Determining hatch dates for skuas: an egg density calibration curve

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Abstract

Key life-history events, such as breeding phenology, underlie much ecological research and inform conservation efforts. Simple methods that improve efficiency during breeding studies are valuable, particularly in remote locations and extreme climates. Building on an earlier study, we investigated the relationship between egg density and incubation progression in two Arctic- and subarctic-breeding seabird species, Arctic Skua *Stercorarius parasiticus* and Great Skua *S. skua*, to statistically test its application as a calibration method. Corresponding with the preceding study we found that the decrease in calculated egg density during incubation can be described by a quadratic relationship with egg development for our populations. In addition, we demonstrate that this relationship was not confounded by multiple egg clutches nor differences in measurement intervals. From this relationship, a calibration curve was constructed to predict hatching dates within an error of c. three days for Arctic Skua and c. four days for Great Skua, using a single measure of the length, breadth and mass of an egg. Furthermore, when combining the data generated in this study, we found model support for a calibration curve independent of species, suggesting that this calibration may have the potential to be extended to other species with similar ecology. This technique can be used to inform the timing of colony visits and thereby maximise research and monitoring efforts for these species with minimal researcher disturbance.

Introduction

Long-term monitoring of seabirds is an important component of nature management and conservation research, partly due to the historical role of seabirds as bioindicators for marine ecosystems (Piatt *et al*. 2007), and partly due to conservation concerns based on large seabird population declines in recent decades (Paleczny *et al*. 2015). Declines in populations have been attributed to changes in the environment, resource availability and anthropogenic disturbance (Halpern *et al*. 2008). As we begin to understand how these trends relate to climate change (Crick 2004), seabird research may aid the understanding of the ecological implications of this phenomenon (Grémillet & Boulinier 2009). Many seabirds are long-lived K-selected species with low annual productivity and delayed sexual maturity. This makes them particularly vulnerable to rapid environmental change (Irons *et al*. 2008; Ainley & Hyrenbach 2010) and poses challenges for research, as population dynamics incur an inherent lag.

A potential environmental factor influencing seabird productivity, driven by warming springs, is a phenological mismatch between breeding initiation and optimal environmental conditions such as weather and food availability for breeding adults and chicks (Lameris *et al*. 2018). Egg laying and hatching dates are measurable parameters for understanding this process, creating a timeframe for the breeding season. Combined with existing estimates for the duration of chick morphological development from hatching until fledging, the knowledge of laying and hatching dates also allows a prediction of fledging dates for chicks, which in turn assists planning of fledging rate surveys and chick-ringing projects.

Obtaining estimates for time-sensitive events such as laying and hatching often demands intensive fieldwork effort, and human disturbance may negatively affect productivity (Anderson & Keith 1980). Minimising researcher presence and interaction is therefore recommended at all times. Considerations for reducing disturbance impose constraints on fieldwork and necessitate the development and refinement of time-efficient and sensitive practical techniques.

There are three main quantitative or qualitative field techniques for estimating hatch dates based on the physical properties of egg development: candling (Lokemoen & Koford 1996), flotation (Rizzolo & Schmutz 2007), and density (Furness & Furness 1981). All methods require some degree of calibration and verification. These techniques are more economical and efficient for general field use than the technology-based monitoring generally utilised for other primary purposes (Grémillet *et al*. 2004; Renfrew & Ribic 2012; Mougeot *et al*. 2014; Islam *et al*. 2015; Eichhorn *et al*. 2017).

The candling technique involves backlighting the egg to visualise its contents through the shell and assess embryonic stage and quality. It is useful in controlled environments such as incubators, but has been used in the field (Deeming 1995; Lokemoen & Koford 1996), and tested comparatively with egg flotation (Reiter & Andersen 2008).

The flotation method assesses the water suspension gradient of the egg throughout development, caused by the increasing ratio of atmospheric gas to wet material. It has been utilised for waterfowl (Reiter & Andersen 2008), waders (Liebezeit *et al*. 2007; Ackerman & Eagles-Smith 2010; Hansen *et al*. 2011), and gamebirds (McNew *et al*. 2007).

The egg density technique is more rarely employed and capitalises on the same principle of water loss underlying egg flotation, but uses egg biometrics to determine density (Westerskov 1950; Barth 1953). Volume and density can be determined from three egg biometrics: length, breadth and mass (Hoyt 1979).

Although this technique has been previously described (Furness & Furness 1981; Yalden & Yalden 1989; Jarrett *et al*. 2003) and is potentially the most time-efficient and least invasive, it has not yet been subjected to rigorous statistical analysis.

Here, we investigate the relationship between egg density and incubation progression of the colonial and ground-nesting Arctic Skua *Stercorarius parasiticus* and Great Skua *S. skua*. Following the methodology of Furness and Furness (1981) for the Faroese population, we test if the relationship, described by a quadratic curve, is reproducible for different populations, and we expand the statistical analysis to account for potential confounding effects of repeated measures of mass and the simultaneous incubation of multiple eggs in the same nest. We assess if a species-specific egg density calibration curve delivers low-error prediction of hatching dates from a single nest visit, and furthermore, we investigate the potential for a global calibration which can be applicable more broadly across related species.

Methods

Arctic Skua egg data were collected on the island of Fugloy, Faroe Islands (62°19’12”N 6°18’36”W), between 2 June and 1 July 2016, and Great Skua egg data were collected on the island of Skúvoy, Faroe Islands (61°45’36”N 6°49’12”W) between 10 May and 11 July 2013. Each nest was visited 1–7 times throughout the incubation period. At first visit, egg length (l) and breadth (b) were measured to 0.05 mm with Vernier callipers, and mass (m) was measured at 0.1 g resolution. At every subsequent visit, m was re-measured. Egg volume (V_E) was calculated using the following formula:

$$V_E = K_V \, x \, l \, x \, b^2$$

where K_V = 0.507, and is an estimated egg-shape constant (Hoyt 1979) following Furness and Furness (1981). Egg density (D_E) was then calculated for each nest visit and measure of m as follows:

$$D_E = \frac{m}{V_E}$$

The range of egg density values for Arctic Skua (0.87–1.04 g/cm^3) corresponded exactly to that of the Arctic Skua data from Foula, Shetland (Furness & Furness 1981). Great Skua egg density values here were slightly wider in range (0.83–1.07 g/cm^3) than both Foula Great Skua eggs (0.86–1.05 g/cm^3) and Arctic Skua eggs (Furness & Furness 1981).

Hatching dates were observed for 25 Arctic Skua eggs (total mass measurements: n = 75) from 17 nests, and 19 Great Skua eggs (total mass measurements: n = 67) from 16 nests. 76% of Arctic Skua nests and 94% of Great Skua nests contained two-egg clutches. Hatching dates were estimated using five observation criteria (Hammer 2016): egg cracked (two days before hatching), egg cracked and chick pipping (one day before hatching), chick wet in nest (hatched same day), chick dry in nest (one day after hatching), chick at ≤ 2 m distance from nest (two days after hatching). Dates of egg measurements relative to hatching date were then expressed as the number of days before hatching (DBH), which serves as a metric of incubation progression.

Mean incubation time was defined as 26 days for Arctic Skua and 30 days for Great Skua (Gilbert *et al*. 1998). From this we calculated the proportion of time before hatching (TBH) in order to combine the dataset for these two species.

For each species individually, the effect of DBH on D_E was analysed using a mixed model approach, where Nest ID and Egg ID nested within Nest ID were *a priori* included in the model as random effects to account for repeated measures of the mass of individual eggs within nests. Ordinal Day was included in the model as an additional fixed effect to test for a confounding effect of simultaneous incubation of multiple eggs in the same nest. We tested the influence of species as a fixed effect in the combined dataset to investigate if differences exist in egg density during embryo development in the two species, also including Nest ID and Egg ID as random effects. Models were defined following backwards stepwise term deletion and ranked by Akaike's Information Criterion (AIC). The relationships between D_E and DBH for all eggs with three or more measurements were plotted for each species to test the assumption of co-linearity (Appendix 1).

All analysis was performed using SAS Software (2014).

Results

We found support in species-specific models of both Arctic and Great Skuas for effects of DBH and DBH^2 on D_E (Table 1, Figure 1). There was no support for Ordinal Day and this parameter was excluded from the calibration curve. For the combined data of both species, the best supported models included a quadratic relationship with time and D_E (Table 1). We found no support for a difference between the two species (model with and without the term Species: AIC 2.3 and 0, respectively; Table 1).

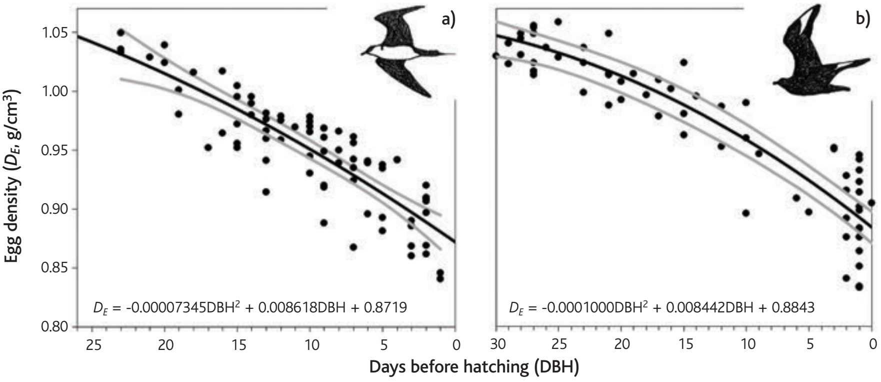

Figure 1. Species-specific egg density data, quadratic calibration curve equations of the relationship between egg density, D_E, and days before hatching, DBH, for (a) Arctic Skua and (b) Great Skua. Observations n = 75 from 25 eggs and 17 nests, n = 67 from 21 eggs and 16 nests, respectively. Black lines represent the predicted egg density, and the grey lines are 95% confidence limits.

Table 1. GLMM results testing for the relationship between egg density and time ranked by AIC-value. Variables, additive and interactions, tested were Days Before Hatching (DBH), proportion of Time Before Hatching (TBH), ordinal day (Day) and Species. Nest ID and Egg ID nested within Nest ID were included as random variables in all models. Best supported models in bold.

Species	Independent variables					df	*F*-values and P-values for each variable					AIC
	IP1	IP2	IP3	IP4	IP5		*F*1; P1	*F*2; P2	*F*3; P3	*F*4; P4	*F*5; P5	
Arctic Skua	**DBH**	**DBH×DBH**				**47**	**229.3; <0.001**	**20.9; <0.001**				**0**
	DBH	Day				47	111.1; <0.001	3.3; <0.0772				8.5
	DBH	DBH×DBH	Day			46	118.2; <0.001	20.8; <0.001	3.2; 0.079			10.1
	DBH	DBH×DBH	Day	DBH×Day		45	29.2; <0.001	33.9; <0.001	5.8; 0.020	9.3; 0.004		21.1
	DBH	DBH×DBH	Day	DBH×DBH×Day		45	133.0; <0.001	7.1; 0.011	4.6; 0.038	11.6; 0.001		25.2
	DBH	Day	DBH×Day			46	2.0; 0.165	2.6;0.114	0.3; 0.584			27.6
Great Skua	**DBH**	**DBH×DBH**				**46**	**95.1; <0.001**	**12.1; 0.001**				**0**
	DBH	Day				47	42.0; <0.001	0.7; 0.423				4.2
	DBH	DBH×DBH	Day			46	47.1; <0.001	11.4; 0.002	0.2; 0.665			12.5
	DBH	Day	DBH×Day			46	4.4; 0.042	0.2; 0.647	0.6; 0.460			23.1
	DBH	DBH×DBH	Day	DBH×Day		45	20.7; <0.001	18.6; <0.001	0.5; 0.492	6.8; 0.013		25.7
	DBH	DBH×DBH	Day	DBH×DBH×Day		45	56.7; <0.001	2.0; 0.161	0.2; 0.648	6.5; 0.014		32.8
Combined	**TBH**	**TBH×TBH**				**95**	**237.2; <0.001**	**23.4; <0.001**				**0**
	TBH	**TBH×TBH**	**Species**			**95**	**243.7; <0.001**	**26.7; <0.001**	**5.6; 0.020**			**2.3**
	TBH	TBH×TBH	TBH×TBH×Species			94	232.1; <0.001	22.4; <0.001	0.2; 0.679			7.3
	TBH	TBH×TBH	Species	TBH×Species		94	240.9; <0.001	25.7; <0.001	4.9; 0.0299	0.0; 0.9772		10
	TBH					96	1580.4; <0.001					14.5
	TBH	TBH×TBH	Species	TBH×Species	TBH×TBH ×Species	93	225.0; <0.001	22.7; <0.001	3.48; 0.065	0.1; 0.754	0.1; 0.739	14.7
	TBH	Species				96	1576.4; <0.001	2.0; 0.158				20.2
	TBH	TBH×Species				95	1264.5; <0.001	0.03; 0.864				22.1
	Species					97	4.5; 0.036					205.7

Prediction error for the calibration curves was calculated as the mean difference between known and predicted DBH for our sample, following Furness & Furness (1981). For Arctic Skua, the overall error was ± 2.85 days, with 17% of the eggs predicted within ± 1 day of observed hatching and 35% within ± 2 days. For Great Skua the error was ± 3.96 days, with 12% predicted within ± 1 day of observed hatching and 21% within ± 2 days.

The quadratic relationship between egg density and incubation progression for both species combined was the most parsimonious. This was used as a calibration curve to predict time until hatching for the two skua species:

$$\mathrm{TBH}_{\mathrm{Skuas}} = \frac{-0.2412 + \sqrt{0.05818 + 0.3175(0.8746 - \mathrm{D_E})}}{-0.1588}$$

Mean prediction error for the combined species calibration curve was ± 3.76 days, with 11% predicted within ± 1 day of observed hatching and 32% within ± 2 days.

Discussion

The quadratic egg density calibration curve for the Faroese populations corresponded to the relationship described for the Scottish populations (Furness & Furness 1981), and the method reliably predicted hatching dates for Arctic Skuas and Great Skuas with errors within c. four days. Prediction errors were of a scale to enable the use of this method to approximate peak periods of hatching and fledging in a colony or population of these species. As such, it can optimise timing of visits for productivity assessments, chick-ringing, observations of incubation and brooding behaviour for these species. Furthermore, it allows low-effort construction of phenological time-series for individual colonies and populations, thereby minimising the risk of nest disturbance during field work. We find some support for the application of a general calibration curve for this species group, with prediction errors within the same range as the species-specific curves (within c. four days).

As a field tool, a prepared egg density calibration curve has the advantage over flotation and candling in that it requires only three simple measurements using callipers and a balance, rather than submersion in water or viewing under controlled lighting. This not only makes it a more time-efficient method but also improves reproducibility between fieldworkers. Compared with candling, this method requires neither specialised or bulky equipment nor expertise in the subjective assessment of embryo development.

A mean prediction error of c. ± 3–4 days corresponds partly with those of flotation studies, which fall between c. ± 0–4 days (Walter & Rusch 1997; Mabee *et al*. 2006; Liebezeit *et al*. 2007; Reiter & Andersen 2008; Ackerman & Eagles-Smith 2010). However, flotation error is known to vary considerably at different stages throughout egg development (Mabee *et al*. 2006; Liebezeit *et al*. 2007; McNew *et al*. 2007). This is apparently not the case for the egg density calibration curves tested here, possibly as it relies on a quantifiable rate of mass loss (Ar & Rahn

Arctic Skua
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1980). The previous study of hatch date prediction using egg density for Arctic and Great Skuas estimated mean errors of c. ± 1–2 days (Furness & Furness 1981). The greater error in our study is most likely a consequence of a substantially smaller sample size, indicating the limitations of this method for small populations or rare species. This should be accounted for in studies of only a few eggs. The accuracy associated with candling was greatest at c. ± 1 day (Reiter & Andersen 2008).

The approach described here, and furthering previous studies (Furness & Furness 1981; Yalden & Yalden 1989; Jarrett *et al*. 2003), has the potential to be used in other birds with similar breeding ecology. In the combined models we found that species contributed little to the calibration curve, suggesting that a global model can be used, certainly for these two closely related skua species. We advocate the preparation of calibration curves following our technique to determine the best fit for any new species. However with further tests including different populations, new species and species groups (e.g. passerines, waders, raptors etc.) a global calibration curve may be developed that can be used more broadly. Variation in natural systems is expected and can be explained by hatching asynchrony, species-specific egg shape and structure, and measurement error. These considerations must be taken into account when describing the limitations in accuracy of this method for skuas and when expanding this technique to other species.

While circadian rhythms and temperature are known to influence embryonic development and incubation duration (Martin *et al*. 2007; Cooper *et al*. 2011), we found no seasonal effect on egg development. This may be in part due to the relatively short breeding season and narrow range of conditions in these high latitude species (del Hoyo *et al*. 2008) or that any influence of ordinal day was within the uncertainty limits of the model or due to low sample size. The quadratic relationship between egg density and time (DBH and TBH, respectively) is possibly driven by the *a priori* inclusion of Nest ID and Egg ID as random variables to account for repeated measures, but this cannot be disentangled for single point measurements.

An important source of prediction error is the potential occurrence of hatching asynchrony: the variation in incubation time for individual eggs within a clutch. Asynchronous hatching has been shown to occur in seabirds ecologically similar to the skuas, including large gulls (Sydeman & Emslie 1992; Kim *et al*. 2010), manifesting in c. two day variation in hatching interval. We *a priori* included nest and egg ID within the model to account for any potential individual effect, and this may explain the range of certainty in predicting hatch dates. For a global calibration an additional source of variation is the accuracy and precision of published mean incubation periods for each species or population.

When combining species in a calibration, employing a non-species-specific egg shape constant for calculating egg volume (Preston 1974; Hoyt 1979) should not be underestimated in its contribution to the variation in calculated density (Furness & Furness 1981; Stoddard *et al*. 2017). Furthermore, for a species-specific calibration curve, intra-species and within-clutch variation in egg volume may account for the observed variation (Preston 1974). Additionally, size measurement errors are likely to be relatively greater for smaller eggs. Because the calculation uses egg breadth squared, the measurement of egg breadth has a particularly strong influence on the estimate of hatching date and should be taken with care. As such, the technique may prove mostly useful for larger species such as skuas, gulls and larger waders, but this remains to be tested.

Inconsistencies in the decrease of egg density may result from natural variation in the rate of egg water loss, which is likely produced by factors such as mass-to-volume ratio upon laying, egg shape, and evaporative capacity. These, in turn, are influenced by eggshell structure, embryonic stage, nest temperature and ambient humidity (Ar *et al*. 1974; Rahn & Ar 1974; Portugal *et al*. 2014). The combined effect of these factors may vary throughout incubation and depend on parental nest attendance and maintenance (Cooper & Voss 2013); however, accounting for them statistically is complex and ultimately unlikely to inform a practical field technique.

Following laying, and before the eggshell is cracked, the decrease in egg mass is well described by the calibration curve. However, as the chick breaks through the shell, the rate of evaporative water loss from the egg increases substantially (Ar & Rahn 1980; Furness & Furness 1981). This may in part explain the large variation in egg densities for near-complete incubation for the Great Skua. Thus, while the egg density curve may be unreliable immediately before hatching, the last two days of developmental progression can be determined by visual inspection (see methods).

The preparation of egg density calibration curves is a valuable tool for studies in which a colony- or population-wide estimation of breeding timing is necessary. Though precision may be improved by other techniques such as candling, obtaining egg-measurements relies substantially less on expertise and no additional specialist equipment is needed. The one-time measurement and reduced handling of the egg density technique is particularly useful in nesting sites of vulnerable species where disturbance should be minimised, in colonies in remote locations with restricted access, or limited workforce. The calibration curves presented here may prove valuable for generating timing estimates of key life-history events for these two skua species, which can be used for productivity assessments, censuses and phenological studies.

Acknowledgements

Danish National Research Foundation supported Center for Macroecology, Evolution and Climate (DNRF96); and Research Council Faroe Islands, Statoil Faroe Islands, and Selskab for Arktisk Forskning og Teknologi (Society for Arctic Research and Technology) supported this study. Field assistance was provided by Kees H. T. Schreven, Høgni Hammer, Levi H. Hammer, Eyð H. Hammer, Jógvan Hammer and Jens-Kjeld Jensen. Land use permits granted by the board of land owners for Southern and Northern Kirkjuhagi, Fugloy. Harry Jensen granted the permit for land use in Skúvoy. Animal work was approved by the Danish Nature Agency by permission to the Copenhagen Bird Ringing Centre (J.nr. SN 302-009). We thank Bo Markussen at the Data Science Lab, University of Copenhagen, for statistics consultation and Robert W. Furness and the two reviewers for valuable comments on the manuscript.

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Appendix 1.

Trendlines for individual eggs with more than three measurements for each species: