

# Is the reduced incubation time for B-eggs in Rockhopper Penguins *Eudyptes chrysocome* linked to egg density variation?

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**Abstract** Crested penguins (genus *Eudyptes*) present a unique reversed egg-size dimorphism and hatching asynchrony, with the larger second-laid egg (B-egg) hatching before the smaller first-laid egg (A-egg). Both a higher water vapour conductance and parental favouritism during incubation could explain the shorter incubation period for the B-egg than for the A-egg. Because the incubation period is increased by the presence of a sibling for A-eggs, but not for B-eggs, and because both egg categories have the same incubation period when they are incubated alone, it has been suggested that the difference in incubation period was largely driven by the parental favouritism for B-eggs during incubation. We tested whether A- and B-eggs show a difference in laying density, density at the beginning of incubation and in density decrease during incubation according to the presence of a sibling. Although density at the start of incubation was significantly higher for B-eggs than for A-eggs, the decrease in density during incubation had the same slope for both egg categories. Moreover, the presence of a sibling did not influence densities. We additionally provide two equations that allow

the back-dating of laying dates for a clutch of Southern-Rockhopper Penguin (*Eudyptes c. chrysocome*) and we discuss the precision of the method ( $3.04 \pm 2.29$  days for A-eggs and  $2.73 \pm 2.10$  days for B-eggs) for penguins which are increasingly being used as marine environmental sentinels.

**Keywords** Egg category · Egg measurements · Southern Rockhopper Penguin · Hatching asynchrony · Hatching date · Laying date

## Introduction

Unique among birds, crested penguins (genus *Eudyptes*) exhibit both reversed egg-size dimorphism and reversed hatching asynchrony (Warham 1975; Williams 1995; St Clair 1998), with the larger second-laid egg (B-egg) hatching before the smaller first-laid egg (A-egg). As a result, even though both eggs can hatch, the chick from the A-egg generally dies of starvation within days of hatching because of sibling competition from the larger B-egg chick (Gwynn 1953).

Eggs consistently lose weight (due to water loss) during incubation (Rahn and Ar 1974), and penguin eggs lose about 13% of their initial mass during the incubation period (Rahn and Hammel 1982; Massaro and Davis 2005). To explain the shorter incubation period for B-eggs of crested penguins, Massaro and Davis (2005) found that water vapour conductance was greater in B- than in A-eggs and suggested that the lower eggshell porosity of A-eggs limits oxygen available to the embryo, prolonging their development in relation to the development of their siblings (B-eggs). The difference in shell porosity between the eggs could thus contribute to the reversed hatching asynchrony.

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However, Poisbleau et al. (2008) observed that the incubation period increased significantly when a sibling-egg was present for A-eggs, but not B-eggs, and that incubation periods were similar for A- and B-eggs when incubated alone. As a result, Poisbleau et al. (2008) suggested that the difference in incubation period between A- and B-eggs is not caused by egg composition, but could be explained by parental favoritism for B-eggs during incubation (see Massaro and Davis 2004). Indeed, crested penguins could adjust the degree of hatching asynchrony by manipulating egg positions (i.e., placing the smaller A-egg in the supposedly thermally disadvantaged anterior position).

According to these observations, differences in water vapor conductance between the A- and B-eggs of crested penguins could partially explain the hatching asynchrony through a difference in density decrease. The density decrease could also be affected by the presence of a sibling-egg during incubation. Therefore, one could predict that there is not only a difference in density decrease between A- and B-eggs (with the decrease being higher for B-eggs), but also a difference in density decrease between A-eggs incubated alone or with a sibling.

Although we are not aware of any study describing the decrease in egg density for penguins, several investigators have used laying and hatching dates as explanatory parameters for chick growth, chick survival, or breeding success in these species (e.g., van Heezik et al. 1993; Viñuela et al. 1996; Moreno et al. 1997). Nevertheless, it is possible to age eggs and to estimate both their laying and hatching dates from their density with only one visit to the nest (Furness and Furness 1981). Although this useful method could significantly reduce disturbance to nests by researchers during incubation, it has not been used as much as it could. One likely reason for this is that, because of inter-species variation in egg shape and composition, a calibration curve must be constructed for each species before this method can be used (Furness and Furness 1981).

The aim of this study is to investigate the effect of the density decrease on the incubation duration, and hence the hatching asynchrony. Because A-eggs have a longer incubation period than B-eggs when they are incubated together, but a similar incubation period when they are incubated alone, we expect a higher density decrease (1) for B-eggs than for A-eggs whether siblings were present or absent, and (2) for A-eggs when incubated alone than when incubated with a sibling. We first test whether A- and B-eggs of Southern Rockhopper Penguins (*Eudyptes c. chrysocome*) show a difference in laying density, density at the beginning of incubation and in density decrease during incubation according to the presence of a sibling. Secondly, we aim to provide an equation that allows the back-dating of laying dates for a clutch of Southern Rockhopper Penguins.

## Methods

Our study was conducted at the Settlement colony at New Island Nature Reserve, Falkland Islands (51°43'S, 61°17'W) during October and November 2006. Female Rockhopper Penguins lay two eggs. The first (the A-egg), laid 4 days before the second (the B-egg), is around 70% in mass of the B-egg (Warham 1975; Williams 1995). Both parents share the incubation (32–34 days) in two alternating long shifts (Raya Rey et al. 2007). From the return of the first male Rockhopper Penguin from the sea after the winter, we visited the colony daily to monitor a sample of 100 nests. When a new egg was detected in a nest, we marked it, measured its length and breadth to the nearest 0.1 mm with vernier calipers, and weighed it to the nearest 0.1 g using a digital balance. As previously described in this species, the laying period was highly synchronised, ranging between 27 October and 10 November, with less than 5% of new A-eggs found after 5 November (see Poisbleau et al. 2008).

Within these 100 nests, we artificially created 24 A- and 22 B-nests by removing their B- or A-egg, respectively (see Poisbleau et al. 2008). Collected eggs were subsequently used for hormone analyses (see Poisbleau et al. 2009a, b). The other 54 nests contained both A- and B-eggs at the beginning of incubation. Afterwards, we checked nests daily and weighed eggs regularly (mean interval of  $6 \pm 3$  (SD) days,  $n = 427$  intervals). This dataset contained only the eggs that hatched, excluding any collected ( $n = 46$ ), sterile ( $n = 9$ ), cracked ( $n = 1$ ) or lost ( $n = 44$ ). We included eggs having a sibling who did not hatch (i.e. not included in the present dataset) but we did not include eggs which lost their sibling before the end of incubation ( $n = 4$ ). Therefore, the final dataset comprised 525 measurements for 96 eggs (46 A-eggs and 50 B-eggs) from 70 different nests. Thirty-two A-eggs and 30 B-eggs had a sibling during the whole incubation period.

We calculated egg volumes ( $V$ , in  $\text{cm}^3$ ) using their length ( $L$ , in cm) and breadth ( $B$ , in cm) as  $V = L \times B^2 \times 0.512$  according to Stonehouse (1966). We determined egg densities ( $D$ , in  $\text{g}/\text{cm}^3$ ) using the equation  $D = M/V$ , where  $M$  is the egg mass (in g). Because all data were normally distributed (one-sample Kolmogorov–Smirnov test, all  $P > 0.14$ ), we tested initial differences between A- and B-eggs using a general linear model (GLM) with egg category (A- or B-egg) as a fixed factor. We also performed GLMs to analyse the effect of egg category (A- or B-egg) and sibling presence throughout incubation on the rate of density decrease during incubation. In these models, egg density (dependent variable) was predicted by egg category (fixed factor), age since the beginning of incubation (covariate), sibling presence (fixed factor) and all interactions. To account for the measures made on both eggs from the same nest, we used nest as a random factor within each GLM. To

allow the future estimation of egg age from density, we used linear regressions of age (assessed by direct observation of laying for all of them) against density to obtain equations for both egg categories, and used the 95% confidence interval of the residuals to assess the precision of this estimation. During incubation, to control for the unequal number of measurements between eggs and to avoid pseudo-replication, we randomly selected the same number of measurements (i.e. four) for each egg and used only these four measurements in the GLM and regression analyses. All statistical analyses were performed using SPSS 15.0. Values are presented as means  $\pm$  SD.

## Results

B-eggs were significantly larger and heavier than A-eggs at laying; however, there was no significant difference in laying density between A- and B-eggs (Table 1). With incubation starting only after the laying of the B-egg, A-eggs (being then  $4.13 \pm 0.54$  days old,  $n = 46$ ) had already lost  $0.53 \pm 0.31$  g ( $n = 46$ ) before the start of incubation. Therefore, A-eggs had a significantly lower initial density than B-eggs at the start of incubation ( $1.080 \pm 0.013$  g/cm<sup>3</sup>,  $n = 46$  vs  $1.092 \pm 0.014$  g/cm<sup>3</sup>,  $n = 50$ ,  $F_{1,25} = 17.5$ ,  $P < 0.001$ ,  $n = 43$ ).

During incubation, the density of Rockhopper Penguin eggs decreased linearly with age for both A- and B-eggs (age effect in Table 2 and Fig. 1), and densities of A- and B-eggs at the beginning of incubation (i.e. y-intercepts) were significantly different (egg category effect in Table 2 and see Fig. 1). However, because slopes were not significantly different between linear regressions for A- and B-eggs (interaction between egg category and age in Table 2), they had a similar density decrease rate (Fig. 1). Moreover, the presence of a sibling during incubation did not significantly influence the decrease in density, either directly or in interaction with egg category (Table 2).

We derived the two following equations for estimating the age since the beginning of incubation (i.e. since laying

of the B-egg) of Rockhopper Penguin A- and B-eggs from their density:

$$\begin{aligned} \text{Age (days)} = & -202.35 \text{ Density (g/cm}^3) \\ & + 221.29 \quad (F_{1,182} = 987.004, P < 0.001) \\ & \text{for A-eggs} \end{aligned}$$

and

$$\begin{aligned} \text{Age (days)} = & -213.19 \text{ Density (g/cm}^3) \\ & + 235.09 \quad (F_{1,198} = 1330.268, P < 0.001) \\ & \text{for B-eggs.} \end{aligned}$$

The mean precision was  $3.04 \pm 2.29$  days for A-eggs and  $2.73 \pm 2.10$  days for B-eggs, with 95% of the estimations having an error lower than  $\pm 7$  days for A-eggs (Fig. 2a) and  $\pm 6.5$  days for B-eggs (Fig. 2b).

## Discussion

Because A-eggs have a longer incubation period than B-eggs when they are incubated together, but a similar incubation period when they are incubated alone, we expected a higher density decrease (1) for B-eggs than for A-eggs whether siblings were present or absent, and (2) for A-eggs when incubated alone than when incubated with a sibling. The present results failed to confirm these hypotheses. We found that A- and B-eggs had a similar density decrease (the same slope) during incubation and the presence of a sibling did not influence this density decrease rate for either the A- or the B-egg. Therefore, it appears that neither the lower water vapor conductance of A-eggs nor parental favoritism for B-eggs had an effect on density decrease. Nevertheless, the effect of the presence of a sibling on density decrease approached significance ( $P = 0.071$ ; Table 2) compared to the egg category effect ( $P = 0.771$ ). This could suggest that the presence of a sibling affects the density decrease whatever the egg category. Additional studies are necessary to test this in more detail.

**Table 1** Size, volume, mass, and density of A- and B-eggs of Southern Rockhopper Penguins (*Eudyptes c. chrysocome*) at the time of laying ( $n = 46$  for A-eggs and  $n = 50$  for B-eggs, mean  $\pm$  SD)

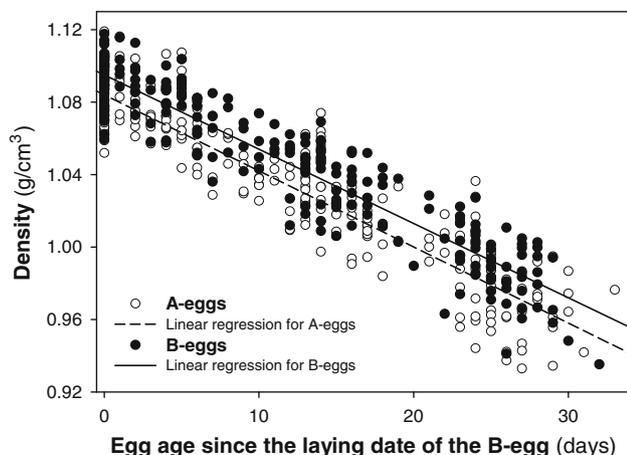
	A-egg	B-egg	Difference
Length (mm)	$65.65 \pm 3.07$	$70.58 \pm 2.20$	$F_{1,25} = 101.3, P < 0.001$
Breadth (mm)	$49.74 \pm 1.93$	$54.32 \pm 1.62$	$F_{1,25} = 497.3, P < 0.001$
Volume (cm <sup>3</sup> )	$83.45 \pm 9.37$	$106.83 \pm 8.51$	$F_{1,25} = 409.9, P < 0.001$
Laying mass (g)	$90.61 \pm 9.86$	$116.71 \pm 9.57$	$F_{1,25} = 447.7, P < 0.001$
Laying density (g/cm <sup>3</sup> )	$1.086 \pm 0.013$	$1.092 \pm 0.014$	$F_{1,25} = 3.7, P = 0.066$

GLMs with egg category as fixed factor and nest as random factor were used to test for differences between A- and B-eggs for each variable

**Table 2** Analyses of the decrease in egg density during incubation

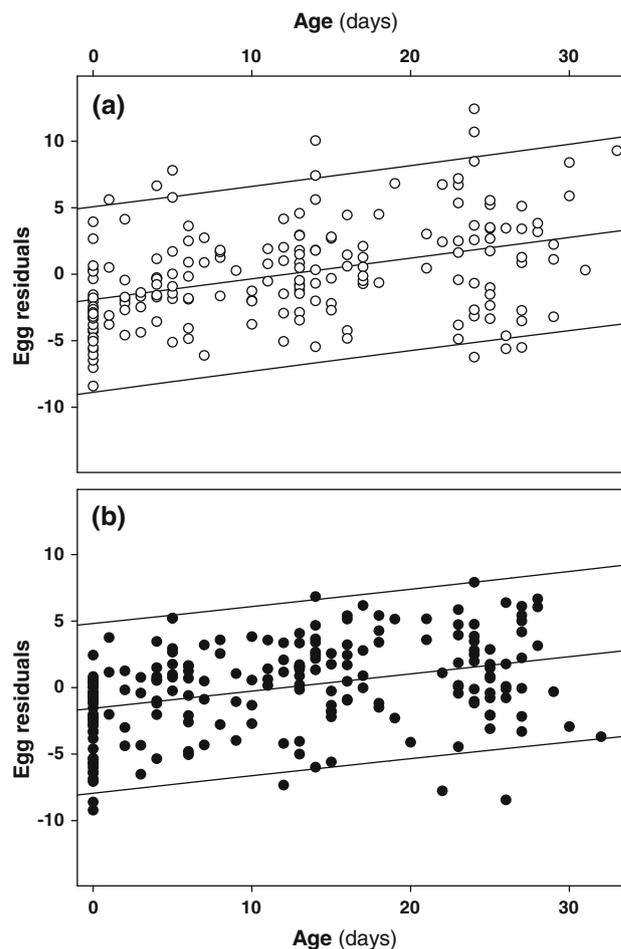
Effect	$F_{1,308}$	$P$	$\eta_p^2$
Age	<b>5,315.4</b>	<b>&lt;0.001</b>	<b>0.945</b>
Egg category (A- or B-egg)	<b>32.3</b>	<b>&lt;0.001</b>	<b>0.095</b>
Egg category $\times$ age	0.09	0.77	<0.001
Sibling presence (0 or 1)	0.81	0.37	0.003
Sibling presence $\times$ age	3.3	0.071	0.011
Egg category $\times$ sibling presence $\times$ age	0.006	0.94	<0.001

Results of a GLM on egg density with age since the beginning of incubation as a covariate, egg category (A- or B-eggs) and sibling presence throughout incubation (0 or 1) as fixed factors and nest as a random factor. Significant  $P$  values are marked in bold. As a measure of effect sizes we used partial Eta-Square values ( $\eta_p^2$ ; i.e. the proportion of the effect + error variance that is attributable to the effect, see [http://web.uccs.edu/lbecker/SPSS/glm\\_effectsize.htm](http://web.uccs.edu/lbecker/SPSS/glm_effectsize.htm)) in case of variables and covariates tested with a GLM



**Fig. 1** Egg density ( $\text{g}/\text{cm}^3$ ) as a function of age (days) since the laying of the B-egg (i.e. the beginning of incubation) by Southern Rockhopper Penguins (*Eudyptes c. chrysocome*). A-egg (open circle): density =  $-0.0042 \text{ age} + 1.084$ , and B-egg (filled circle):  $-0.0041 \text{ age} + 1.095$

Many authors have studied the mysterious role of the A-egg in crested penguins, but the results are often contradictory (see Burger and Williams 1979; Lamey 1990; St Clair 1998; Poisbleau et al. 2008). At present, it remains unclear whether egg composition, parental incubation favoritism, or both produce the reversed hatching asynchrony. The use of the density decrease tested in this study failed to confirm any of these hypotheses. However, we showed previously that Rockhopper Penguins in the Falkland Islands are sometimes able to raise two chicks to fledging (Poisbleau et al. 2008), which is apparently unique for this species. Moreover, among all the populations of Rockhopper Penguins, the least dimorphic eggs are those from the Falkland Islands population (volume ratio A-egg/B-egg = 0.79 in the Falkland Islands compared to 0.68–0.77 for other populations;



**Fig. 2** Residuals and 95% confidence intervals of the regression between density and age since the laying of the B-egg for **a** A-eggs (open circle) and **b** B-eggs (filled circle)

Demongin et al. 2010). Furthermore, this population has the second least dimorphic eggs of all crested penguins after the Fiordland Penguin (*Eudyptes pachyrhynchus*) (volume ratio = 0.85; Williams 1995). Consequently, the differences between A- and B-eggs in the Falkland Islands population might not be strong enough to be detected by the method of the density decrease. This study is based on only one breeding season, and we may argue that egg density could vary between different years. However, in avian species, egg size appears to be an individual characteristic, the effects of age, female body condition or food availability having only a small effect on this trait (Christians 2002). As a consequence of this inter-population and inter-individual variation in egg measurements, the proposed equations are to be considered and used with caution and should (perhaps) be restricted to the colonies at the Falkland Islands.

Because B-eggs had a higher initial density than A-eggs at the beginning of incubation, two different equations are necessary to estimate egg age since the beginning of incubation (laying date for B-eggs) from egg density. Because

A-eggs are laid  $4.1 (\pm 0.5)$  days before B-eggs (see “Results” and Poisbleau et al. 2008), the age since laying of an A-egg may be estimated by adding 4 days to its estimated age since the beginning of incubation. The presence of a sibling does not need to be accounted for in the calculation. With this method, we can age an egg with a mean accuracy of about  $\pm 3$  days, but with still 95% of the estimations having an error up to  $\pm 7$  days. This value represents around 20% of the incubation period with an associated maximum error reaching up to 40%. This lack of accuracy could not be explained reasonably by observer or equipment effects because the same observer (L.D.) carried out all of the measurements and always used the same scale. Neither were temporal desertions of the nest responsible, as incubating birds never left their nest during incubation, except for quick exchanges between parents. We observed that the variability in egg shape between Rockhopper Penguin females (i.e. between clutches, irrespectively of egg category) is large (observed width/length ratio range: 0.66–0.86), and this may have caused a lack of accuracy in the calculation of egg volumes (Furness and Furness 1981). Calculating the egg volume from shell thickness and mass could increase the accuracy of the volume calculation (see Paganelli et al. 1974; Rahn and Paganelli 1989). However, this equation requires knowing initial egg mass of each egg and then to be present at laying. Alternative methods to measure egg sizes, such as water displacement (Hoyt 1976) or photographic techniques (Bridge et al. 2007), require more complex methodologies and thus are hardly applicable under (our) field conditions. When both eggs are in the nest, one useful possibility to reduce the error in the determination of the beginning of incubation is to estimate this date for both A- and B-egg using the equations provided here and then to consider the range of overlap to be the most plausible period. Nevertheless, we additionally propose to use these equations to determine breeding dates at the population scale. Indeed, since penguin colonies are often located in places of difficult access, a sufficiently large sample obtained from only one visit to the breeding site could provide very valuable information for population monitoring of penguins, a group of species having many advantages as marine environmental sentinels (Boersma 2008).

## Zusammenfassung

Steht die kürzere Bebrütungszeit bei B-Eiern von Felsenpinguinen *Eudyptes chrysocome* in Verbindung mit Unterschieden in der Ei-Dichte?

Pinguine der Gattung *Eudyptes* zeigen einen einzigartigen Ei-Größe-Dimorphismus und eine Asynchronie beim Schlupf, wobei das größere und später gelegte Ei (B-Ei) vor

dem früher gelegten kleineren Ei (A-Ei) schlüpft. Sowohl eine höhere Wasserdampf-Leitfähigkeit als auch eine elterliche Präferenz während des Brütens könnte die kürzere Bebrütungszeit für die B-Eier im Vergleich zu den A-Eiern erklären. Weil sich die Bebrütungszeit für A-, nicht aber für B-Eier in Anwesenheit eines Geschwisters erhöht und weil beide Ei-Typen gleich lang bebrütet werden, wenn sie allein bebrütet werden, wurde angenommen, dass der Unterschied in der Bebrütungsdauer im wesentlichen von einer elterlichen Bevorzugung der B-Eier herrührt. Wir untersuchten, ob A- und B-Eier einen Unterschied in der Dichte zeigen zum Zeitpunkt des Legens, des Beginns der Bebrütung und in der Dichteabnahme während des Brütens unter Berücksichtigung des Vorhandenseins eines Geschwisters. Obwohl die Dichte zum Anfang des Brütens für B-Eier signifikant höher war als für A-Eier, war die Dichteabnahme für beide Ei-Typen gleich. Darüber hinaus beeinflusste das Vorhandensein eines Geschwisters die Dichten nicht. Außerdem stellen wir zwei Gleichungen vor, die es erlauben, das Legedatum eines Geleges beim südlichen Felsenpinguin zu bestimmen und wir diskutieren die Genauigkeit dieser Methode ( $3.04 \pm 2.29$  Tage für A-Eier und  $2.73 \pm 2.10$  Tage für B-Eier) für Pinguine, die zunehmend als marine Indikatorarten Verwendung finden.

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