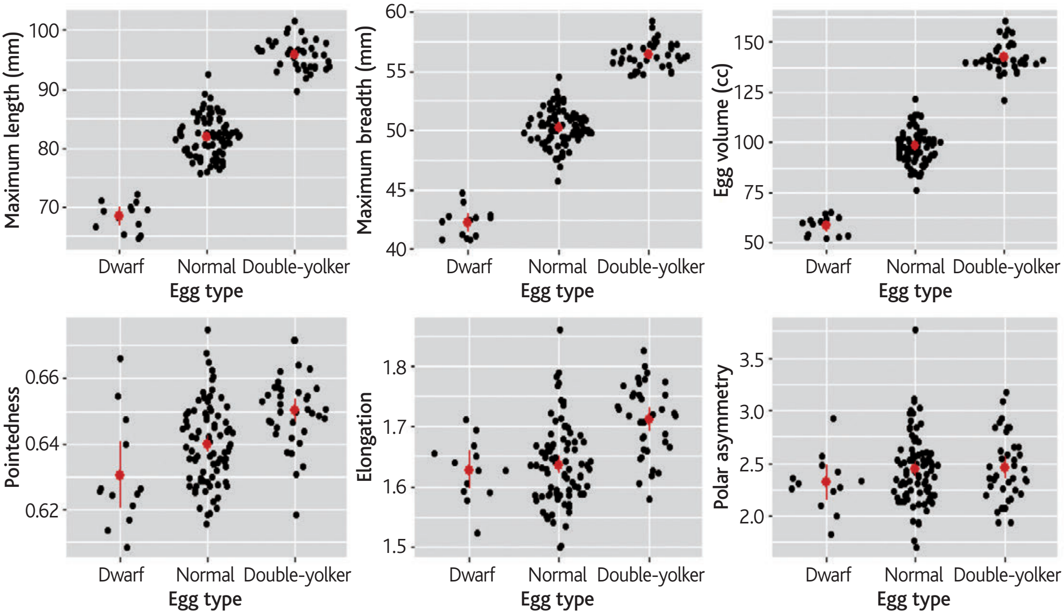

Figure 1. Shape and size of dwarf, normal and double-yolked Common Guillemot *Uria aalge* eggs. The red circle is the mean ± S.E. (see Supplementary Material for sample sizes statistical comparisons).

(ii) Eggs with unusual surface

Some eggs have additional calcium deposits, either as near-uniform 'pimples' over the egg's surface, or as one or more additional deposits that appear as bulges, usually at one end of the shell (Figure 3).

Figure 2. Dwarf, normal and double-yolked Common Guillemot *Uria aalge* eggs (left to right) in the Natural History Museum at Tring. Note the irregular surface of the dwarf egg.

Figure 3. Common Guillemot *Uria aalge* eggs with abnormal surfaces (extra calcium deposition). The lower four eggs are probably from the same female and collected in four separate years. All eggs from the Natural History Museum at Tring.

(iii) Banded eggs

One of the drawers in Lupton's collection contains 15 'banded eggs'. A note in that drawer, says "These eggs show natural breaks as laid, not cliff-rubbed". In other words, the single, pale band lying around the short axis of the egg that characterises this particular abnormality is 'natural' and not a consequence of abrasion from the substrate in the field. Indeed, since the band is apparent on any part of the egg (Figure 4a), and not just that region that would be in contact with the substrate (see for example Birkhead *et al*. 2018), it is very unlikely that bands could be the result of abrasion. The mean width of the pale band on 14 eggs (one was not measurable) was: 14.4 mm ± 6.0 (S.D.).

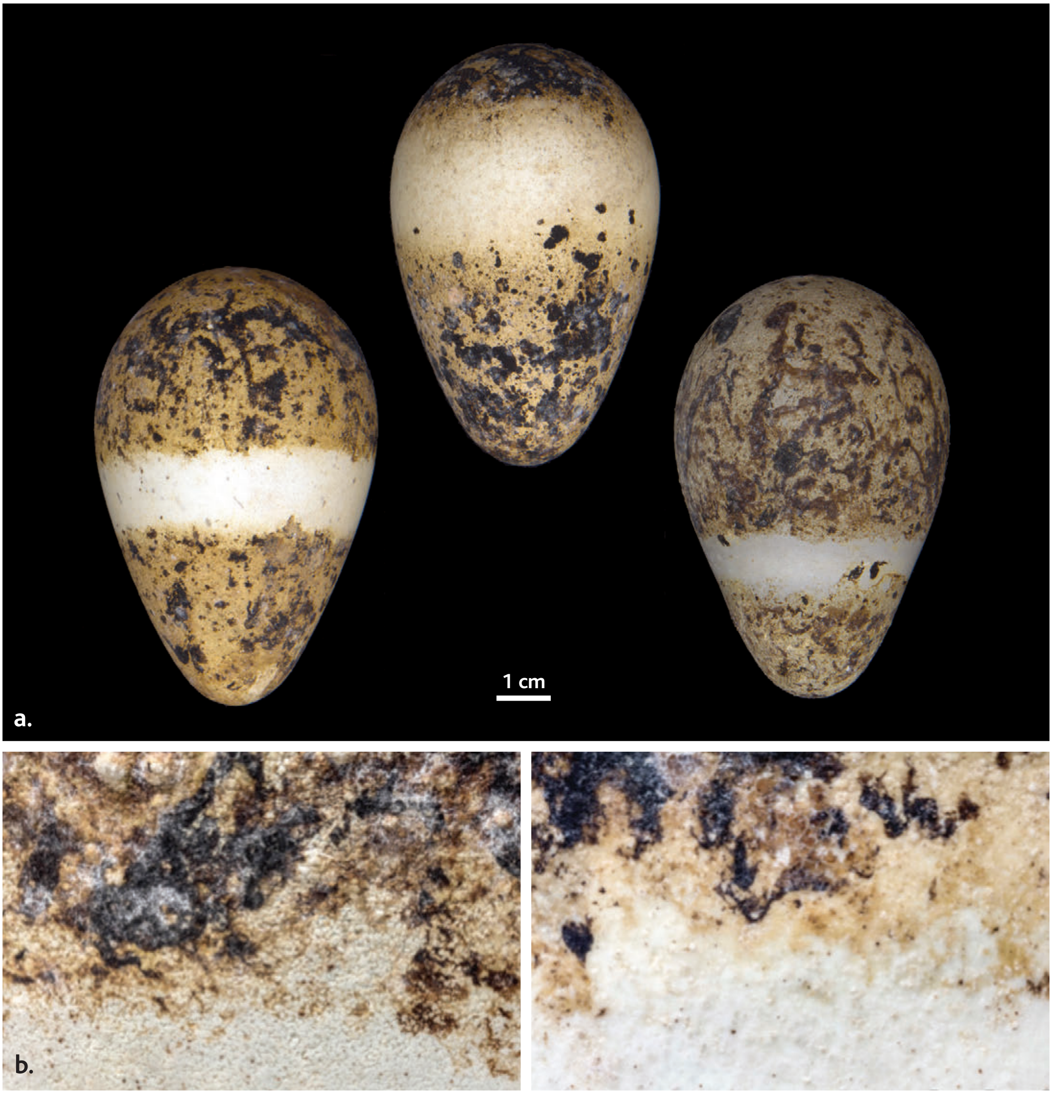

Figure 4. (a) Three examples of banded Common Guillemot *Uria aalge* eggs and **(b)** close ups of the banded and unbanded regions of two Common Guillemot eggs in the Natural History Museum at Tring.

Examination of several banded eggs using a dissecting microscope showed the banded region had a much smoother surface than adjacent regions (Figure 4b), suggesting that the banded region lacks the normal surface accessory material and pigment (see Board & Scott 1980). One of the most striking aspects of the banded eggs was that almost all of them had virtually the same cream ground colour (one egg had a blueish tinge) with brown or reddish maculation. Even allowing for the fact that the ground colour of Guillemot eggs in museum collections fade somewhat, this similarity in pigmentation suggests some link between ground colour and banding.

Figure 5. Examples of misshapen Common Guillemot *Uria aalge* eggs from Bempton, Yorkshire, UK, in the Natural History Museum at Tring.

(iv) Unusually-shaped eggs

Several eggs in Lupton's collection are of curiously distorted shapes: relatively long or relatively broad, compressed and curved (Figure 5). One egg of abnormal shape (Figure 6) also appears to have suffered a crack and a subsequent repair within the oviduct. Repaired breaks have also been recorded in chicken eggs (Romanoff & Romanoff 1949).

Discussion

As far as we are aware, Lupton left no written records of the eggs in his collection. However, the diary of a contemporary egg collector, G. Rickaby, transcribed and published by Whitaker (1997) refers to Lupton and to several types of abnormal Guillemot eggs taken by the climmers at Bempton. These include dwarf (runt) eggs, double-yolked eggs (Whitaker 1997) and those with an unusual surface (Whitaker 1997). Although there is no mention of banded eggs, the different Guillemot egg types he refers to include one with a 'salmon zone' (Whitaker 1997) and another with a 'grey spotted zone' (Whitaker 1997), where zone refers to a band, and these may be similar to the banded eggs in Figure 4. Rickaby makes no mention of unusually shaped eggs (Whitaker 1997). Nelson (1907) also mentioned dwarf and double-yolked Guillemot eggs at Bempton, but no other abnormal types.

Figure 6. An example of a misshapen Common Guillemot *Uria aalge* egg that has been broken and repaired within the oviduct, in the Natural History Museum at Tring.

Incidence of abnormal eggs

With the exception of dwarf eggs, which are the commonest form of abnormality among birds in general (Koenig 1982a; Crick 1995), the incidence of abnormal eggs is difficult to quantify. Crick (1995) estimated that among passerines, dwarf eggs occurred approximately once in every 600 eggs (0.17%), and for non-passerines, once in every 300 eggs (0.33%). Among wild birds, other kinds of abnormality seem to be much less common. One instance we know of involved two abnormally shaped eggs in the same nest of a Herring Gull *Larus argentatus* (R. Nager, pers. comm.).

It would have been feasible to quantify the incidence of abnormal Guillemot eggs when the climmers (or those collecting Guillemot eggs elsewhere) were active, but this was never done. Since the collecting of eggs — of Guillemots or any other species — became illegal in Britain following a change in the law in 1954, the possibility of estimating the incidence of abnormal eggs has been lost (but see below). Observations of Guillemots from a distance to record the timing of breeding and breeding success without disturbance (e.g. Birkhead & Nettleship 1980) provide limited opportunity to see abnormal eggs. Three independent observers that have spent decades doing this have never recorded an abnormal egg (M. P. Harris (Isle of May, Scotland), M. Heubeck (Shetland) pers. comm. and T. R. Birkhead (Skomer Island, Wales), pers. obs.).

The causes of abnormal eggs

Studies of the domestic fowl show convincingly that abnormal eggs are often the result of females experiencing some kind of stressful event during the egg formation process (Hughes *et al*. 1986; Mills *et al*. 1987). Koenig (1980a, b) similarly attributed the high frequency (4.3%) of dwarf eggs in the Acorn Woodpecker *Melanerpes formicivorus* to the stress resulting from the extreme competition between females as a result of their communal breeding system.

By typically breeding at high densities, Guillemots may experience levels of stress greater than many other birds, although if they do, they have clearly evolved to cope with it. The Guillemots at Bempton however, were subject to an additional source of stress from climmers visiting the breeding ledges every few days throughout the laying period, flushing the birds from their breeding sites each time, and remaining in the vicinity of the breeding ledges for several hours at a time. On their initial visit early in the season the climmers threw any eggs present into the sea, ensuring that on subsequent visits all eggs present were fresh, that is, had not been incubated for more than three days (Vaughan 1998). This was also common practice at other Guillemot colonies (Tuck 1961) but, as far as we know, at no other colony other than Bempton were oologists regularly on hand to purchase eggs for their collections. Unlike many passerine birds that lay in the early morning (Schifferli 1971; Weidmann 1964), Guillemots show no diurnal pattern in egg laying, with eggs being laid at any time (certainly during the daylight hours) (T.R. Birkhead, pers. obs.). This means that when the Bempton climmers descended the cliffs and disturbed the Guillemots there will have been some females at all stages of egg formation.

There is circumstantial evidence consistent with this disturbance hypothesis. Although the harvesting of Guillemot eggs at Bempton ceased in the 1950s, harvesting has continued at some other locations elsewhere in the North Atlantic, including the Faroes and Iceland (Anon. 2005). We contacted two experienced ornithologists (Bergur Olsen and Aevar Petersen) at these two locations and asked them to speak directly with men involved with the egg harvest, to ask them about abnormal eggs. We provided the two ornithologists with photographs of the different types of abnormal eggs (using the images in this paper) as a reference, but we did not inform them of our hypothesis. We simply asked whether the egg harvesters had ever encountered abnormal Guillemot eggs.

B. Olsen contacted two men, Óla Jákup Hentze, born in 1933 and Meinhard Hentze, born in 1941, who participated in harvesting tens of thousands of Guillemot eggs on the island of Skúvoy, Faroes, in the past. They said "they do not remember having seen or heard about misshaped eggs, but they have heard about dwarf eggs, but only one for each 1,000 eggs or more".

A. Petersen contacted two men who have each collected tens of thousands Guillemot eggs over several decades from two different locations in Iceland. The first, Halldór Halldórsson, who collected eggs on Langanes peninsula in northeast Iceland, reported finding abnormal eggs of different kinds every year: "Runt [dwarf] eggs are not many but more eggs of greatly variable shape… eggs with bent narrower end are found. Sometimes eggs that have a flat broader end and wrinkled shells around the broad end". The second Icelandic collector Sveinn Eyjólfur Tryggvason, a harvester at Látrabjarg in northwest Iceland for 20–30 years, reported that abnormal eggs are found "every year and of various kinds: runt (small, in size similar to Arctic Tern *Sterna paradisaea* or Redshank *Tringa tetanus* eggs), large with two yolks (larger than normal eggs), elongated eggs, [and] sometimes eggs with hardly any shell, look like the membrane only (not collected, [because they] break)."

An important difference between the Faroes and Iceland is in the style of harvesting. On Skúvoy, Faroes, the harvest was undertaken on just a single visit. In Iceland the colonies are visited multiple times, weather permitting, throughout the egg-laying period, much as at Bempton in the early 1900s. The Guillemots in Iceland, therefore, experienced more disturbance than those on the Faroes, which is consistent with the idea that disturbance is associated with a higher incidence of abnormal eggs. Previously however, on the island of Stóra Dímun in the Faroes, eggs were "collected three times in a row [presumably first eggs, first and second replacement eggs, as at Bempton], but because there was blood on the [surface of the] eggs from the third collection they stopped using this method a long time ago. This was called 'blóðræning' or 'blood egging' (B. Olsen, pers. comm., Nørrevang 1977). This information comes from an interview conducted by Arne Nørrevang in 1977 with an egg harvester Jógvan (Joen) Joensen, born in 1896, who worked on Stóra Dímun between 1915 and 1918. Nørrevang was told by Joensen that 'a long time ago' (i.e. before 1915–18) when they harvested three times, the eggs from the third collection were both bloody and very small (B. Olsen, pers. comm.)[1]. At other colonies first replacement Guillemot eggs are about 5% less in volume than first laid eggs (T. R. Birkhead and J. E. Thompson, pers. obs.), but we have been unable to obtain data on the volume of second replacement eggs, and whether the 'blood eggs' on the Faroes would constitute dwarf eggs using Koenig's definition, i.e. having less than 75% of the volume of 'normal' eggs, is unclear. However, the presence of blood on the surface of these Faroese eggs suggests that the birds were stressed by either being disturbed and/or by laying additional eggs. We can find no reference to anything equivalent to 'blood eggs' at Bempton (Nelson 1907; Wade 1907).

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[1] This is an audio recording in the archive of the Faroese University - Fróðskaparsetur Føroya, Føroyamálsdeildin (the Faroese linguistic department) tape number 854, recorded by Arne Nørrevang in 1977.

Mechanics of abnormal egg production

The timing of the formation of different components of a normal egg provides a clue as to when the different abnormalities in Guillemot eggs might arise. The eggs of most birds are formed over a period of 24 hours in the oviduct (Romanoff & Romanoff 1949). Examination of the germinal disc of seven Guillemot eggs within 24 hours of laying is also consistent with an egg formation period (in the oviduct) of approximately 24 hours (N. Hemmings & T. R. Birkhead unpubl. observation; see also Birkhead *et al*. 2010).

At ovulation, the ovum (i.e. the yolk) is released from the ovary into the infundibulum where fertilisation occurs, after which it travels into the magnum of the oviduct where the albumen is added. Then, some six hours after ovulation, the albumen-encased ovum enters the isthmus of the oviduct, where the shell membranes are deposited and the egg's shape determined. In the isthmus, water is also added to the albumen. The still shell-less egg then enters the uterus or shell gland where it remains for around 16 hours as the calcareous shell is deposited onto the outer shell membrane. It is during the last few hours in the uterus that the shell accessory material and pigment are applied on to the shell (see Board & Scott 1980). Approximately 24 hours after the ovum's release from the ovary the completed egg is laid (for more details, see Nys & Guyot 2011).

The precise way that disturbance or stress disrupts the normal process of egg formation is unknown. Here we discuss some possible mechanisms.

Disturbance prior to, or at, ovulation may result in the simultaneous formation and release of two ova, resulting in a double-yolked egg. Conversely, disturbance may result in the failure to release an ovum at all, resulting in a yolkless dwarf egg (see Crick 1995).

When female domestic fowl experience stressors just before, or at the time of, the initial phase of calcium deposition (i.e. shell formation), while the still-forming egg is in the isthmus or uterus, this can result in eggs with abnormal surfaces and misshaped eggs (Hughes *et al*. 1986; Reynard & Savory 1999). Hughes *et al*. (1986) report that in domestic fowl, stress can elicit endocrine changes that result in uterine contractions and, in some cases, retention of the egg in the oviduct.

Hughes *et al*. (1986) also suggest that banded eggs in domestic fowl are the result of delayed oviposition, creating a superficial layer of amorphous calcium deposited on top of the shell that may reduce hatching success. However, the banded Guillemot eggs that we examined appear to lack pigment in the band rather than having an extra layer of calcium. Mills *et al*. (1991) and Nys *et al*. (1991) reported that in domestic fowl, stress can result in 'egg whitening' as a result of the premature termination of shell pigmentation. It is not known exactly how the colour or shell accessory material is applied to birds' eggs inside the shell gland (Birkhead 2016), but banding may provide some insight into this process. The pale, pigment-poor band in Guillemot eggs suggests that in normal egg formation a

Common Guillemot with egg.
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wave of ground colour application or shell accessory material deposition passes over the length of the egg, but that during a disturbance this is disrupted or temporarily halted. Another possibility is that after the surface accessory material has been deposited and is still wet, it is rubbed off in one region around the egg's girth, possibly as a result of the egg being shunted within the uterus.

We also considered the possibility that banded eggs were fabricated by the collectors, but examining the eggshells' surface using a dissecting microscope, we saw no sign of abrasion in the pale band indicating that fabrication is unlikely.

Disturbance prior to pigment deposition might also influence the egg's orientation or rotation with the oviduct. In some birds at least, the egg rotates through 180 degrees along its long axis within the shell gland one hour or so before laying (Bradfield 1951). In Guillemots, and indeed the majority of birds, the heaviest maculation is almost always deposited towards the blunt end of the egg. Very occasionally in Guillemots, the maculation is concentrated towards the pointed end of the egg, a pattern the Bempton climmers referred to as a 'nose cap' (Whitaker 1997). In a study of egg colour in a small number of captive Guillemots, Hauber *et al*. (2019) illustrate one such 'nose cap' egg among three other normal eggs laid (each a year apart) by the same captive female (bird M23) at the Oregon Coast Aquarium. Guillemots are rarely kept and even more rarely breed successfully in captivity, possibly because they often appear nervous and find captivity stressful (T. R. Birkhead pers. obs.). Given that in this same, small captive population another Guillemot was photographed in the process of laying with the large end of the egg emerging first (aquarium.org/tag/common-murre) — instead of the pointed end as is consistently the case among wild Guillemots (T. R. Birkhead pers. obs.) — this strongly suggests that some of these captive birds experienced a degree of stress. This may therefore account for the reversal in the deposition of the maculation on one of M23's eggs. This is confirmed by some observations by Taschenberg (1894) who dissected a number of Rooks *Corvus frugilegis* with an egg in the shell gland. In most cases the egg was orientated 'normally', with its pointed end towards the cloaca, and the densest deposition of maculation on the blunt end of the egg. However, Taschenberg recorded at least one case in this species where the egg was orientated the other way, and where most maculation had been deposited at the pointed end of the egg. Figure 7 illustrates the situation as it probably occurs in the Guillemot.

Disturbance close to the time of egg laying may cause some Guillemots to leave the breeding ledge and deposit their (normally sized and shaped) egg at sea. For ardent oologists, Guillemot eggs dredged from the seabed off the Bempton cliffs were at one time especially favoured by collectors and it was sometimes (bizarrely) assumed that laying at sea was normal (Nelson 1907; Wade 1907; see also Birkhead & Thompson 2019). Most birds are able to retain an egg in the oviduct only for a few hours beyond the normal time of laying, and do so in response to stress (Reynard & Savory 1999). Guillemot eggs are sometimes found by scuba divers on the sea floor beneath breeding cliffs (J. R. Hart, pers. comm.; Motyer &

Narirn 2006), but these are very likely to be eggs that have rolled off, or been washed off the ledges by high seas, rather than laid at sea by birds disturbed at the point of laying, as we suggest for birds at Bempton.

At undisturbed colonies, female Guillemots spend relatively little time at the breeding colony in the four days before they lay (Birkhead *et al*. 1985; Hatchwell & Pellatt 1990; Wanless & Harris 1986). However, the resolution of the data in those studies is insufficient to know what proportion of females are at the colony and for how long during the 24 hours before the egg is laid, while the egg is forming in the oviduct. Presumably a number of female Guillemots were at the Bempton colony during the period of egg formation when they were disturbed by the climmers. Female Guillemots may minimise the amount of time at the colony during the 24 hours before laying to reduce the risk of experiencing any disturbance while the egg is being formed.

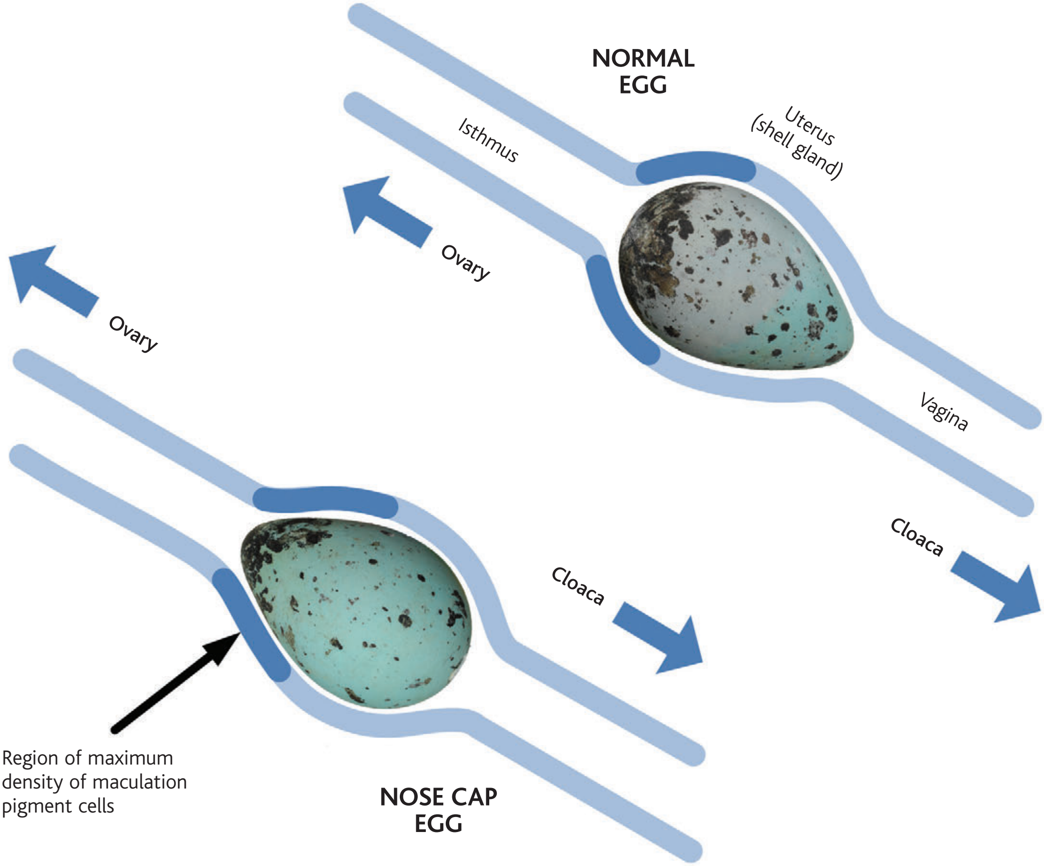

Figure 7. Comparison of the orientation of a normal (upper) and a 'nose cap' (lower) Common Guillemot *Uria aalge* egg in the oviduct. The nose-cap egg is orientated in a reversed position within the shell gland. The zone of maximum maculation cells is presumed, based on the deposition of maculation on the egg (see text). These eggs were laid by the same female (M23) at the Oregon Coast Aquarium in 2013 (normal) and 2014 (nose cap); M23 laid a normal egg in both 2015 and 2016.

Not all abnormal Guillemot eggs collected at Bempton are necessarily the result of stress and disturbance (see also Hughes *et al*. 1986). Lupton's collection includes four pimply eggs dated 1899, 1900, 1902 and 1903 (Figure 3), that — judging from their similar appearance and knowing that climmers often took distinctive eggs from the same site year after year — were probably laid by the same female. This suggests that this female was predisposed to lay such eggs regardless of disturbance. There are similar records of individual females of other species producing dwarf eggs year after year (see Crick 1995).

Fitness consequences of abnormal eggs

The abnormal Guillemot eggs taken at Bempton obviously never hatched, but Narushin & Romanov (2002) have shown that in poultry, abnormal eggs of the types discussed here, have reduced hatching success and that chicks that hatch have reduced post-hatching survival. As these authors state, the avian egg is a 'highly integrated biological system' such that the disruption of any one component can result in hatching failure. Dwarf eggs fail to hatch mainly because most have no yolk and we have found no records of dwarf eggs hatching (see Crick 1995). Double-yolked eggs usually fail to produce twins that survive to or beyond hatching, because double-yolked eggs contain insufficient albumen (Salamon & Kent 2013). Eggs with shells that are thicker or thinner than normal, or with additional calcium deposits may fail to hatch because: (i) the shell breaks or is crushed during incubation, as with pesticide-induced egg-shell thinning (Newton 1979), or (ii) shell porosity and gas exchange is disrupted (Narushin & Romav 2002). Eggs of abnormal shape have reduced hatching success because deviations from the normal shape disrupts the axial orientation of the embryo (Narushin & Romanov 2002). These authors also report reduced 'fertility' of abnormal eggs, but this statement must be considered carefully. Eggs that appear 'infertile' are usually the result of very early embryo mortality rather than an absence of sperm (Birkhead *et al*. 2008; Hemmings & Evans 2020). It is possible that stress (as at Bempton) reduces the probability of fertilisation, but because pairs copulate frequently over two weeks or so, and females store sperm, it seems more likely that it causes early embryo mortality.

In addition to reduced hatching success and reduced post-hatching survival of chicks from abnormal eggs (Narushin & Romanov 2002), the survival of females producing an abnormal egg may also be reduced. It is well known for example, that relatively large human neonates increase the risk to mothers, and it is plausible that the production of double-yolked Guillemot eggs (which are 12% wider than normal eggs) stretch the avian oviduct (specifically the isthmus, uterus and vagina) in a detrimental way.

Conclusions

Although it is well known that certain environmental factors, such as pesticides and acid rain can directly or indirectly, disrupt egg formation in birds (Newton 1979; Green 1998), it has not been generally recognised — despite the extensive evidence from poultry research (above) — that different types of stress can have a similarly disruptive effect on the size, shape, surface texture and hatching success of avian eggs. While the types of stress and the different types of abnormalities discussed here in Guillemot eggs are quite extreme, by recording the incidence of eggshell anomalies, either in museum collections or in field studies, researchers have the potential to detect other forms of environmental stress in birds. Writing in the 1600s, Sir Francis Bacon recommended that we record all the monsters and prodigious products of nature, of every novelty, rarity or abnormality, not for their own sake, but for what they reveal about the normal laws of nature (Bacon 1620).

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Supplementary Table 1. Mean shape and size (mm) measurements of dwarf, normal and double-yolked Common Guillemot *Uria aalge* from Bempton Cliffs, Yorkshire, UK held in the Natural History Museum at Tring, Hertfordshire, UK.

	Mean (95% CI)		
	Dwarf (N = 13)	**Normal (N = 83)**	**Double-yolked (N = 37)**
Pointedness*	0.631 (0.620–0.641)	0.640 (0.637–0.643)	0.650 (0.647–0.654)
Elongation†	1.628 (1.597–1.659)	1.637 (1.622–1.651)	1.711(1.691–1.731)
Polar Asymmetry§	2.318 (2.156–2.481)	2.444 (2.372–2.516)	2.461 (2.356–2.565)
Maximum Length	68.408 (66.912–69.903)	81.995 (81.263–82.728)	95.857 (94.995–96.718)
Maximum Breadth	42.262 (41.512–43.011)	50.277 (49.940–50.615)	56.319 (55.946–56.692)
Egg Volume	58.496 (55.619–61.373)	97.946 (96.129–99.764)	142.398 (139.907–144.889)

* **Pointedness** is the length from the point where the egg is widest to the more distant end divided by the overall length. † **Elongation**: ratio of the length to the width at the widest point. § **Polar Asymmetry** is the ratio of the diameter of the largest circle that can 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 (Biggins *et al*. 2018). Mean pointedness (ANOVA: $F_{2,130} = 14.82$, $P < 0.0001$) and elongation (ANOVA: $F_{2,130} = 18.87$, $P < 0.0001$) significantly differ between the three egg types. Whilst post-hoc Tukey comparisons showed each egg type to significantly differ between one another for mean pointedness ($P < 0.05$), although Tukey comparisons between the double-yolked egg type and each of the other two egg types showed significant differences in mean elongation ($P < 0.05$), differences between the mean elongation of dwarf and normal egg types did not ($P = 0.896$). Mean polar asymmetry did not significantly differ between the three egg types (ANOVA: $F_{2,130} = 1.012$, $P = 0.366$) and post-hoc Tukey comparisons showed no significant differences in any separate pair comparisons of the three egg types ($P > 0.05$). Mean maximum length (ANOVA: $F_{2,130} = 455.1$, $P < 0.0001$), maximum breadth (ANOVA: $F_{2,130} = 520.6$, $P < 0.0001$) and egg volume (ANOVA: $F_{2,130} = 683.4$, $P < 0.0001$) all significantly differed between the three egg types and all post-hoc Tukey comparisons also showed significant differences between separate paired comparisons ($P < 0.0001$).