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ARTICLE

Relaying propensity and characteristics of replacement clutches of Leach's Storm-Petrels (*Oceanodroma leucorhoa*)

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Abstract: Animals with low fecundity, such as seabirds, invest heavily into one or a few eggs per breeding attempt. The loss of these eggs can mean that individuals abandon breeding or invest in a replacement clutch. However, the ability of females to replace clutches may be costly and so replacement clutches may be delayed and they may differ in nutrient content. Replacement clutches are rarely documented conclusively in storm-petrels, and most avian replacement clutches are smaller and differ in composition from original eggs. We removed eggs from Leach's Storm-Petrel (*Oceanodroma leucorhoa* (Vieillot, 1818)) nests on Gull Island, Witless Bay, Newfoundland and Labrador, Canada, and monitored nest sites for replacement clutches. Leach's Storm-Petrels use locally acquired nutrients to lay a single egg that weighs 20% of a female's body mass. Nearly 70% of pairs (17/26) produced a replacement egg after 22 days and two pairs produced a third egg after a further 21 days. Replacement eggs were nearly identical to original clutches, except for small decreases in length (2%) and volume (3%). We found that Leach's Storm-Petrels were able to acquire sufficient nutrients to produce a second (and in two cases, a third) egg, likely from endogenous nutrients, but delays of 3–6 weeks in breeding may have detrimental effects on fledging success and offspring survival.

Key words: egg composition, exogenous nutrients, income breeding, Leach's Storm-Petrel, *Oceanodroma leucorhoa*, Witless Bay.

Résumé : Les animaux présentant une faible fécondité, comme les oiseaux marins, investissent beaucoup dans la production d'un ou quelques œufs par tentative de reproduction. La perte de ces œufs peut signifier que les individus abandonnent la reproduction ou investissent dans une couvée de remplacement. La capacité des femelles de remplacer les couvées peut toutefois être coûteuse, de sorte que les couvées de remplacement peuvent être retardées et avoir un contenu en nutriments différent. Des couvées de remplacement ont rarement été documentées de manière conclusive chez les océanites, et la plupart des couvées de remplacement d'oiseaux se distinguent des couvées initiales par leur taille plus petite et la composition différente de leurs œufs. Nous avons retiré les œufs de nids d'océanites culblancs (*Oceanodroma leucorhoa* (Vieillot, 1818)) dans l'île Gull de la baie Witless, à Terre-Neuve-et-Labrador (Canada), et surveillé l'apparition de couvées de remplacement dans les nids. Les océanites utilisent des nutriments acquis localement pour pondre un unique œuf faisant 20 % de la masse corporelle de la femelle. Près de 70 % des couples (17/26) ont produit un œuf de remplacement après 22 jours et deux couples ont produit un troisième œuf 21 jours plus tard. Les œufs de remplacement étaient presque identiques à ceux des couvées initiales, à l'exception de légères diminutions de leur longueur (2 %) et de leur volume (3 %). Si nous avons constaté que les océanites culblancs étaient capables d'acquérir suffisamment de nutriments pour produire un deuxième (et, dans deux cas, un troisième) œuf, vraisemblablement à partir de nutriments endogènes, le fait que la reproduction est retardée de 3 à 6 semaines pourrait avoir des effets adverses sur le succès d'envol et la survie des oisillons. [Traduit par la Rédaction]

Mots-clés : composition des œufs, nutriments exogènes, reproduction reposant sur les revenus, océanite culblanc, *Oceanodroma leucorhoa*, baie Witless.

Introduction

Among species with low fecundity, the production of a few (or even a single) large eggs relative to the female's body size is energetically expensive (Monaghan and Nager 1997; Monaghan et al. 1998; Nager et al. 2000). The loss of such a large investment produces two possible outcomes: abandon breeding in a given year or invest again in a replacement clutch. This decision will be a function of an individual's age (as well as that of its mate), the availability of resources to attempt breeding again, and the timing of egg loss (within the incubation period and the breeding season resource pulse, especially at higher latitudes; Hegyi and Sasvári 1998; Hipfner et al. 2008).

Individuals that choose to reinvest in a replacement clutch face additional constraints of a shorter period in which to complete breeding, mismatching chicks' provisioning requirements with seasonal prey availability, and lower chick survival (Hipfner et al. 1999, 2003; Gasparini et al. 2006; Hipfner 2008; Jakubas and Wojczulanis-Jakubas 2013). Females laying extra eggs may compromise their chicks' immunocompetence or survival (Sorci et al. 1997). Replacement clutch production may also be hindered by the time required by females to acquire the necessary nutrients (Astheimer 1986) or the catabolism of nutrients from body reserves (Hobson 2006). Species that use exogenous nutrients for egg production ("income breeders") must spend considerable time and energy foraging to form a new egg (Drent and Daan 1980; Thomas 1983). Replacement clutches are often smaller, with proportionally smaller yolks and thinner eggshells, which can contribute to decreased offspring quality and survival (Nager et al. 2000; Hipfner et al. 2003; Jakubas and Wojczulanis-Jakubas 2013).

Procellariiform seabirds are among the least fecund birds—females lay a single egg every 1–2 years, representing up to 25% of

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their body mass (Rahn and Whittow 1988; Brooke 2004). Adults have a late age of first breeding, high survival, and long lifespans (Warham 1990; Brooke 2004). Females embark on lengthy "exodus" flights for several weeks between mating and laying to acquire the necessary nutrients for egg production, and replacement clutches are generally rare (Warham 1990). These factors are expected to reduce the likelihood of a replacement clutch or to result in eggs with less nutrient investment.

Prey availability will also affect the ability of females to acquire sufficient nutrients to form a replacement clutch, and the composition of any replacement eggs themselves (Cairns 1987; Ardia et al. 2006). This will, however, be mediated by individual quality, behaviour, and the willingness of the mate to attempt breeding again following egg loss (Naves et al. 2007; Ludwig and Becker 2008; Ismar et al. 2010).

Among the Procellariiformes, relaying is most prevalent in the storm-petrels (Hydrobatidae), since they do not generally undertake an exodus flight prior to laying like other groups do such as the Procellariidae (Warham 1990). Leach's Storm-Petrel (*Oceanodroma leucorhoa* (Vieillot, 1818)) is a highly pelagic, cosmopolitan species in northern temperate waters of the Atlantic and Pacific oceans that subsists on a diet of mesopelagic fish and euphausiids (Linton 1979; Huntington et al. 1996; Hedd et al. 2009). Adults breed at large offshore colonies, where females use exogenous resources to lay an egg that represents 22% of their body mass, and both parents care for the egg and chick for approximately 13–16 weeks (Montevecchi et al. 1983; Watanuki 1985; Huntington et al. 1996; Bond and Diamond 2010). Replacement clutches laid by Leach's Storm-Petrels have been reported previously (Wilbur 1969; Morse and Buchheister 1979; Huntington et al. 1996), but the identity of the pairs was not always known (e.g., Campos and Granadeiro 1999). Experimental removal of eggs can induce large proportions of females to lay again (Huntington et al. 1996). Our objectives were to examine the relaying propensity and timing of Leach's Storm-Petrels following experimental egg removal and to compare the composition of first and replacement clutches in relation to each other, as well as the size of the female. We predicted that replacement eggs would be smaller, contain a smaller lipid fraction, and potentially have thinner eggshells than original clutches.

Materials and methods

We collected fresh eggs (<7 days) from 10 to 15 June 2012 at Gull Island, Witless Bay Ecological Reserve, Newfoundland and Labrador (47°15′N, 52°46′W), after capturing and banding both parents in 25 burrows. Adult birds were weighed and measured, and a small blood sample taken from the brachial vein and placed on sterile filter paper for genetic sexing (see below). After eggs were collected, we visited burrows every 7 days to check for replacement eggs. Once a replacement egg was found, the burrow was checked daily until we also found an adult (no more than 3 days), indicating that the egg was a replacement egg and not a different breeding pair that had taken over the nest site. We assumed pairs would not divorce within the season given their biparental care for young and their long-lasting pair bonds (Warham 1990; Brooke 2004). Leach's Storm-Petrels lay a single egg per clutch, so we designated the first egg "A", the second (first replacement) egg "B", and the third (second replacement) egg "C".

Egg length and breadth were measured to the nearest 0.1 mm using dial callipers, and measurement error assessed by repeated measurements of eggs was 0.1 mm for both length and breadth. We determined egg volume using the formula and coefficient for birds in general: volume (mL) = length × breadth^3 × 0.51 (Hoyt 1979).

Egg mass, to the nearest 0.1 g, was determined using an electronic balance, and measurement error assessed by repeated measuring of the same egg was <0.1 g. Eggs were then boiled for 15 min, placed in sterile polyethylene bags, and frozen until further analysis. Boiling allows for easier separation of the egg components, with only marginal loss of water from albumen (Ricklefs 1982).

We also examined which pairs attempted breeding the following year (2013) by visiting burrows once during incubation (17 June 2013) and once during chick rearing (17 August 2013).

Egg composition

To determine egg composition, egg components (albumen, yolk, shell + membrane) were separated and weighed to the nearest 0.01 g using an electronic balance. Albumen loses water with boiling, so we took the mass of the albumen to be the fresh egg mass minus the sum of the other components (which do not lose water; Ricklefs 1982; Williams et al. 1982; Hipfner et al. 2003). We measured the thickness of eggshell at the egg's equator using a micrometer to the nearest 0.01 mm, and measurement error was ±0.01 mm ($n = 4$). Components were dried (to a constant mass) for 48 h using a freeze dryer and then weighed again to determine percent moisture and dry mass. The lipid fraction of yolk was extracted using repeated washes of a 2:1 chloroform:methanol solution (Bligh and Dyer 1959) and weighed as described above.

We determined the energetic content of eggs following Montevecchi et al. (1983) and assumed that carbohydrates were a negligible component of Leach's Storm-Petrel eggs. We assigned a value of 20 kJ/g to the protein fraction of albumen and yolk and 38 kJ/g for yolk lipid (Ricklefs 1974).

Molecular determination of sex

DNA was extracted from the filter paper using the DNeasy Blood and Tissue Kit (Qiagen Inc., Toronto, Ontario, Canada) and following the manufacturer's protocol. Sex was determined by amplifying the chromo-helicase-DNA 1 gene (*CHD1*), which is linked to both sex chromosomes, but when amplified with primers 2550F and 2718R (Fridolfsson and Ellegren 1999), different-sized bands are produced for each sex chromosome. Polymerase chain reactions (PCRs) were carried out in a volume of 25 μL containing 1× Promega PCR master mix (Promega Corp., Madison, Wisconsin, USA), 2.5 μmol/L of each primer, and approximately 25 ng of DNA. Thermal cycling was performed in a GeneAmp 9700 (Applied Biosystems Inc., Foster City, California, USA) under the following conditions: 95 °C for 5 min, followed by 30 cycles of 94 °C for 1 min, 45 °C for 1 min, and 72 °C for 1.5 min, and a final extension at 72 °C for 5 min. PCR products were stained (EZ-Vision Three DNA dye; Amresco LLC, Solon, Ohio, USA) and visualized on a 2% agarose gel by electrophoresis. Individuals with two bands (*CHD1W* and *CHD1Z*, approximately 450 and 650 bp in size, respectively) were scored as female and those with one band (*CHD1W* band only) were scored as male.

Statistical methods

We tested for differences in egg composition between A-eggs and B-eggs only, as only three C-eggs were found (Table 1). We used paired t tests to examine differences in egg size and composition in R version 3.0.2 (R Core Team 2014). We also tested for differences in A-eggs that were replaced and in A-eggs that were not replaced using unpaired t tests. A generalized linear model with binomial error structure was used to test for the relationship between the number of eggs laid and breeding the following year. We determined whether female condition, assessed by body mass measured to the nearest 2 g with a spring balance, differed based on how many eggs they laid using an analysis of variance (ANOVA). Differences were considered significant when $p < 0.05$.

Results

We captured one male and one female in each nest, and all replacement eggs were attended by one of these originally banded individuals. Of the 25 nests, 17 (68%) produced a replacement egg (B-egg) and 3 (12%) produced a second replacement egg (C-egg). B-eggs appeared 22 ± 4 days (range: 15–29 days) after the first egg

Table 1. The composition of A-, B-, and C-eggs (mean ± SD) from Leach's Storm-Petrels (*Oceanodroma leucorhoa*) breeding on Gull Island, Witless Bay, Newfoundland and Labrador, in 2012.

	A-egg (not replaced)	A-egg (replaced)	B-egg	C-egg	$t_{[23]}$*	p	$t_{[16]}$†	p
n	8	17	17	3				
Whole egg								
Length (mm)	32.8±1.0	33.3±0.9	32.7±0.9	32.4±1.4	1.51	0.14	5.54	<0.001
Breadth (mm)	23.8±0.4	23.8±0.7	23.7±0.7	24.0±0.4	0.15	0.88	0.93	0.36
Volume (mL)	9.5±0.4	9.7±0.8	9.4±0.8	9.6±0.1	0.82	0.42	2.75	0.014
Fresh mass (g)	10.2±0.3	10.4±0.8	10.2±0.9	10.3‡	0.41	0.69	1.45	0.17
Percent female body mass	19.6±1.8	19.8±2.0	19.4±1.4	19.1‡	0.26	0.80	1.55	0.14
Percent moisture§	69.7±2.9	68.4±3.5	70.2±1.9	66.7±3.9	–0.9	0.36	–1.60	0.13
Eggshell								
Mass (g)	0.84±0.10	0.90±0.13	0.87±0.12	0.87±0.17	1.05	0.30	0.83	0.42
Mass (% of whole egg)	8.6±1.5	9.3±1.1	8.9±1.1	9.9±1.7	1.18	0.25	1.22	0.24
Thickness (mm)	0.17±0.01	0.18±0.01	0.17±0.01	0.18±0.01	0.72	0.48	1.31	0.21
Percent moisture§	28.7±6.0	28.6±6.7	29.6±3.6	29.2±4.7	–0.02	0.99	–0.54	0.60
Albumen								
Mass (g)	4.28±0.98	4.02±0.97	4.45±1.06	3.75±0.96	–1.22	0.24	–1.07	0.30
Mass (% of whole egg)	43.2±7.5	41.3±7.8	44.8±6.4	42.2±5.3	–0.59	0.56	–1.34	0.20
Percent moisture§	81.8±5.7	81.6±6.4	84.4±3.4	82.3±4.0	–0.10	0.91	–1.53	0.14
Yolk								
Mass (g)	4.71±0.63	4.75±0.64	4.50±0.43	4.17±0.11	0.11	0.91	1.37	0.19
Mass (% of whole egg)	48.1±6.5	49.5±7.5	46.3±5.9	47.8±5.0	0.43	0.67	1.37	0.19
Percent moisture§	64.9±4.9	63.8±3.3	63.7±2.7	60.5±2.1	–0.75	0.46	–0.05	0.96
Percent lipid (% of wet mass)	24.4±3.9	24.9±2.8	24.5±2.3	26.2±1.6	0.35	0.73	0.27	0.79
Percent lipid (% of dry mass)	71.0±3.5	69.1±4.1	68.3±3.5	69.0±0.1	–1.12	0.27	0.39	0.70
Yolk:albumen (wet mass)	1.17±0.39	1.28±0.47	1.08±0.34	1.15±0.04	0.56	0.58	1.31	0.21

*Student's t test comparing "replaced" and "not replaced" A-eggs.

†Paired t test for replaced A-eggs and B-eggs.

‡n = 1.

§Percent moisture as a weighted average of the percent moisture of each component.

was removed; C-eggs appeared 21 ± 0 days after the second egg was removed. The following year (2013), there were breeding attempts by the same birds in 10/25 nests (40%), with new adults found in 2 nests, and in one case, found paired with the previous year's female. The number of eggs laid by a pair had no effect on their breeding attempt the following year ($F_{[1,23]} = 0.55$, $p = 0.47$). Female mass was not related to the number of eggs laid ($F_{[2,22]} = 0.36$, $p = 0.70$).

Composition of original and replacement clutches

There were no differences between A-eggs that were replaced and A-eggs that were not replaced (Table 1). There was no significant difference in any measure of egg size or composition, with the exception of egg length and egg volume (which is a function of length). B-eggs were 2% shorter and 3% smaller than A-eggs (Table 1). The energy content was similar between A-eggs (68.69 ± 6.43 kJ) and B-eggs (65.78 ± 6.59 kJ) ($t_{[40]} = 1.43$, $p = 0.17$).

Discussion

We found relatively high rates of replacement clutches in Leach's Storm-Petrel nests with experimentally removed eggs. These results are similar to those reported from Great Island, Witless Bay, Newfoundland and Labrador, where 78% of females who lost their egg within the first week replaced it 10–20 days later (Huntington et al. 1996). Unlike Huntington et al. (1996), however, we found little difference in the size and no difference in the energetic investment of first and replacement eggs.

Among other storm-petrels, relaying has been little studied, except for Fork-tailed Storm-Petrels (*Oceanodroma furcata* (Gmelin, 1789)) where 11/36 nests (31%) where the original egg was removed resulted in a replacement clutch 21 days following removal. Fork-tailed Storm-Petrel replacement eggs were significantly smaller than first eggs, but no different from A-eggs laid late in the season (Boersma et al. 1980). Other studies suggest that replacement clutches may occur, but are relatively rare in storm-petrels, or could not be proven conclusively (Harris 1969; Beck and Brown 1972; Everett 1991; Mínguez 1997; McClelland 2007), or did not find any evidence of clutch replacement (Wasilewski 1986; Underwood and Bunce 2004). Instances of two-egg clutches in storm-petrels are likely the result of two inexperienced females laying a single egg each, or females' recognition of one infertile egg that is not ejected from the nest (Plant 1989; Marchant and Higgins 1990; Ryan et al. 2007).

It takes roughly 15–16 days for Leach's Storm-Petrels to form an egg yolk, determined using Astheimer and Grau's (1990) general equation for Procellariiformes, and a mean egg mass of 10.5 g. There is little intraspecific variation around these estimates (Astheimer and Grau 1990), indicating that rapid yolk development in Leach's Storm-Petrel starts almost immediately after egg loss, with little to no lag time, and this fixed rate is responsible for the bulk of the time required to produce a replacement clutch.

We found no difference in the composition of A-eggs and B-eggs. In contrast to Montevecchi et al. (1983), who found that wet albumen was greater than wet yolk (yolk:albumen mass ratio of 0.71 ± 0.10), we found considerably more variation (range of yolk:albumen mass ratio between 0.74 and 2.55), with yolk being larger than albumen in 25/45 (56%) of A-eggs and B-eggs combined. The energetic content of eggs in 2012 (67.52 ± 6.58 kJ), however, was only slightly less than those analysed in the 1978 (72.42 ± 5.54 kJ) (Montevecchi et al. 1983). The eggs are otherwise nearly identical (Table 1).

The proportion of yolk fits with the semialtricial development of storm-petrels (Sotherland and Rahn 1987; Brooke 2004), which is generally found throughout the Procellariiformes, especially those that lay smaller eggs (Williams 1994; Deeming 2007). And as would be expected, there was a high proportion of yolk to total egg mass, which is typical of small procellariiform eggs (Warham 1983).

Leach's Storm-Petrels are resilient to egg loss, and can produce replacement eggs relatively rapidly and in a majority of cases. The

3-week delay in breeding, however, may affect chick survival and condition (Ydenberg 1989; Gaston 1998; Hipfner and Gaston 1999; Gaston 2003), as eggs that hatch later in the season are less likely to result in a fledged chick or a chick in good condition, and later fledging chicks or chicks in poorer condition often have reduced juvenile survival compared with early-hatching individuals (Brooke 1978; Ollason and Dunnet 1986; Morrison et al. 2009; Krist 2011). As income breeders (Bond and Diamond 2010), most Leach's Storm-Petrels were able to acquire the nutrients required to produce a replacement clutch nearly identical in composition to their original egg. No studies have, to our knowledge, found such similar replacement clutches and our results suggest that nutrients were not limiting in Leach's Storm-Petrel reproduction.

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