Two-egg clutches in the Fulmar

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Abstract Members of the seabird family Procellariidae (albatrosses, petrels and shearwaters) typically produce a single-egg clutch. Two-egg clutches have been recorded occasionally in some of those species, but it is not known whether they were laid by a single female. In this study we examined eight two-egg clutches of the Fulmar *Fulmarus glacialis* in the Faroes, to assess whether those eggs may have been laid by the same female. Using data from eggs laid in different years by the same 100 females on Eynhallow, Orkney, we first confirmed that the egg measurements were repeatable from year to year. Second, using egg length, breadth, volume and three indices of shape, we compared the eggs from the eight two-egg clutches with (i) 100 pairs of eggs sampled at random from 111 single-egg clutches from the Faroes, and (ii) eggs laid in different years by 100 females on Eynhallow. Our analyses focused on differences between eggs in each pair. Differences in the eggs of two-egg clutches were more similar to those of pairs of eggs taken at random than to pairs of eggs from the same female in different years. We infer from this that the eggs in two-egg clutches were laid by different females.

All Procellariiformes (albatrosses, petrels, shearwaters) typically produce a single-egg clutch (Warham 1990), but occasionally two eggs occur at the same nest site. Although it is often assumed that these are laid by two different females (Warham 1990; Ryan *et al.* 2007), it has occasionally been asserted that the two eggs were laid by the same female (reviewed in Tickell & Pinder 1966).

The incidence of two-egg clutches in populations of the Fulmar *Fulmarus glacialis* varies from zero to around 15%. Lockley (1936) reported that in the Vestmannaeyjar (Westmann Islands), Iceland, 10–15% of Fulmar nest sites contained two eggs, although for the same locality Einarsson (cited in Fisher 1952) reported a much lower incidence, of 1.6% (67/4,150 nest sites). Similarly, Jensen (1989) reported that 0.82% (25/3,047) of Fulmar nest sites on the Faroes contained two eggs. He suggested that these were laid by the same female because: (i) the eggs were similar in shape (assessed visually); and (ii) at one nest site, two eggs had been found in four consecutive years. On the other hand, Fisher (1952), commenting on two-egg clutches in this species, wrote:

> In 1947, on a holm in West Shetland, the oologist *Peregrine* [Frank Watmough – Jim Whitaker, pers. comm.] found one of the rare two-egg clutches of the Fulmar. 'One egg was very long' he writes, 'and the other much more round' and… On landing at the same place in 1948 'lo and behold, the Fulmar was in the self-same spot and again with two eggs, one long and the other round' (Birdland 1948).

The most obvious ways to establish whether or not two-egg clutches in the

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55. Participants in the traditional Faroes harvest of Fulmar *Fulmarus glacialis* eggs for human consumption, in May 2010.

Fulmar are laid by the same or two different females would be: (i) to witness the eggs being laid by individually recognisable females (which would be very difficult, but see Tickell & Pinder 1966); or (ii) to use molecular techniques to ascertain the maternity of both eggs by obtaining DNA from the shell membrane, from the shell itself or from the developing chicks (Grealy *et al.* 2019). It is easier to establish that two eggs or offspring have different mothers than it is to demonstrate that they have the same mother, but molecular analyses of either type require: (i) DNA from both the focal eggs and the putative mother as well as the general Fulmar population; (ii) considerable technical skill; (iii) sufficient financial resources to undertake the analyses; and (iv) a sufficient number of molecular markers (Waits *et al.* 2001; Jones & Ardren 2003).

An additional method that may allow us to distinguish between the two hypotheses is to compare the dimensions and shape of eggs in two-egg clutches on the well-verified assumption that individual females typically lay eggs more similar in shape, volume and linear dimensions than two eggs laid by different females (Romanoff & Romanoff 1949; Petersen 1992 and references therein; Mónus & Barta 2005; Birkhead *et al.* 2017). Thus, we predicted that, if the eggs in two-egg clutches were laid by the same female, they would be less different in all or most of the six size and shape traits than pairs of eggs taken at random from the population.

Methods

The traditional Faroes harvest of Fulmar eggs for human consumption is still undertaken (Jensen 2012) and this local access can provide important insights into the breeding biology of Fulmars. Although two-egg clutches in Fulmars on the Faroes have been known to occur historically, and at low frequency, in 2019 local egg-collectors noted that among 34 clutches found in Byrgisgjógv, Sandavágur, there were five or six two-egg clutches, while on Lonin, Sandoy, collectors reported approximately 15 two-egg clutches among 160 eggs.

In 1988 and 1989, JKJ enlisted the assistance of close friends involved in the traditional Faroes Fulmar egg harvest to collect any two-egg Fulmar clutches they encountered. A total of eight two-egg clutches was collected, with each pair of eggs placed immediately in a sealed bag and kept separate from the other Fulmar eggs. These eggs

from the two-egg clutches were later labelled in pencil and then emptied, washed and dried and retained by JKJ. In 2019, we measured (to the nearest 0.1 mm) the maximum length and breadth of these eggs using Vernier calipers and photographed them individually under standardised conditions (see Biggins *et al.* 2018). From these photographs (fig. 1), we used the method described in Biggins *et al.* (2018) to quantify the volume and three shape parameters – elongation, pointedness (sometimes called asymmetry) and polar asymmetry – of each egg. Elongation is length/width; pointedness is the degree to which the maximum width of the egg deviates from the midpoint of its length; and polar asymmetry is a measure of the relative size of the two ends of the egg.

To assess whether the eggs from the two-egg Fulmar clutches were more similar to each other than was the case for pairs of eggs taken from other females, we made two comparisons. First, we compared those eggs to pairs of randomly chosen eggs from the same Faroes population. To do this we photographed and quantified (as described above) 111 Fulmar eggs collected haphazardly during 17th–21st May 2019. To simulate two-egg clutches from this sample, we randomly chose two eggs (without replacement) and repeated this 100 times with replacement. If the two eggs in real two-egg clutches were laid by the same female, we would expect them to be more similar, on average, than two eggs that were each selected from a different, randomly chosen female.

Second, we compared the eggs in real clutches to two eggs laid by the same female in different years. To do this, we analysed the measurements of 200 eggs laid by 100 individually marked females from the long-term study of Fulmars on Eynhallow, Orkney (Michel *et al.* 2003). These data comprised linear measurements of eggs laid by the same marked females in different, though not always consecutive years, during the periods 1975–84 and 2002–05. All but two of the birds laid the two eggs within one of those periods (mean 3 years), but the eggs from two females were collected 18 and 23 years apart. When their second egg was collected, these 100 females were 1–35 years (mean 10.8 years) after their age of first breeding. We used the egg length and breadth to calculate both volume (using the formula in Michel & Thompson 2003) and elongation. We did not have standardised photographs of Eynhallow Fulmar eggs so we were not able to quantify pointedness or polar asymmetry. If the two eggs in two-egg clutches were laid by the same female, we would expect them to be as similar to each other, on average, as two eggs laid by the same female in different years.

We created 100 simulated clutches from the Faroes to match the sample of paired Eynhallow eggs so that the statistical comparisons between the real two-egg clutches and the other two samples would have similar power. We compared the median of the real two-egg clutches to the medians of the other two samples using separate nonparametric Wilcoxon tests to avoid any issues with outliers and non-normal distributions (see fig. 2).

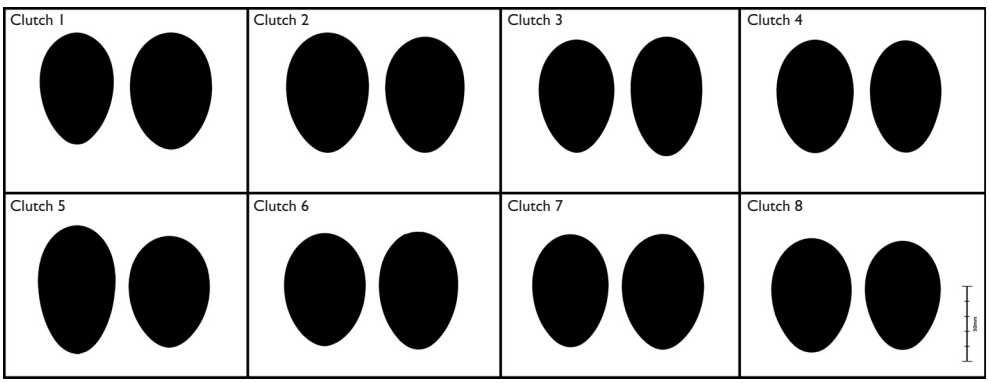

Fig. 1. Silhouettes of the eight pairs of Fulmar *Fulmarus glacialis* eggs collected from the Faroes in 1988–89. The eggs are photographed correctly for shape analysis (see text) and are to scale.

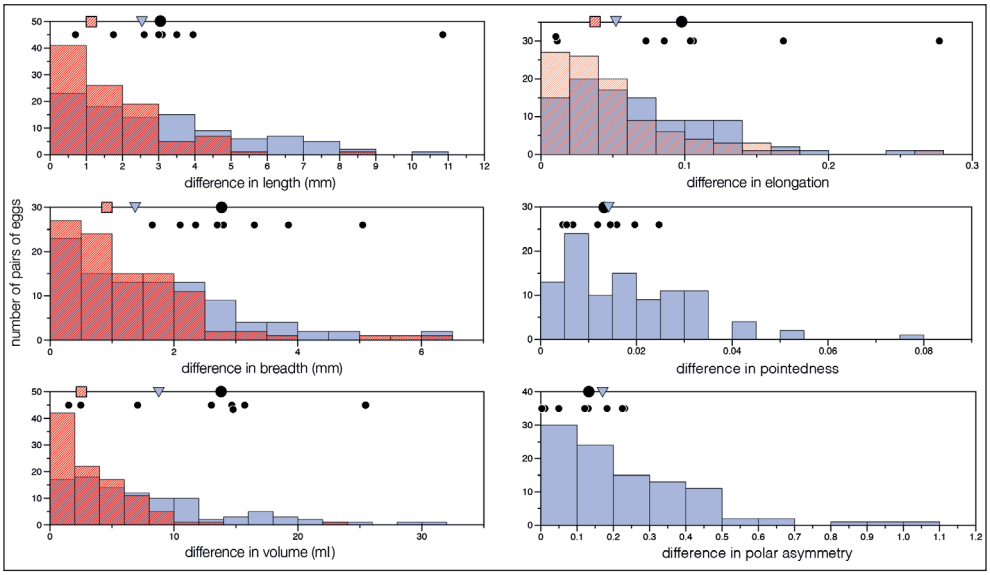

Fig. 2. Differences between pairs of eggs in eight real two-egg Fulmar clutches from the Faroes (black circles), 100 simulated clutches with each egg chosen from a random female on the Faroes (solid blue bars and triangles), and 100 pairs of eggs laid by females in different years on Eynhallow (hatched red bars and squares). Symbols on the top axis of each graph indicate medians (see table 3).

Results

Pairs of eggs laid by the same female on Eynhallow provide some insights into the extent of within-female variation in egg size and shape. The measurements of these eggs were significantly repeatable within females, with repeatabilities ranging from moderate (0.50) to high (0.75) (table 1). None of these egg measurements varied significantly with the year of laying (r = -0.04–0.08, P = 0.29–0.43, n = 200), or the age of the laying female (relative to age of first breeding) for the second egg measured (r = -0.08–0.05, P = 0.36–0.76, n = 100). Nor did the differences between any of the measurements of the two eggs vary significantly with the number of years between the laying of the first and second egg measured (r = -0.04 –0.11, P = 0.29–0.68, n = 100).

Eggs from Eynhallow were significantly smaller than those from the Faroes, although the mean differences were slight and there was no significant difference in elongation (table 2). Furthermore, correla-

Table 1. Repeatability of egg measurements from eggs laid in two different years by each female Fulmar *Fulmarus glacialis* on Eynhallow, Orkney (n=100). Confidence limits calculated by bootstrapping; P-value (from likelihood ratio test) tests whether repeatability is different from zero.

variable	repeatability	95% CL	P
length (mm)	0.75	0.65–0.83	<0.0001
breadth (mm)	0.50	0.34–0.64	<0.0001
volume (ml)	0.70	0.59–0.79	<0.0001
elongation	0.59	0.45–0.71	<0.0001

Table 2. Mean [95% CL] measurements of 16 Fulmar eggs in real two-egg clutches on the Faroes (n = 8 clutches), 111 random eggs collected in the Faroes and 200 eggs laid in different years by the same 100 females on Eynhallow, Orkney. For each variable, means with same letter superscript are not significantly different (Tukey posthoc tests from linear models).

variable	two-egg clutches	Faroes	Eynhallow
length (mm)	73.7^{ab} [73.1–74.0]	74.4^{a} (74.0–75.0]	73.6^{b} [73.1–74.0]
breadth (mm)	50.0^{ab} [48.7–51.2]	50.7^{a} [50.4–51.0]	49.7^{b} [49.5–50.0]
volume (ml)	95.1^{a} [89.6–100.6]	99.5^{b} [98.1–100.9]	97.2^{a} [96.3–98.1]
elongation	1.48^{a} [1.43–1.52]	1.46^{a} [1.45–1.48]	1.48^{a} [1.47–1.49]

tions between the differences between eggs laid by the same female and their mean size measurements were small and not significant (for max. length r = 0.07, P = 0.48; for max. breath r = -0.20, P = 0.09; for volume, r = -0.18, P = 0.08; n = 100 pairs of eggs from Eynhallow). Thus, comparisons of differences between the sizes and shapes of pairs of eggs from the Faroes and Eynhallow populations should not have been influenced by the small mean differences in the overall size of their eggs.

The differences (with respect to length, breadth, volume and elongation) between the two eggs in real two-egg clutches were significantly larger than the differences between two eggs from the same female from Eynhallow (table 3, fig. 2). With one exception (maximum breadth), the median differences in size and shape between the eggs in the real two-egg clutches were not significantly larger than the differences between eggs in the simulated two-egg clutches from the Faroes (table 3, fig. 2). Note also that, with respect to each of these differences within pairs of eggs, the real clutches are more similar to the randomly chosen pairs of eggs than they are to the eggs laid by the same females on Eynhallow (tables 3 & 4). Overall, these results suggest that the eggs in the eight two-egg clutches from the Faroes were laid by different females.

Table 3. Differences in measurements between the two eggs in eight real two-egg Fulmar clutches on the Faroes, 100 pairs of eggs taken at random from the Faroes, and 100 pairs of eggs from the same female on Eynhallow in different years. Values in parentheses are P-values from Wilcoxon tests for comparisons with the two-egg clutches.

variable	two-egg clutches	Faroes	Eynhallow
length (mm)	3.05	2.30 (0.29)	1.15 (0.008)
breadth (mm)	2.75	1.63 (0.0002)	0.90 (0.0001)
volume (ml)	13.84	8.22 (0.18)	2.60 (0.002)
elongation *	0.095	0.065 (0.09)	0.039 (0.045)
pointedness	0.013	0.015 (0.37)	–
polar asymmetry	0.130	0.23 (0.04)	–

* Note that elongation, pointedness and polar asymmetry are dimensionless values (see Biggins *et al.* 2018).

Table 4. Mean [95% CL] differences in measurements between the two eggs in real two-egg clutches on the Faroes (n = 8 clutches), in two eggs sampled at random from the Faroes (n = 100 pairs of eggs), and in two eggs laid in different years by the same female on Eynhallow (n = 100 pairs of eggs). For each variable, means with same letter superscript are not significantly different (linear models, with length and breadth log10-transformed to normalise residuals).

variable	two-egg clutches	Faroes	Eynhallow
length (mm)	3.68^{a} [1.11–6.25]	2.99^{ab} [2.52–3.45]	1.58^{b} (1.30–1.87)
breadth (mm)	2.98^{a} [2.07–3.88]	1.81^{b} [1.53–2.10]	1.21^{c} [0.99–1.43]
volume (ml)	11.83^{a} [5.24–18.43]	8.25^{ab} [7.04–9.46]	3.58^{b} [2.91–4.26]
elongation	0.10^{a} [0.03–0.18]	0.07^{ab} [0.06–0.08]	0.05^{b} [0.04–0.06]
pointedness	0.013^{a} [0.007–0.019]	0.017^{a} [0.015–0.020]	–
polar asymmetry	0.119^{a} [0.043–0.195]	0.258^{b} [0.219–0.296]	–

Discussion

The data from individually marked female Fulmars on Eynhallow confirmed that individual females lay eggs of similar linear dimensions, volume and elongation in different years. Significant repeatabilities show that eggs laid by the same female were more similar than the measurements of randomly chosen pairs of eggs from the same population.

For the two-egg clutches on the Faroes, the fact that these were more different than pairs of eggs laid by the same female in different years on Eynhallow is consistent with the idea that the two eggs in the eight Faroes clutches were laid by different females. This conclusion is further supported by the similarity of differences between eggs in the real and simulated two-egg clutches from the Faroes (table 3).

There is a further, albeit remote, possibility, which is that a Fulmar laying two eggs in the same season does so as the result of a pathological condition that also results in the two eggs being dissimilar in size and shape.

Future researchers may be able to use molecular techniques to further investigate this. While it is certainly possible that any of the two-egg clutches could have been laid by the same female, the most parsimonious conclusion, based on our analyses and knowledge of the breeding biology of this species, is that they were laid by different females.

If two-egg clutches are the product of two females, it remains to be explained why this occurs. There are several possibilities: (i) two monogamously paired females both 'assume' that they own the egg-laying site, and in some cases do so in consecutive years; (ii) egg-dumping, or intraspecific brood parasitism, in which a female deliberately deposits an egg in another's nest to avoid the energetic cost of rearing the chick (although in species laying a single egg and only ever rearing a single chick, egg-dumping seems unlikely); and (iii) some Fulmars form female-female pairs (a situation that occurs in some Laysan Albatrosses *Phoebastria immutabilis* and some gull and tern species) and produce supernormal clutches, some of which contain fertile eggs. As in Laysan Albatrosses (Young *et al.* 2008) and these gulls and terns (Hunt & Hunt 1977; Conover *et al.* 1979), the eggs in some two-egg Fulmar clutches on the Faroes contained developing embryos (Jensen 1989).

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References

Biggins, J. D., Thompson, J. E., & Birkhead, T. R. 2018. Accurately quantifying the shape of birds' eggs. *Ecol. & Evol.* 8: 9728–9738.

Birkhead, T. R., Thompson, J. E., & Biggins, J. D. 2017. Egg shape in the Common Guillemot *Uria aalge* and Brünnich's Guillemot *U. lomvia*: Not a rolling matter? *J. Orn.* 158: 679–685.

Conover, M. R., Miller, D. E., & Hunt, G. L. 1979. Female-female pairs and other unusual reproductive associations in Ring-billed and California Gulls. *The Auk* 96: 6–9.

Fisher, J. 1952. *The Fulmar*. Collins, London.

Grealy, A., Bunce, M., & Holleley, C. E. 2019. Avian mitochondrial genomes retrieved from museum eggshell. *Mol. Ecol.* 19: 1052–1062.

Hunt, G. L., & Hunt, M. W. 1977. Female-female pairing in Western Gulls (*Larus occidentalis*) in Southern California. *Science* 196: 1466–1467.

Jensen, J-K. 1989. Toægs-kuld hos færøske Mallemukker. [Two-egg clutches of Fulmars in the Faroes]. *Dansk Ornitologisk Forenings Tidsskrift* 83: 83–88.

— 2012. *Mallemukken på Færøerne*. [The Fulmar on the Faroe Islands]. Torshavn.

Jones, A. G., & Ardren, W. R. 2003. Methods of parentage analysis in natural populations. *Mol. Ecol.* 12: 2511–2523.

Lockley, R. M. 1936. On the breeding birds of the Westmann Islands. *Ibis* 13: 712–718.

Michel, P., & Thompson, P. M. 2003. A simple photogrammetric technique for estimating egg volume from field measurements. *Atlantic Seabirds* 5: 31–34.

—, Ollason, J. C., Grosbois, V., & Thompson, P. M. 2003. The influence of body size, breeding experience and environmental variability on egg size in the Northern Fulmar (*Fulmarus glacialis*). *J. Zool.* 261: 427–432.

Mónus, F., & Barta, Z. 2005. Repeatability analysis of egg shape in a wild Tree Sparrow (*Passer montanus*) population: a sensitive method for egg shape description. *Acta Zoologica Academiae Scientarium Hungaricae* 51: 151–162.

Petersen, M. R. 1992. Intraspecific variation in egg shape among individual Emperor Geese. *J. Field Ornithol.* 63: 344–354.

Romanoff, A. J., & Romanoff, A. L. 1949. *The Avian Egg*. Wiley, New York.

Ryan, P. G., Cuthbert, R., & Cooper, J. 2007. Two-egg clutches among albatrosses. *Emu* 107: 210–213.

Tickell, W. L. N., & Pinder, R. 1966. Two-egg clutches in albatrosses. *Ibis* 108: 126–129.

Waits, L. P., Luikart, G., & Taberlet, P. 2001. Estimating the probability of identity among genotypes in natural populations: cautions and guidelines. *Mol. Ecol.* 10: 249–256.

Warham, J. 1990. *The Petrels: their ecology and breeding systems*. Academic Press, London.

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