

Clutch Size in *Eudyptes* Penguins

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Apart from the King *Aptenodytes patagonica* and Emperor *A. forsteri* Penguins which lay only a single egg, all other penguins normally lay a clutch of two eggs. However, there is considerable variation in this rule. In the pygoscelid penguins three-egg clutches are infrequent but are regularly reported, especially if the first egg is lost before the second is laid (Bagshawe 1938; Gwynn 1953; Sladen 1958) and single-egg clutches may be laid if the first clutch has been lost (Murphy 1936; Gwynn 1953). Sladen's data indicate that single-egg clutches may be not unusual in the Adelie Penguin *P. adeliae*. However, the only other penguin, apart from *Aptenodytes*, known to lay single-egg clutches with any frequency is the Yellow-eyed Penguin *Megadyptes antipodes*, in which 38% of two-year-olds, breeding for the first time, were found to lay single-egg clutches (Richdale 1957). Richdale also noted that the eggs of two-year-old birds were significantly lighter and narrower than those of older birds, but that there was no clear difference in length (Richdale 1949). Gwynn (1953) found that in the Gentoo Penguin *Pygoscelis papua* the first egg was generally slightly larger than the second; this appears to be the case in all other penguins apart from *Eudyptes* (Williams 1981).

The *Eudyptes* penguins normally lay a two-egg clutch in which the first (the A egg) is markedly smaller than the second (the B egg), an arrangement which appears to be unique in the avian world (Gwynn 1953; Warham 1975; Williams 1980a, 1981). It should be noted that several early observers believed that the Macaroni Penguin *E. chrysolophus* laid single-egg clutches (Murphy 1936; Falla 1937) but it is now accepted that this was because colonies were visited when most A eggs had already been lost (Williams 1982). Similarly, early statements that the Rockhopper Penguin (*E. chrysosome*) normally laid three-egg clutches are now discredited, though this was firmly believed by the Tristan da Cunha islanders, who harvest the eggs; Murphy (1936) cites somewhat contradictory reports on the subject and, as Williams (1981) has pointed out, the belief that the Rockhopper lays three-egg clutches has persisted mainly on the basis of Elliott's

statement in 1957: 'despite Hagen's doubts, C/3 is much more usual than C/2'. However, Williams implies that Elliott may have had second thoughts on the subject and his own work on Gough Island (Williams 1980b) and on Tristan da Cunha (Williams & Stone 1981) has laid this error firmly to rest. At the latter island, out of 410 clutches examined, only four contained three eggs and the possibility that one of these was derived from a neighbouring nest could not be excluded. The belief in three-egg clutches undoubtedly arose from the Rockhoppers' tendency to include in their own clutch eggs displaced from neighbouring nests, a frequent occurrence, especially if the colony was the subject of much disturbance.

Though all students of *Eudyptes* since Gwynn (1953), e.g. Warham (1975) and Williams (1981), agree that the normal *Eudyptes* clutch is two eggs, Gwynn has stated that true three-egg clutches occasionally occur in the Rockhopper and in the Macaroni (in Downes *et al.* 1959). On the other hand, Williams (1981) has legitimately questioned the existence of three-egg clutches, as he never encountered one in his extensive experience of these two species and Warham (*in litt.*) never saw one in his own detailed study of the Rockhopper at Macquarie Island (Warham 1963). It is the purpose of this paper to consider such evidence.

For complete confidence in the validity of a three-egg clutch, it would be necessary to have a clutch from a marked female under daily observation and each egg marked as laid from which the date of laying of each egg can be accurately known and followed by an internal examination of the female after completion of the clutch. However, circumstantial evidence of three kinds can be adduced. First, Rockhoppers often nest in broken, rocky ground, so that many nests are isolated in such a way as to make it physically impossible for a stray egg to be derived from another nest; two of the three clutches mentioned by Gwynn (1953) were considered to fulfill this criterion. Secondly, there is considerable variation in the shape of Rockhopper eggs, independently of size (Gwynn 1953 Plate 2) and this is constant in any one clutch. This is quite obvious in the

field, so that a stray egg from another nest can often be easily recognised. Thirdly, in a normal two-egg clutch the ratio between first (A) and second (B) eggs of any one clutch is remarkably constant (Gwynn 1953 Fig.1). In the one three-egg clutch for which data are available, the ratio by weight between first and third eggs lies almost exactly on the axis in Gwynn's (1953) Figure 1; the ratio between second and third egg lies just outside the range shown by normal two-egg clutches — in other words, it is intermediate in weight for that clutch. As pointed out by Williams (1981), both first and second eggs of this rather small clutch would normally be classed as A eggs; the weight of the third egg (there is an unfortunate but obvious error in the published measurements of this egg) is within the range for B eggs of normal two-egg clutches (Gwynn 1953 Tables 1 & 3). During two seasons at Heard Island, I saw a few other three-egg clutches and formed the opinion that true three-egg clutches, though rare, could usually be identified in the field by the criteria given above. The evidence for three-egg clutches in the Rockhopper is therefore circumstantial and, although it can be convincing in the field, awaits further critical evaluation.

In the Macaroni Penguin, the difference between the A and B eggs is even more extreme than in the Rockhopper. As stated in Downes *et al.* (1959), 'intermediate-sized' eggs were occasionally found — i.e. eggs that appeared too large to be A eggs, yet too small to be B eggs (Gwynn 1953). Evidence for three-egg clutches in the Macaroni Penguin is based on dissections of six laying females, two of which had laid such 'intermediate' eggs.

1. H53/B5 was sitting in an empty nest. Dissection revealed one yolk in the oviduct, the gelatinous envelope of a ruptured follicle, and three large ripening

follicles (Table 1). The ovary also contained numerous small follicles with yolks up to 7 mm diameter, the envelopes of many being loose, gelatinous and much more bulky than their contents, and the peritoneal spaces were filled with watery fluid.

2. H53/B6 was sitting on one egg. A second egg, complete with membrane but no shell, was low in the oviduct; two ruptured follicles, already regressing, were 12 mm and 22.5 mm wide; one ripening follicle (Table 1) was attached to the ovary, which also contained numerous follicles up to 8 mm in diameter. There was a small quantity of fluid in the peritoneal spaces.
3. H53/B7 was collected within 20 hours of completing a two-egg clutch. The ovary contained two burst follicles, 14 and 10 mm across, with mouths 10 and 5 mm wide, and one large flaccid follicle which had evidently contained a large yolk but was now a fig-shaped body (measuring 34 x 25 mm, operculum 19 mm wide, weight 6.45 g) and a second atretic follicle, 18 x 16 mm (flattened) operculum 9 mm wide. Smaller follicles were also regressing.
4. HD was sacrificed three days after the first egg had been recorded (laid since previous afternoon). On dissection, the B egg was in the shell gland, complete except for the usual chalky accretion and surrounded by a little milky fluid. There were two large intact follicles, one, probably once the larger of the two, already flaccid and wrinkled, weighed 21.8 g; the second, still spherical, 38 mm in diameter (with a 9 mm cyst in the follicle wall) weighed 32.2 g, but was not as tense as developing follicles in the preceding cases. Smaller follicles were also showing regression.
5. 7541 was collected within 24 hours of completion of a two-egg clutch (Gwynn 1993). It was taken because of its large ('intermediate') A egg (weight 116.7 g). The oviduct was empty, and there were three burst follicles (two 16 mm across, one 13 mm across, with mouths 8 mm, 9.5 mm and 8 mm wide). There was also one flaccid follicle, resorption well advanced, 32 mm across.
6. 7551 was collected on 24 November, also on account of its large A egg (laid 15-16 November, weight 123.4 g). and was now sitting on its B egg (Gwynn 1993). Regression of the ovary was well advanced; three burst follicles had mouths 4 mm, 6 mm and 9 mm across, the last almost the full width of the follicle. No other follicle appeared to have

Table 1 Details of ripening follicles at onset of laying in *Eudyptes chrysolophus*.

Clutch number	Follicle number	Mean diameter (mm)	Weight (g)	Volume (ml)
H53/B5	1+	—	25.6	25
	2	39	30.0	28
	3	36	23.2	22
	4	29	12.3	11.5
H53/B6	2+	—	32.3	30
	3	37	26.3	25

+ Yolk in oviduct.

been greatly enlarged; one fig-shaped follicle 10 mm across showed advanced atresia.

Of this series, it is probable that H53/B5 and H53/B6 would have laid normal two-egg clutches and that all remaining follicles would have been resorbed. H53/B7 and HD were clearly in course of laying normal two-egg clutches as the remaining follicles were already regressing. However, 7541 and 7551 had each evidently laid three eggs, of which the first was never found. In both these clutches, the second egg was 'intermediate' in size and, in both, the second and third eggs were highly conformable.

Provisionally, it would seem that: (i) in preparation for laying, three or four follicles become conspicuously enlarged; (ii) the second follicle bursts at some uncertain interval after the first egg is laid (Grau 1984 indicates that the time spent in the avian oviduct is generally short and unrelated to the lag period, between the end of yolk deposition and laying); and (iii) that regression of the ovary begins before the final (normally the second) egg is laid, probably after the bursting of the second follicle.

What circumstances, then, might cause a Macaroni Penguin to lay three eggs? The first point to note is the third egg, in the two cases described, was not a pygmy egg as has been recorded in the Rockhopper Penguin (Murphy 1936; Elliott 1957) but an apparently normal B egg. Secondly, it is remarkable that such an unusual event should have occurred twice in a small group of about 20 pairs under close observation; in both cases, the female in question was selected for dissection on account of the 'intermediate' size of the first discovered egg. One possible hypothesis would be that gross disturbances of the colony (in this case, banding) could have switched off the biological clock when the first egg was lost, and that when normal conditions returned, the female, possibly with a new mate at another site, could have started again, resulting in the second follicle which had begun to develop, continuing to form an unusually large A egg, allowing the third follicle to develop into a normal B egg. This would explain the production of three eggs by one bird twice in such a small group. In discussing egg formation in the Fiordland Crested Penguin, Grau (1982) points out that though they do not eat during the egg formation period, the total egg weight in that species represents only 6% of the female's weight when she starts breeding, so that egg production in *Eudyptes* is not a major problem, even to a fasting bird.

Gilbert (1979) discusses the resorption of post-

ovulatory follicles and atresia of developing follicles at the end of egg-laying. After referring to the fact that egg-laying normally ceases once the bird completes the clutch size characteristic of her species, he states that the precise causal relationship between the end of egg-laying and the onset of incubation has not been completely determined, but that the change from egg-laying to incubation is associated with considerable changes in the appearance of the ovary, since the normal mechanisms for the growth and maturation of the oocyte no longer operate.

One other feature in the dissections that should be recorded was the large quantity of intraperitoneal fluid, together with the gelatinous appearance of the burst follicle (and of some smaller follicles) found in H53/B5, the earliest in the laying cycle. H53/B6 which had laid one egg, the second complete with membrane in the shell gland, had a small quantity of free intraperitoneal fluid; in the other four birds, at more advanced stages, there was no free intraperitoneal fluid. This raises the question as to whether this could be a normal mechanism for fluid storage in preparation for the long fast, during which a large quantity of albumen had to be secreted for the two eggs. I put this question to C.R. Grau, who after consultation with some colleagues, could find no record of any similar observation.

Cassin's Auklet *Ptychoramphus aleuticus*, one of the few species in which internal examination of laying birds has been done, presents a completely different picture (Astheimer 1986). This species lays a one-egg clutch and only one follicle enlarges. Only if the first egg is lost will another follicle enlarge and a second egg be laid, after an appropriate interval.

It would appear that the eudyptid penguins offer an interesting area for further research into the physiology of egg formation and clutch limitation in birds.

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Egg Composition in the Macaroni Penguin *Eudyptes chrysolophus*

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The *Eudyptes* penguins are unique in laying two-egg clutches in which the first (A egg) is consistently smaller than the second (B egg; Gwynn 1993). This divergence is seen in its most extreme form in the Macaroni Penguin *E. chrysolophus* and Royal Penguins *E. schlegeli*, in which the second egg is about 60% heavier than the first egg (Gwynn 1953 Table 2).

In the course of studies on breeding Macaroni Penguins on Heard Island in 1953 (Downes *et al.* 1959), dissections were made of six laying females (Gwynn 1993). The composition of a series of known first and second eggs was examined to determine whether there was a difference in composition between them, and the status of the 'intermediate' eggs laid by two of the females examined. Elsewhere, Williams *et al.* (1982)

have since given the composition of A and B eggs in a series of eight Macaroni Penguin clutches from Marion Island and Grau (1982) has studied egg formation in the fiordland Crested Penguin *Eudyptes pachyrhynchus*.

In the present study the composition of five known clutches was examined. The technique was to separate the yolk from albumen in a saucer, rinse it in water, blot it on filter paper and then weigh it. The shells were washed, dried and weighed, and the weight of albumen calculated by difference (Table 1).

Because the first three appeared to be normal three-egg clutches, these were treated separately from 7541 and 7551, in which the first known egg was unusually large and the birds were subsequently found to have ovulated three times (Gwynn 1993). Table 1 shows that