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Geographical variation in egg size dimorphism in rockhopper penguins

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Abstract All crested penguins present a unique reversed hatching asynchrony: the larger second-laid egg (B-egg) hatches before the smaller first-laid egg (A-egg). Although both eggs often hatch, the A-chick generally dies of starvation within days after hatching. However, within rockhopper penguins, the population at the Falkland Islands is unique in that some birds manage to raise both chicks. Although it has been suggested that the egg size dimorphism between A- and B-eggs may explain how long both eggs and chicks survive, this hypothesis has never been explicitly tested. We expect that both eggs are retained longer in the less dimorphic clutches than in the more dimorphic ones. In this paper, we have compiled egg measurements for three rockhopper penguin species (*Eudyptes chrysocome*, *E. filholi* and *E. moseleyi*) in order to compare the intra-clutch egg size dimorphism among these species. Furthermore, we have collected new data to compare egg size dimorphism between two populations of *E. chrysocome* (Falkland Islands versus Staten Island). A-egg volumes are more variable between species and populations than B-egg volumes. *E. chrysocome* and especially the population from the Falkland Islands produces the largest A-eggs and the least dimorphic eggs. Nevertheless, as differences in A-egg volumes between species and between the populations of Falkland Islands and Staten Island are stronger and more significant than differences in egg dimorphism, we suggest that A-egg volume, more than egg dimorphism, could be one of the factors influencing the prevalence of twins. A large A-egg and/or reduced egg dimorphism is probably necessary to enable rockhopper penguins to raise two chicks, but other reasons may also be involved which enable them to keep both eggs and chicks.

Keywords Rockhopper penguin · Egg dimorphism · Geographical variation · Chick survival

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Introduction

All crested penguins (genus *Eudyptes*) exhibit brood reduction: two eggs are laid but only one chick usually fledges (Stonehouse 1975). They also present a unique reversed hatching asynchrony among birds (Warham 1975): the larger second-laid egg (B-egg) hatches before the smaller first-laid egg (A-egg). Although both eggs often hatch, the A-chick generally dies of starvation within days after hatching (Gwyn 1953; Lamey 1990). The eggs of erect-crested *E. sclateri*, macaroni *E. chrysolophus* and royal *E. schlegeli* penguins are highly dimorphic and generally only one egg hatches as the A-egg is usually lost before the B-egg is laid (Warham 1975; Williams 1980a; St Clair et al. 1995). In comparison, Snares *E. robustus* and Fiordland *E. pachyrhynchus* penguins have been shown to be able to raise occasionally two chicks because their eggs are the

least size dimorphic within the genus *Eudyptes* (Stonehouse 1971). Indeed, McLean (2000) has suggested that Fiordland penguins could raise twins in 12% of nests during unusually good years, and at least one pair over 114 nests fledged two chicks (S.M. Phillipson *in* McLean 2000).

Rockhopper penguins have a circumpolar distribution and are the most widespread of the crested penguins (Fig. 1); they breed on many isolated islands of the Southern oceans (Marchant and Higgins 1990). Like all penguins, they have a high site fidelity to their natal colonies (e.g. Williams 1995). Based on genetic evidence (Jouventin et al. 2006), BirdLife International formally separated in 2007 the Northern rockhopper penguin *E. moseleyi* from the Southern rockhopper penguin *E. chrysocome* including the sub-species *chrysocome* and *filholi*. To go one step further, a separation into three different species based on molecular, geological and palaeoceanographic data has recently been proposed and validated (Banks et al. 2006; de Dinechin et al. 2009). Therefore, the three rockhopper penguin taxa should now be considered and treated as three different species: *E. moseleyi*, *E. chrysocome* and *E. filholi*.

Only two cases of *E. filholi* raising two chicks have been documented at Campbell Island (52°33′S, 169°09′E) (Marchant and Higgins 1990) and none for *E. moseleyi* (Williams 1995). However, at the Falkland Islands

(52°00′S, 59°30′W) it is not unusual for *E. chrysocome* to raise two chicks (Strange 1982; Pütz et al. 2001; Clausen and Pütz 2002). In 2006–2007, for example, three of 114 nests (2.6%) raised two chicks until fledging (Poisbleau et al. 2008). In the same breeding population, more than 80% of pairs retained both eggs until at least one hatched successfully (Strange 1982; Lamey 1993). This proportion is higher than for all other rockhopper penguin populations (20–60%, Williams 1995). According to the suggestion made by Stonehouse (1971), a possible reason why *E. chrysocome* in the Falkland Islands retains both eggs until hatching is that their eggs are less dimorphic than those of the other rockhopper penguin populations. If this is the case, the size difference between both chicks at hatching should also be reduced, with the chick size at hatching being correlated with egg size (Warham 1975; Reid and Boersma 1990; Alquati et al. 2007). These cumulative conditions may be necessary to enable A-chicks to compete with B-chicks, the latter being generally favoured by the hatching asynchrony (Lamey 1990; St. Clair 1996).

To test this hypothesis, we have compiled egg measurements for the three species of rockhopper penguins from different populations, and we also provide new egg measurements for *E. chrysocome*. We first compared the extent of intra-clutch egg dimorphism between species testing whether

Fig. 1 Distribution map for *E. moseleyi*, *E. filholi* and *E. chrysocome*. *Circle E. moseleyi*, *Triangle E. filholi*, *Square E. chrysocome*. Each symbol represents one population. Staten Island is one of the South American islands. No data are available for Auckland, Antipodes and Bounty islands (*white triangles* without name)
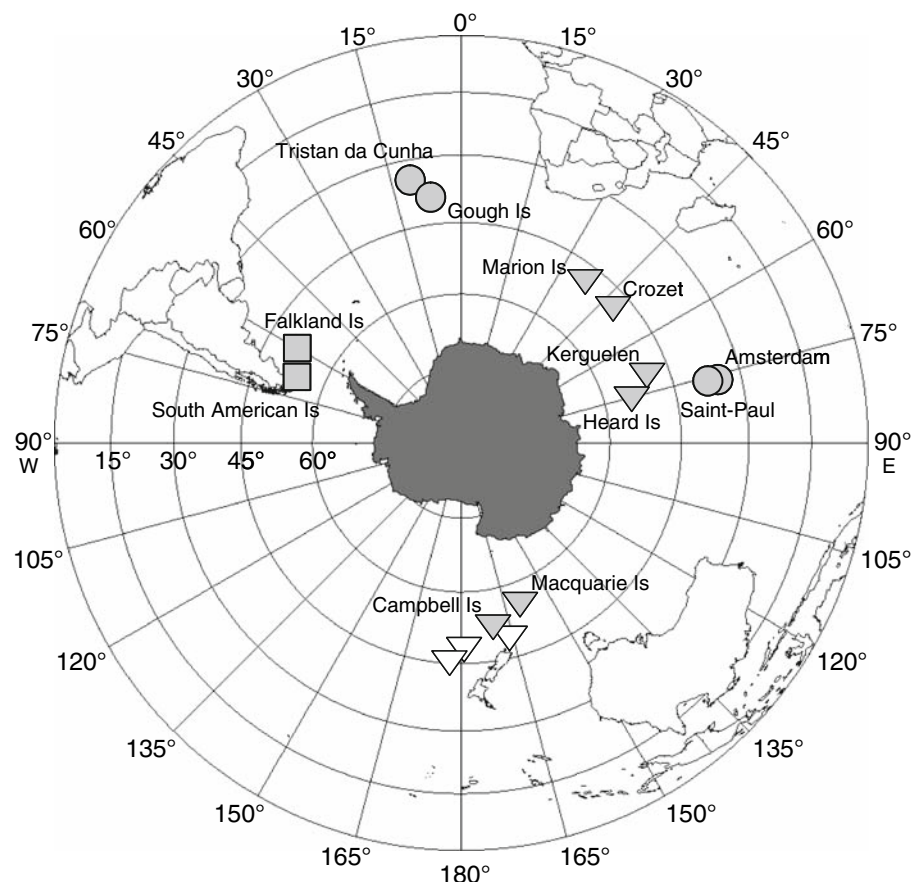
E. chrysocome had lower dimorphic clutches than the two other species. We further examined whether the Falkland Islands population of *E. chrysocome* had lower dimorphic clutches than the Staten Island population of the same species.

Methods

Egg data were obtained both from field studies and the published literature. As it is extremely rare to obtain individual data from the literature, we, here, dealt with the means supplied by the different studies. In the Falkland Islands, the study was carried out in the "Settlement Colony" on New Island (51°43′S, 61°17′W) during three consecutive austral summers from October 2006 to November 2008. The colony has approximately 5,000 breeding pairs of *E. chrysocome*. When a new egg was detected, we marked it with a unique code, measured its length and breadth to the nearest 0.1 mm with vernier callipers and weighed it to the nearest 0.1 g with a digital balance (for more information see

Poisbleau et al. 2008). In Argentina, the fieldwork was conducted during the austral summer 1998–1999 at Bahía Franklin, Staten Island (54°50′S, 64°40.5′W), in a sub-colony located above the Arroyo Pedro where >500 pairs breed (Schiavini 2000).

We calculated egg volume (cm^3) as length (cm) × breadth^2 (cm) × 0.512 (Stonehouse 1966). Although the fresh mass of the egg may be a better indicator of its total size than its volume, the mass data available in the literature are incomplete for a comparison. We, therefore, used egg volumes and the ratio between A-egg volume and B-egg to compare eggs between species and the two *E. chrysocome* populations.

Two studies present a ratio well outside the range of the other populations (Table 1) and should be considered with caution. For Tristan da Cunha (Williams 1995), the sample size is reduced. Furthermore, contradictory reports on the clutch size of this population have led to the belief that rockhopper penguins lay three eggs, some having unusual size (Williams 1981b); these data come from secondary

Table 1 Egg measurements for *E. moseleyis*, *E. filholi* and *E. chrysocome* (mean)

Species	Population	Sample size		Length (mm)		Breadth (mm)		Mass (g)		Volume (cm^3)		Volume ratio	
		A-egg	B-egg	A-egg	B-egg	A-egg	B-egg	A-egg	B-egg	A-egg	B-egg	A-egg/B-egg	
moseleyi	Tristan da Cunha	8	8	63.9	71.8	46.6	56.1	–	–	71.0	115.7	0.61	Williams (1995)*
filholi	Crozet	23	18	61.2	72.0	47.9	53.7	–	–	71.9	106.3	0.68	Despin et al. (1972)
filholi	Heard Is	9	9	63.6	71.7	46.2	52.9	76.1	110.8	69.5	102.7	0.68	Gwynn (1953)**
filholi	Heard Is	13	13	63.1	71.3	46.5	52.5	77.2	110.2	69.9	100.6	0.69	Woehler and Gilbert (1990)
filholi	Marion Is	122	119	62.3	70.2	46.8	52.9	–	–	69.9	100.6	0.69	Williams (1981b)
filholi	Marion Is	9	9	63.5	71.3	47.7	53.9	80.5	115.6	74.0	106.1	0.70	Rand (1954)
filholi	Macquarie Is	7	11	64.3	71.5	47.5	53.8	80.9	114.2	74.3	106.0	0.70	Gwynn (1953)
moseleyi	Gough Is	30	30	65.2	73.0	49.2	55.2	–	–	80.8	113.9	0.71	Williams (1980b)
filholi	Campbell Is	41	39	63.5	70.5	48.0	53.7	79.6	112.0	74.9	104.1	0.72	Marchant and Higgins (1990)
filholi	Crozet and Kerguelen	31	31	63.5	70.3	47.4	52.9	79.0	108.7	73.0	100.7	0.73	Tollu (1978)
filholi	Crozet	20	20	63.5	70.4	47.3	52.4	–	–	72.7	99.0	0.73	Stahl et al. 1985
moseleyi	Amsterdam	44	44	63.2	70.1	49.7	54.6	–	–	79.9	107.0	0.75	Duroselle and Tollu (1977)
moseleyi	Amsterdam and Saint-Paul	49	49	63.4	70.4	50.0	54.6	88.4	118.4	81.2	107.5	0.76	Tollu (1978)
chrysocome	Staten Is	14	14	63.8	69.5	49.4	54.2	–	–	80.2	104.7	0.77	This study
filholi	Macquarie Is	141	130	64.0	71.0	49.0	53.0	88.2	115.2	78.7	102.1	0.77	Hull et al. (2004)
chrysocome	Falkland Is	545	394	66.1	71.1	50.2	54.6	92.5	118.4	85.4	108.7	0.79	This study
chrysocome	Falkland Is	10	10	67.2	70.7	49.4	52.5	–	–	84.0	99.8	0.84	Strange (1982)*

Populations are classed according to increasing volume ratio between A-egg volume and B-egg volume. No data are available for Auckland, Antipodes and Bounty islands

* Studies removed from the statistical analysis (see Methods)

** Gwynn (1953) used two types of clutches for weight and measurements: nine clutches were "unselected" and two "additional clutches were selected because of their unusual sizes or shapes". In the present paper, we have kept only the nine "unselected" clutches as the two additional clutches were not appropriate for our aims

literature without indication of the original source and are not verifiable. In the study of Strange (1982), the eggs were not marked as soon as they were laid; hence it is possible that some eggs have rolled from one nest to another, a frequent case in the New Island colony (pers. obs.), misrepresenting the identity of A- and B-eggs. Moreover, another study with a large sample size in the same colony provided the same egg mass as the present study (A-egg: 91.8 ± 9.36 g, $n = 119$; B-egg: 118.6 ± 9.27 g, $n = 112$; St. Clair 1996). Therefore, we did not include these two studies in the statistical analysis.

All egg measurements followed a normal distribution (tested with Kolmogorov–Smirnov tests). After examining the correlation of the volumes between A- and B-egg within the three species with a Pearson's correlation, we performed General Linear Models (GLM) based on type III sum of squares with species as fixed factor to test the difference in volumes (A-egg volume, B-egg volume and ratio between both volumes) among the three species. We used post-hoc Tukey HSD tests with species as the grouping variable to highlight the difference between species. Second, we compared egg measurements of the two populations with available individual measurements (i.e. *E. chrysocome* at Staten and at Falkland Islands) using independent-samples t-tests. To obtain comparable sample sizes for the two populations in t-tests, we randomly selected 14 A-eggs and 14 B-eggs from the Falkland Islands population.

Results

Comparison between species

Published data for *E. moseleyi*, *E. filholi* and *E. chrysocome* as well as data from this study are summarised in Table 1
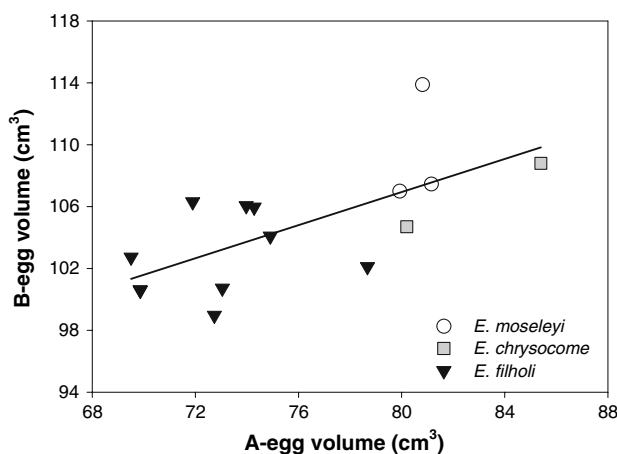
Fig. 2 Relation between the volume of A-eggs and B-eggs for *E. moseleyi*, *E. filholi* and *E. chrysocome*. Each data point represents one population (see Table 1)

for each population. Mean volumes of A- and B-eggs are positively correlated within these three species (Pearson Correlation, $r = 0.675$, $P = 0.006$, $N = 15$ studies, Fig. 2). The coefficient of variation (CV) between populations is 6.50% for A-egg volumes and 3.73% for B-egg volumes. This result shows that A-egg volumes are more variable between different populations for the three species than B-egg volumes (Fig. 2).

We observed a significant difference between species in A-egg volumes, in B-egg volumes and in the ratio between
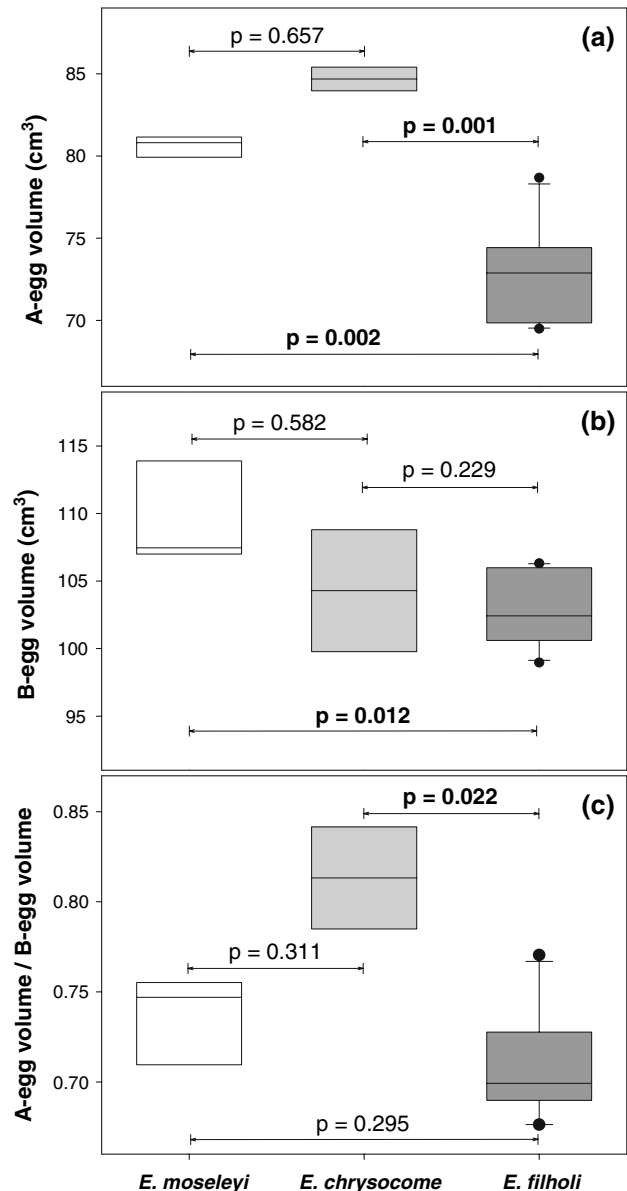
Fig. 3 Differences in **a** A-egg volumes, **b** B-egg volumes and **c** ratio between these both volumes according to species. *Boxes* show medians, 25 and 75% quartiles; *whiskers* indicate the range between the 10th and 90th percentiles. *Filled circle* data outside the 10th and 90th percentiles. Sample sizes are 3, 2 and 10, respectively. Results of post-hoc Tukey HSD tests with species as the grouping variable are presented above or under respective boxes. Significant P-values are marked bold

Table 2 Egg measurements for *E. chrysocome* (mean ± SD)

Population	Sample size		Length (mm)		Breadth (mm)		Volume (cm^3)		Mass (g)	
	A-egg	B-egg	A-egg	B-egg	A-egg	B-egg	A-egg	B-egg	A-egg	B-egg
Staten Is	14	14	63.8 ± 3.73	69.5 ± 2.81	49.4 ± 2.49	54.2 ± 1.94	80.2 ± 12.58	104.7 ± 10.97	–	–
Falkland Is	545	394	66.1 ± 2.69	71.1 ± 2.55	50.2 ± 1.72	54.6 ± 1.67	85.4 ± 8.13	108.7 ± 9.11	92.5 ± 8.68	118.4 ± 9.97
T-test			$t_{26} = 2.737$ $P = 0.011$	$t_{26} = 1.081$ $P = 0.290$	$t_{26} = 2.287$ $P = 0.031$	$t_{26} = 0.843$ $P = 0.407$	$t_{26} = 2.489$ $P = 0.020$	$t_{26} = 0.987$ $P = 0.333$		

We compare egg lengths, breadths and volumes of the two populations of this study using independent-samples *t*-tests. While means and SD are given for the entire dataset, we randomly selected 14 A-eggs and 14 B-eggs from the Falkland Islands population in order to obtain comparable sample sizes for the two populations in *t*-tests

both volumes, the differences in A-egg volumes being more significant than the differences in B-egg volumes and in the ratio ($F_{1,12} = 17.722$ $P < 0.001$, $F_{1,12} = 6.576$, $P = 0.012$ and $F_{1,12} = 5.408$, $P = 0.021$, respectively). *E. filholi* has the smallest eggs (Fig. 3a and b). *E. chrysocome* has the largest A-eggs (Fig. 3a), while *E. moseleyi* has the largest B-eggs (Fig. 3b). As a result, *E. chrysocome* exhibiting the highest ratio between A-egg volume and B-egg volume has the least dimorphic clutches, while *E. filholi* exhibiting the lowest ratio has the most dimorphic clutches (Fig. 3c).

Egg characteristics and prevalence of twins
in two populations of *E. chrysocome*

Egg lengths, breadths, volumes and fresh masses of *E. chrysocome* collected in this study are given in Table 2. A-eggs from the Falkland Islands had significantly greater lengths, breadths and, therefore, also volumes than A-eggs from Staten Island (Table 2, Fig. 4a). However, there was no significant difference between both populations for any of the characteristics of B-eggs (Table 2, Fig. 4b). As a result, even if the ratio between A-egg volume and B-egg volume seems higher for the Falkland Islands than for Staten Island (Fig. 4c), this difference is not significant ($t_{26} = 1.777$, $P = 0.250$).

For the 2002–2003 and 2003–2004 breeding seasons at Staten Island, the breeding success was, respectively, 31 and 23% (Raya Rey et al. 2007). These rates were low and no twins were raised. In 2006–2007 in the Falkland Islands, the breeding success was 69% for 54 nests, and 2.6% of 114 nests raised two chicks until fledging (Poisbleau et al. 2008).

Discussion

Variations in volumes

Interestingly, although mean volumes of A- and B-eggs were positively correlated within rockhopper penguins, we observed a higher coefficient of variation in volumes for A-eggs than for B-eggs. We also observed more significant difference between species in A-egg volumes than in B-egg volumes. Similarly, differences between the Falkland Islands and the Staten Island populations were significant for A-eggs, while they were not for B-eggs. All these observations indicate that B-egg volumes are more consistent between species and populations than A-egg volumes are, the latter being twice more variable than B-eggs. This also means that differences in volume dimorphism between A- and B-eggs are mainly driven by variation in A-egg volumes.

Intra-clutch egg dimorphism between species

As a result of differences in egg volumes, we observed that *E. filholi* had the most dimorphic eggs while *E. chrysocome* has the least dimorphic ones. Among all populations of rockhopper penguins (Table 1), we similarly noted that the least dimorphic eggs were those from the Falkland Island population. In this study, the A-egg averaged 0.79 of the B-egg volume, a value between the Snares penguin and the Fiordland penguin species (0.77 and 0.85, respectively, Warham 1974a, b; Massaro and Davis 2005). This population has, therefore, the second least dimorphic eggs of all crested penguins after the Fiordland penguin. The trend for *E. chrysocome* to have less dimorphic eggs than others was also confirmed by the data from Staten Island that were equalled only by those of one study from Macquarie Island (Hull et al. 2004), although another study from this population found a much higher egg dimorphism (Gwynn 1953).

The species with highly dimorphic eggs (erect-crested, macaroni and royal penguins; A-egg/B-egg volume: 0.55–0.64; Gwynn 1953; Williams 1995) almost never keep both eggs until hatching, while the species with more equal eggs (Snares and Fiordland penguins; 0.77–0.85, Warham 1974a, b) often hatch two chicks (Warham 1975; St. Clair et al. 1995). Rockhopper penguins present an intriguing intermediate pattern with significant differences between species and populations.
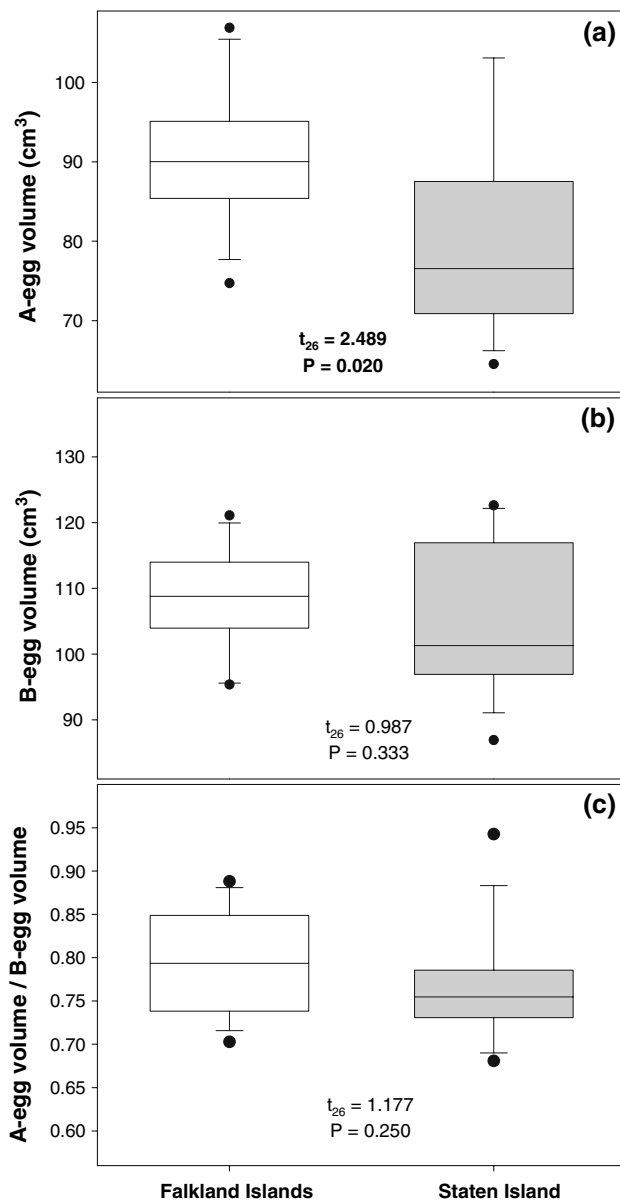
Fig. 4 Differences in **a** A-egg volumes, **b** B-egg volumes and **c** ratio between both of these volumes between Falkland Islands and Staten Island. *Boxes* show medians, 25 and 75% quartiles; *whiskers* indicate the range between the 10th and 90th percentiles. *Filled circle* data outside the 10th and 90th percentiles. Sample sizes are 14 for both populations. Results of *t*-tests with population as the grouping variable are presented under respective boxes. Significant *P*-values are marked bold

Interestingly, *E. chrysocome* from the Falkland Islands presents the higher hatching rate of both eggs and is the only rockhopper population likely to rear two chicks (Lamey 1993; Williams 1995; Poisbleau et al. 2008). Our results fit well the Stonehouse's hypothesis that intra-clutch egg dimorphism could influence the prevalence of twins in a population (Stonehouse 1971).

The fact that the difference in egg dimorphism between the *E. chrysocome* populations from Falkland Islands and Staten Island was not significant does not corroborate this

hypothesis. However, A-eggs from the Falkland Islands population are significantly larger than A-eggs from Staten Island, while no significant difference was detected for B-eggs. Moreover, the A-eggs from the Falkland Islands were the largest of all the populations. This result could explain the higher hatching rate for A-eggs and the higher survival rate for A-chicks in this population. Thus, we can suppose that the A-egg volume, whether in combination with the B-egg volume through the egg dimorphism or not, could be a factor influencing the prevalence of twins in a population.

In most avian species, egg size appears to be an individual characteristic, with the effects of age, female body condition or food availability having only a small effect on this trait (Christians 2002). Although we cannot exclude that the accumulation of these effects could bias egg size, especially when sample size is small, the potential impact is probably slight and not measurable, and therefore does not affect the overall patterns described here. Many hypotheses have been proposed to explain why the first-laid egg is smaller than the second (see for example Williams 1980a; Johnson et al. 1987; Williams 1989; Johnson and Bednarz 1989; Williams 1990; Lamey 1993; St. Clair 1998 and see Williams 1995 for a review), but no consensus was reached yet. Williams (1990) suggested that egg-size dimorphism in the genus *Eudyptes* tends to be greater at higher latitudes. If this hypothesis is valid for rockhopper penguins, *E. moseleyi* should have the least dimorphic eggs and *E. chrysocome* the most dimorphic, which is clearly not supported by our results.

Prevalence of twins

Factors explaining the amount of time two chicks may coexist are numerous. The most important one is probably the degree of hatching asynchrony (Williams 1980a; Williams 1981a; Lamey 1990): the larger the size difference between both chicks, the less the smallest chick may survive. This difference may be reduced if the egg dimorphism is low and/or if the time elapsed between both hatchings is short (Seddon and van Heezik 1991a, b; Williams and Croxall 1991; Moreno et al. 1994). When twins are present in the nest, an important factor in their survival may be the ability of the parents to provide a substantially greater amount of food than if they were rearing only one chick (Warham 1974b). In this context, the distance to foraging grounds and the food availability are probably important determinants for the reproductive performance and these may vary annually (Raya Rey et al. 2007). Differences in the degree of predation, often by skuas, are also responsible for egg and chick loss and may vary strongly between colonies (Williams 1980b; St. Clair and St. Clair 1996).

Given all of these factors, even if both eggs are able to hatch in many populations of rockhopper penguins, the probability that twins reach the fledging age remains low. It is possible that the overall situation would be more favourable in the Falkland Islands than in other populations. Thus, the breeding success for *E. moseleyi* and *E. filholi* is usually less than 0.61 chicks per breeding pair (Williams 1980b; Williams 1995), while the average per year can be as high as 0.95 chick per breeding pair in the Falkland Islands (Huin 2005). Although rearing twins to fledging is undoubtedly a rare event in rockhopper penguins, this phenomenon should receive more attention and it can no longer be stated that it never occurs. Clearly, the study of the prevalence of twins in other populations could help to clarify our understanding of the reversed hatching asynchrony in the crested penguins.

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