

The influence of body size, breeding experience and environmental variability on egg size in the northern fulmar (*Fulmarus glacialis*)

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Abstract

Procellariiform seabirds provide a good model for studies of the causes and consequences of variability in avian egg size, because females can only adjust reproductive investment by breeding intermittently, or by altering the size of their single egg. Maternal characteristics such as age, breeding experience and body size, as well as environmental variability, can influence egg size, but the effect of these factors has rarely been assessed simultaneously in the same study. Previous studies in Scotland have shown that the egg size of northern fulmars *Fulmarus glacialis* increased in relation to breeding experience. At this colony the influence of breeding experience, body size and inter-annual variability upon egg size was tested simultaneously. Data collected over seven breeding seasons between 1975 and 2002 showed that egg size varied significantly both between years and in relation to the length of the breeding experience of females, but that female body size explained most variation in egg size. Inter-annual variability in egg size was not related to the winter North Atlantic Oscillation, which had recently been shown to influence other measures of reproductive success at this colony. Larger eggs also seem to be more likely to produce successful fledglings. These findings are discussed in relation to the relative contribution of egg quality and parental quality on increased reproductive success.

Key words: egg volume, seabirds, body-size, senescence, reproductive success, *Fulmarus glacialis*

INTRODUCTION

Maternal age or breeding experience (Davis, 1975; Ollason & Dunnet, 1986; Croxall, 1992), body size (Sedinger, Flint & Lindberg, 1995), and inter-annual variability in environmental conditions (Croxall, 1992; Perrins, 1996; Weidinger, 1996) can all influence avian egg size. In many species, for example, the size of the egg has been found to vary with age and/or experience, as older and more experienced females lay broader eggs (Davis, 1975; Furness, 1983; Ollason & Dunnet, 1988; Lequette & Weimerskirch, 1990; Weimerskirch, 1990; Croxall, 1992; Weidinger, 1996). Large body size also enables females to store larger reserves (Sedinger *et al.*, 1995), and interannual variations in egg size suggest that environmental conditions, particularly food availability during the period of yolk formation, play a role in determining egg-size (Croxall, 1992; Perrins, 1996; Weidinger, 1996). However, most of these studies have focused on just one or two of these factors, and the influence of experience, body size and environmental conditions on variability in egg size have rarely been assessed simultaneously.

Consequently, variability linked to environmental conditions may confound or obscure the relationships with individual characteristics and vice versa.

Variations in egg size may in turn have consequences for hatching and fledging success. Egg size can influence the nutrient reserves available to chicks (Weidinger, 1996), and egg size and shape may affect embryonic metabolism and influence gas, water and heat exchange between the egg and its environment (Perrins, 1996). Thus, larger eggs retain heat better, and cool down more slowly than smaller eggs when not incubated (Perrins, 1996). Relationships between egg size and hatching success have been empirically demonstrated in kittiwake *Rissa tridactyla* (Thomas, 1983), wandering albatross *Diomedea exulans* (Croxall, 1992) and oystercatcher *Haematopus ostralegus* (Jager, Hulscher & Kersten, 2000). In contrast, in studies of fulmar (Ollason & Dunnet, 1988), Nazca booby *Sula granti* (Clifford & Anderson, 2002), and roseate tern *Sterna dougallii* (Ramos, 2001), breeding success was not influenced by egg volume. These results may reflect real species differences. Alternatively, variations in environmental conditions may make it difficult to detect any influence of egg size on subsequent reproductive success. For example, Perrins (1996) suggested that it is advantageous to have smaller eggs when feeding

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conditions are poor, because smaller young require less food and are therefore more likely to produce fledglings in poor years. Another problem inherent in understanding the influence of egg size on reproductive success is the role of parental quality (Perrins, 1996), because observed relationships between hatching success and egg size may simply reflect improvements in hatching success resulting from female age or experience (Ollason & Dunnet, 1986; Croxall, 1992; Weidinger, 1996).

Species which lay only a single egg provide a good model for studies of the causes and consequences of variability in egg size, because females can only adjust reproductive investment by breeding intermittently or by altering the size or composition of eggs (Weidinger, 1996). In this study, earlier work on the northern fulmar at a Scottish breeding colony, which had shown that female age or experience influenced egg size, was extended (Ollason & Dunnet, 1988). Recent analyses of data collected at this colony showed that there was marked inter-annual variation in reproductive success, which was in turn related to variability in the winter North Atlantic Oscillation (NAO) (Thompson & Ollason, 2001). The main aim of this study was simultaneously to test the effects of breeding experience, body size and inter-annual variability in environmental conditions on egg size. In addition, we aimed to collect a larger dataset to explore the relationship between egg size and reproductive success.

STUDY AREA AND METHODS

Fieldwork was conducted at a fulmar colony on Eynhallow, a 1 km² uninhabited island, in Orkney, Scotland (59°08'N, 03°08'W). Visits to the study colony were made in late May or early June to count occupied nests, in mid-July to estimate hatching success and to individually colour-ring and measure successful new recruits, and in mid-August to estimate fledging success (Dunnet, 1991; Thompson & Ollason, 2001). Observations of colour-ringed adults in attendance at each nest were made during each visit to document individual reproductive histories (Ollason & Dunnet, 1988).

The length and breadth of eggs were measured to the nearest 0.1 mm, using callipers, in 1975, 1976, 1978, 1979, 1982, 1984 and 2002. In all years except 2002, only the eggs of colour-ringed breeders were measured, meaning that these samples may be biased towards more experienced birds. In 2002, eggs were measured at all accessible nests. However, even in this year, some eggs would have been lost before our first visit to the colony and the sample may remain slightly biased towards more experienced birds. Field measurements were made by both PMT and PM in 2002, whereas earlier measurements were generally made by JO and co-workers. To assess the extent of any between-observer measurement error that could influence assessments of inter-annual variation, these 3 authors independently measured the length and breadth of 12 chicken eggs before the 2002 field season.

In July 2002, the volume of 19 eggs was estimated directly by water displacement. Each egg was placed in an

empty 250 ml flask, which was then filled with water to 250 ml using a 100 ml graduated flask. These direct estimates of egg volume were then used to find the most effective formula for predicting volume from measurements of length and breadth. Linear regression indicated that 66.23% of the variation in egg volume within this sample could be explained by applying field measurements of egg length and breadth measurements to equation 1:

$$\text{volume} = 0.0063(\text{length} * \text{breadth})^{1.1753} \quad \text{equation 1}$$

In contrast, the use of published formulae (Romanoff & Romanoff, 1949; Narushin, 2001) for estimating egg volume from measurements of length and breadth all produced r^2 values ≤ 0.5 . Consequently, equation 1 was used to estimate egg volume from all field measurements.

For the whole dataset of egg size measurements, only 21 females were of known age (i.e. ringed as chicks) and there was little variability in the age of these birds as all but 2 were between 30 and 40 years of age. Consequently, breeding experience was only used as a proxy of age. This measure was based on the number of years since they were first recorded breeding, and was available for the much larger number of females that had been colour ringed as new recruits to the colony. Therefore, as in previous studies at this colony (Ollason & Dunnet, 1988), these data did not allow the separation of effects owing to age and breeding experience.

The sex of colour-ringed breeders was determined using a discriminant function based on measurements of bill length and bill depth (Dunnet & Anderson, 1961). When sexing was uncertain owing to similar values for both members of a pair, weight or tarsus measurements were used to determine which was the largest member of the pair, and this was assumed to be the male. This discriminant function was also used as an index of body size, as data on body weight were not available for all females.

The extent of inter-annual variation in different measures of egg size was first determined using ANOVA. The combined effects of year, breeding experience and body size on egg volume were then analysed using general linear models. In the first analysis, egg volume was entered as the dependent variable, against year as a fixed factor, and the body size index, and breeding experience as covariates. The quadratic effect of breeding experience was also included as a possible factor in the model to determine whether there was any evidence of a relationship that reflected a decline in egg size amongst the oldest females. A second analysis excluded the year factor and instead incorporated the winter NAO index as a covariate. In both models we also tested for possible interactions between the different factors. Values for the winter NAO Index were obtained from the website of the National Geophysical Data Centre, U.S.A. (<http://www.cgd.ucar.edu/~jhurrell/nao.html#seasonal>).

The influence of egg volume on subsequent reproductive success was analysed using logistic regression. Hatching success is here defined as the probability of an egg subsequently producing a chick, whereas reproductive success is defined as the probability of an egg producing a

Table 1. Summary showing the inter-annual variations in mean (± 1 SD) values for length, breadth, and volume of northern fulmar *Fulmarus glacialis* eggs measured at nests on Eynhallow. Results are also given for the ANOVA tests carried out to determine whether the significance of inter-annual variation in each variable

Year	<i>n</i>	Length (mm)	Breadth (mm)	Volume (cm ³)
1975	28	74.07 \pm 2.85	49.80 \pm 1.51	98.89 \pm 5.29
1976	29	72.57 \pm 3.54	49.46 \pm 2.24	95.91 \pm 8.61
1978	42	72.59 \pm 3.02	49.35 \pm 1.67	95.58 \pm 6.22
1979	79	73.09 \pm 2.89	49.93 \pm 1.49	97.70 \pm 6.22
1982	40	73.45 \pm 3.29	50.78 \pm 1.39	100.30 \pm 7.56
1984	64	74.13 \pm 2.59	50.55 \pm 1.73	100.84 \pm 7.11
2002	132	74.11 \pm 2.78	49.76 \pm 1.91	98.86 \pm 6.58
<i>F</i>		3.00	4.27	4.05
<i>P</i>		< 0.01	< 0.001	< 0.001

chick that was present in the nest during the mid-August visit. Losses were rare after this stage, and all chicks present during August were assumed to have fledged (Ollason & Dunnet, 1988). All analyses were carried out in SPSS.

RESULTS

Overall variability in measurements and egg size

Test measurements made of chicken eggs by different observers were significantly correlated (*P* values for all comparisons were < 0.001), with slightly higher *r*² values for measurements of length (*r*² > 0.99) than for breadth (*r*² > 0.96). CVs of the three repeated measurements were all < 0.5%, for egg length and < 1.4% for egg breadth.

Field measurements of the length of fulmar eggs for the complete dataset were normally distributed (Anderson–Darling normality test, *A*² = 0.523, *P* = 0.18) and averaged 73.59 mm (CV = 4.0%; range 63.20–81.80 mm.). Egg breadth measurements, on the other hand, were negatively skewed (Anderson–Darling normality test *A*² = 1.187, *P* < 0.01), and averaged 49.95 mm (CV = 3.6%; range 21.90–54.60 mm). Egg volume values were normally distributed, following a similar pattern to egg length frequency distribution. They averaged 98.55 cm³, but were more variable (CV = 7.0%; range 69.02–115.61 cm³). There was significant variation in all three variables between years, with the lowest values recorded in 1976 and 1978, and highest values in 1984 (Table 1).

Effects of body size, age and inter-annual variability

Body size, and breeding experience had a significant influence on egg volume, whether interannual variability in environmental conditions was modelled using a year effect or using the winter NAO index (Table 2). In both cases, there was also support for a quadratic influence of breeding experience, suggesting that egg volumes increased until females had been breeding for *c.* 18 years, after which

Table 2. Results of the two general linear models comparing the effect of body size, breeding experience and inter-annual variability upon northern fulmar *Fulmarus glacialis* egg volume. Model 1, inter-annual variability modelled using year as a categorical variable; model 2, inter-annual variability modelled using the winter NAO index as a continuous variable

	d.f.	<i>b</i>	<i>F</i>	<i>P</i>
Model 1				
Intercept		28.055	4.31	< 0.05
Body size index	1	0.979	22.38	< 0.001
Breeding experience	1	0.32	4.04	< 0.05
Breeding experience ²	1	−0.0145	6.06	< 0.01
Year	6		3.10	< 0.01
Total	9		4.88	< 0.001
Model 2				
Intercept		31.055	4.52	0.034
Body size index	1	0.947	20.24	< 0.001
Breeding experience	1	0.333	4.26	< 0.05
Breeding experience ²	1	−0.0136	5.13	< 0.05
Winter NAO	1	0.297	1.12	0.29
Total	4		6.33	< 0.001

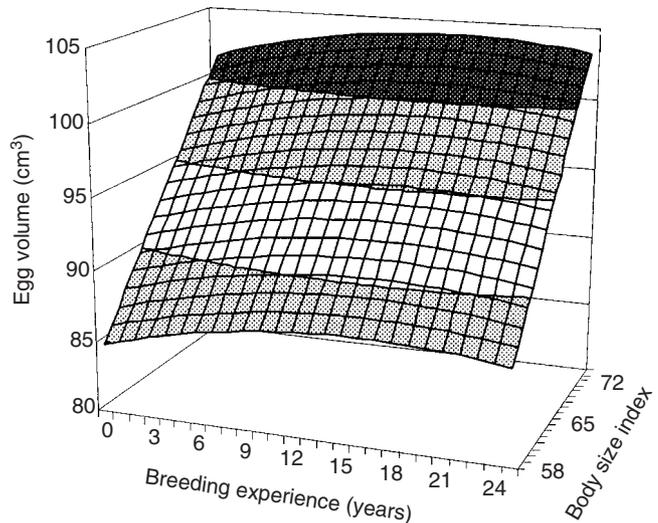


Fig. 1. Fitted values from the general linear model (see Table 2) showing the relative influence of body size and breeding experience on northern fulmar *Fulmarus glacialis* egg volume.

size decreased with experience (Fig. 1). However, body size always had a much stronger effect on egg volume than breeding experience. There was significant inter-annual variability in egg volume when this was modelled as a year effect, but there was no evidence that this variability was related to inter-annual variability in the winter NAO (Table 2).

Influences of egg size on reproductive success

Using the complete dataset, there was a positive but insignificant relationship between egg volume and subsequent hatching success (change in log likelihood ratio, $\chi^2 = 3.28$, d.f. = 1, *P* = 0.07) and overall reproductive

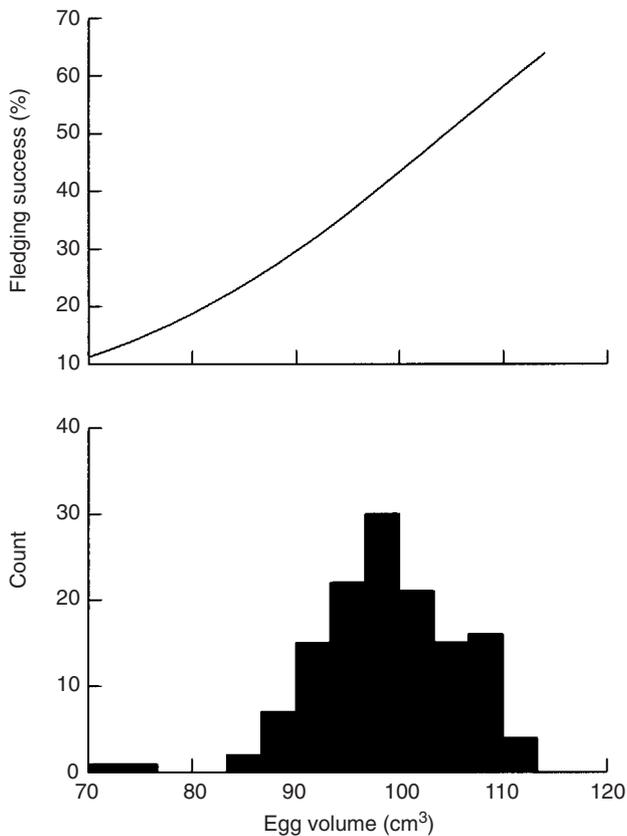


Fig. 2. Estimated probability of a northern fulmar *Fulmarus glacialis* egg producing a successful fledgling in relation to egg volume. Also presented is the frequency distribution of different sizes of eggs. Data are all from the 2002 breeding season.

success (change in log likelihood ratio, $\chi^2 = 3.69$, d.f. = 1, $P = 0.055$). There was also no significant interaction between year and egg volume. However, the positive influence of egg volume on both hatching success (change in log likelihood ratio, $\chi^2 = 4.27$, d.f. = 1, $P = 0.04$) and overall reproductive success (change in log likelihood ratio, $\chi^2 = 5.08$, d.f. = 1, $P = 0.024$) was significant when restricted to the larger set of data collected during the 2002 breeding season (Fig. 2).

DISCUSSION

Factors influencing egg volume

Previous studies at this colony have shown that there was a significant relationship between egg volume and breeding experience, primarily because experienced females tended to lay broader eggs (Ollason & Dunnet, 1988). Similarly, egg volume has been shown to increase with age or breeding experience in Antarctic fulmars *Fulmarus glacialis* (Weimerskirch, 1990) and several other seabird species (Davis, 1975; Thomas, 1983; Croxall, 1992; Weimerskirch, 1992). Our data confirmed the pattern found by Ollason & Dunnet (1988), and further indicate that egg volume decreased slightly amongst older females

(Fig. 1), as seen in some other petrels (Weimerskirch, 1992). In some studies, it has been argued that age-related changes in reproductive performance can be confounded with trends in environmental conditions (Nisbet, 2001). However, we tested for this quadratic effect of breeding experience in the presence of a year effect, suggesting that this reflects a genuine change in reproductive effort due to age.

Whilst the influence of breeding experience or age on egg size has been shown to be significant in several petrel species, these studies have all reported considerable individual variation in egg size within age-classes (Brooke, 1978; Ollason & Dunnet, 1988; Croxall, 1992). Our analyses indicate that much of this additional variability may be explained by differences in female body size, which proved to be a more significant influence on egg size than breeding experience (Table 2, Fig. 1). Furthermore, because measures of body size were based upon measurements made when females first recruited to the colony, this effect should be independent of age. Studies of the cape petrel *Daption capense* also found that body size influenced egg volume (Weidinger, 1996), but data were not available to simultaneously test for any influence of age or experience. Indeed, most studies of this kind have tended to look at the effect of either breeding experience or body size. In other species, the effect of body size on eggs from larger clutches can be significant, but tends to be weak (Jager *et al.*, 2000). The magnitude of these effects can differ between years, with the influence of both age and body size on egg volume being greatest when feeding conditions are poor (Hakkarainen & Korpimäki, 1993; Weidinger, 1996; Ratcliffe, Furness & Hamer, 1998). No significant interaction, however, was found between the influence of either body size or breeding experience and inter-annual environmental variability.

Christians & Williams (2001) demonstrated that the size of the female organs involved in the production of the yolk and supply of nutrients had no effect on egg variations. Together, these findings suggest that the influence of body size on egg volume may be less of a physiological constraint, and more an indication of differential levels of female investment. Slight, but significant, differences were found in the size of eggs in different years (Table 1), which may reflect differences in female reproductive investment in relation to inter-annual variation in environmental conditions. Similarly, temporal variability in egg size has been recorded in other petrels, and is believed to reflect changes in food availability (Croxall, 1992; Chastel, Weimerskirch & Jouventin, 1995; Weidinger, 1996). Previous work at this study colony assumed that environmental conditions were fairly stable from year to year (Ollason & Dunnet, 1980, 1986), but more recent analyses have shown that climate variation, reflected by the winter NAO Index, can influence reproductive success (Thompson & Ollason, 2001). However, we found no evidence that observed inter-annual variations in egg size (Table 1) were explained by variations in the NAO. Typically, relationships between the NAO and ecological variables have only been detected using long time series (Ottersen *et al.*, 2001; Stenseth *et al.*, 2002).

Thus, the lack of a significant relationship in this study (Table 2) may reflect a lack of power when using only a 7-year dataset on egg size.

Given the observed influence of body size on egg size (Table 2), inter-annual variation in mean egg size at the colony could reflect differences in the sample of females successfully laying in each year, rather than changes in individual reproductive effort. Because eggs have been measured in only a few years, with samples generally collected several years apart, we were unable to make more detailed analyses of the extent of within-female variation in egg size. Further work is now planned to address this, and to explore why variability in egg size is so much greater than variability in body size.

Influences of egg volume on reproductive success

In contrast to previous studies at this colony (Ollason & Dunnet, 1988), egg volume was found to positively influence the probability both of the egg hatching and of the egg subsequently producing a fledgling. This relationship was only significant, however, when our analysis was restricted to the data collected in 2002 (Fig. 2). The stronger effect in 2002 may reflect the larger sample size in this year, slight differences in the extent of this effect in different years (e.g. Ratcliffe *et al.*, 1998), or the more representative sample of eggs measured from both ringed and unringed breeders in 2002. Differences between these findings and earlier studies could also result from methodological differences and other confounding effects resulting from the use of many nests for manipulative experiments (Ollason & Dunnet, 1986). In the present study, a new formula was derived for estimating egg volume from measurements of length and breadth, which provided a more powerful estimator of volume than the equations of Romanoff & Romanoff (1949) that were used previously. In addition, Ollason & Dunnet's (1988) earlier work involved within-female comparisons for a smaller sample of known breeders, whose eggs had been measured on two occasions. This study, particularly those data from 2002, involved a wider range of data for both egg size and female breeding experience. Whatever the reason for these differences, descriptive studies such as ours cannot be used to determine whether the observed effects stem from variations in egg size per se, or whether they simply reflect differences in other aspects of female quality. Larger eggs have been found to have higher hatching success in several previous studies (Croxall, 1992; Weidinger, 1996; Jager *et al.*, 2000). Increased hatching success amongst larger eggs may result from a higher surface to volume ratio that makes them less susceptible to fluctuations in temperature or water loss (Clifford & Anderson, 2002). However, including eggs that have been predated may lead to spurious relationships between egg size and hatching success (Clifford & Anderson, 2002). In future, better discrimination between the different causes of failure, together with other measures of egg shape or quality, should provide better insights into the link between egg

size and reproductive success. Given the observed link between body size and egg size, it is possible that increased success of large eggs may reflect some other advantage of large body size. Body size will influence fasting ability in these birds, and it is probable that body size will also affect attendance patterns and, consequently, the risk of egg predation. Ultimately, the relative importance of parental body size and egg size on reproductive success will best be assessed by extending earlier experiments designed to compare the effects of breeding experience and egg quality (Ollason & Dunnet, 1986).

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