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Short Note
The timing of egg loss in macaroni penguins

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Introduction

Brood reduction, in which last-hatched chicks compete poorly for food and only survive in years when resources are sufficient to raise two chicks, is common among bird species (Lack 1947, Ricklefs 1965). Some species show obligate brood reduction in which one or more offspring do not survive and may serve only as an insurance policy (Mock 1984, Forbes & Mock 2000). All crested penguin species, genus *Eudyptes*, show obligate brood reduction (Warham 1975), first-laid eggs are smaller than second-laid eggs and egg size dimorphism is extreme among bird species (Gwynn 1953, Warham 1975, Slagsvold *et al.* 1984). The most dimorphic eggs of all crested penguin species are found in the macaroni penguin *Eudyptes chrysolophus* Brandt (Warham 1975). The first egg is always lost before hatching and generally before the second egg is laid; this species therefore undergoes clutch reduction (Gwynn 1953, Williams 1980, Williams 1989). The timing of egg loss is very synchronous with most eggs being lost on the day before or the day the second egg is laid (Williams 1980, Williams 1989). In some cases at least, egg loss is by deliberate rejection from the nest (Downes 1955).

In this study the timing of egg loss in macaroni penguins is investigated in order to try to understand the mechanisms involved in egg loss. Using an experimental approach, clutch size is artificially increased at two different stages of laying to determine the effects on egg loss. First, clutch size is artificially increased at the start of laying by adding an experimental egg to nests to investigate the effects on timing of loss of both eggs. Second, clutch size is artificially increased to two at the end of laying by adding an experimental egg to nests to investigate whether macaroni penguins will incubate two eggs.

Methods

The study was conducted at the macaroni penguin colony on Goldcrest Point, Bird Island, South Georgia (38°02'W, 54°00'S), in November and December 1998. Study nests were marked and checked daily from early November to determine laying dates of first and second eggs. Each egg was weighed to the nearest 1 g using a Pesola spring balance, and maximum length and breadth were measured to the nearest 0.1 mm using callipers. Egg size, an estimate of volume, was calculated as length x (breadth)^2. Each egg was marked with indelible ink with an individual code. Each nest was assigned to one of three groups randomly in rotation to keep samples evenly distributed over the laying period. Experimental first and second eggs were collected from elsewhere in the colony and were kept in an insulated box at ambient temperature until required.

The three groups were as follows. First, a control group in which nests were checked daily for eggs ($n = 24$). Second, a group in which clutch size was increased early by adding an experimental second egg to the nest the day after the first egg was laid ($n = 12$). Third, a group in which the clutch size was increased late by adding an experimental first egg to the nest the day after the second egg was laid ($n = 12$). Sample sizes in each group were small due to the difficulties found in collecting and keeping experimental second eggs when they were required.

Once all eggs were laid and experimental eggs added, the study nests were checked daily for the first week, then every two days until hatching so that failures could be recorded. Differences in egg mass and size were investigated between the three groups to ensure that all groups contained representative nests. ANOVAs were carried out on variables that conformed to the appropriate assumptions: i.e. were normally distributed and showed heterogeneity of variance (Zar 1984). Non-parametric Kruskal-Wallis tests were used for variables that did not conform to the above assumptions. Statistical analysis was carried out using Minitab.

Results

There were no differences among the three groups in mass of first egg ($F_{2,47} = 0.98$, $P = 0.38$), size of first egg ($F_{2,47} = 0.04$, $P = 0.97$), mass of second egg ($F_{2,47} = 0.90$, $P = 0.41$), size of second egg ($F_{2,47} = 0.08$, $P = 0.93$), egg size ratio ($H = 1.45$, $P = 0.48$, df = 2) or laying interval ($F_{2,47} = 0.23$, $P = 0.80$) (Table I).

Table I. First and second egg data from all ($n = 48$) study nests. See Methods for definition of egg size. 'No. days first egg' is the number of days for which the first laid egg survived.

	Mean	s d	Range
First egg mass / g	94	9	76–110
First egg size / cm^2	172	17	134–207
No. days first egg	3	1	1–5
Second egg mass / g	145	12	120–172
Second egg size / cm^2	274	20	225–311
Egg mass ratio	1.60	0.1	1.2–1.9
Laying interval / days	4	0.6	2–5

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Table II. Timing of egg loss shown by the percentages of eggs lost on each day from control (n = 36) and experimental (n = 12) nests.

No. days from second egg laying	-4	-3	-2	-1	0	1
First egg loss, control group	6	8	6	36	44	0
First egg loss, experimental group	0	0	0	67	33	0
Second egg loss, experimental group	0	0	9	33	58	0

The timing of egg loss in the early increased clutch size group compared to the control group is shown in Table II. The late increased group was included in the control group as the treatment on the two groups was the same at this stage. In all cases, most egg loss (more than 80%) occurred the day before or the day of laying of the natural second egg, regardless of the size of the egg lost. In no case did either the first or added second egg survive until after the natural second egg was laid. These proportions are significantly higher than would be expected if eggs were lost at random during the laying interval (Kolmogorov-Smirnov $P < 0.01$). There was no difference in the number of days that the natural first egg and experimental second egg were retained in the nest (paired $t = 0.69$, $P = 0.50$). The addition of the experimental second egg had no effect on the laying interval compared with the control group ($t = 0.4$, $P = 0.69$, df = 46).

In the late increased clutch size group, one nest failed after four days. The failure rate in this group was 8%, a value similar to a failure rate of 22% in the remaining 36 nests in the study. Of the remaining 11 nests in the late increased clutch size group, the extra first egg was retained for between 1 and 15 days (mean = 6, s d = 5); in four of these the extra egg was recorded in the nest for only one day.

Discussion

The egg sizes and egg size ratio recorded in this study agree with previous data collected from macaroni penguins (Gwynn 1953, Downes 1955, Williams 1990) and there were no difference between the groups in the experiment. The timing of first egg loss was also similar to previous studies (Williams 1980, Williams 1989), and all first eggs were lost before the second eggs were laid. An early increase in clutch had no effect on the timing of egg loss: both experimental second eggs and natural first eggs were lost at the same time. Williams (1989) suggested that the laying of the second egg acts as a stimulus for the loss of the first egg. The early addition of an experimental second egg did not provoke early first egg loss, but this is perhaps not surprising as simple experimental addition of eggs does not mimic the hormonal changes involved in laying (Williams 1989, St Clair *et al.* 1995). The interesting observation here, however, is that all eggs are lost on or around laying of the penguin's own second egg. The cue for egg loss appears to be the arrival of the second egg and results in loss of all other eggs in the nest, regardless of their size, and therefore possibly their potential value. Further work is required to determine the proximate mechanism that regulates egg loss and the functional mechanisms that result in it. In particular, the cause of egg loss, not investigated in this study, needs to be determined.

A late increase in clutch size had no effect on failure rate in the nests, although sample sizes were small to detect such a change. The additional egg remained in the nest for a very short period, however, compared to the incubation period of 35 days (Williams & Croxall 1991). This suggests that there are costs to having two eggs in the nest of a macaroni penguin. It was not observed whether the extra egg was removed from the nest deliberately by the incubating penguins (St Clair *et al.* 1995) or lost accidentally due to neglect during incubation, although the latter would be surprising as the birds lie fully prone over the eggs (Williams 1989). However, it was observed that the smaller experimental egg was always in the anterior incubation position in the nest. Also, in no case was the natural egg lost and the experimental egg kept. This study shows that the arrival and/or presence of the macaroni penguins' own second egg leads to any other egg being lost. The mechanisms responsible for this still need to be determined.

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