Breeding success, brood reduction and the timing of breeding in the Fiordland crested penguin (*Eudyptes pachyrhynchus*)

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Abstract I visited 10 breeding sites across the range of Fiordland crested penguins (*Eudyptes pachyrhynchus*) in 1995. Based on the developmental stage of chicks at each of the sites, breeding begins progressively later in more northern colonies. Fiordland crested penguins had unusually high hatching success on Taumaka I. (Open Bay Islands) in 1995, and I suggest from anecdotal observations made at the nine other sites that 12% of pairs may have raised two chicks in that year. Together, these observations suggest that Fiordland crested penguins had an unusually good breeding season in 1995. The suggestion that rare "good" years occur, allowing two chicks to be raised, has implications for explanations of brood reduction in crested penguins.

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INTRODUCTION

Following Warham (1975) it has become the rule to assume that all crested penguins (Eudyptes spp.) lay two eggs, yet raise one chick, with that chick typically being from the second-laid and larger egg. Subsequent research has confirmed and extended Warham's results. We now know that only three species (E. chrysocome, E. robustus, E. pachyrhynchus) regularly hatch both eggs, whereas most or all pairs of the other species lose the first-laid egg early in incubation or even before incubation has begun (reviews in Lamey 1990; St Clair et al. 1995). Even for crested penguins that may hatch two eggs, only one egg hatches in many nests (Warham 1975; Lamey 1990; this paper). Evolutionary explanations for the 2-egg, 1chick system remain elusive, especially for those species that never hatch two eggs (St Clair et al. 1995). Gwynne (1953) and Warham (1974, 1975) hypothesised that the first-laid egg provided 'insurance', in the event either that the second-laid egg was lost, was incubated to term but

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was not viable, or the chick died within a few days of hatch ('insurance reproductive value', Mock & Parker 1986).

Fiordland crested penguins E. pachyrhynchus are the most northern in distribution, and show the least egg dimorphism, of all the crested penguin species (Warham 1975; Lamey 1990). Suggestions that they do the most near shore foraging (Warham 1975; Lamey 1990) remain to be substantiated. Pairs of Fiordland crested penguins that hatch two eggs have a higher probability of fledging a chick than pairs that hatch only one egg (St Clair 1991; Phillipson 1992), supporting the insurance hypothesis. Together, these characteristics make Fiordland penguins the most likely crested penguin species to occasionally raise two chicks (if this can ever be achieved) by taking advantage of occasional 'good' years (Lack 1968; thereby obtaining 'extra reproductive value', Mock & Parker 1986). In this sense, 'good' is likely to mean that food is unusually abundant and/or accessible. Crested penguins live in remote locations and are rarely studied intensively enough either for nests with two surviving chicks to be detected, or for rare 'good' years to be detected. I believe

that such a 'good' year occurred for Fiordland crested penguins in the 1995 breeding season. Presented here is the limited evidence that I can provide to support that assertion, along with other details about breeding gleaned from a species-wide survey conducted in that year.

METHODS

I and my students studied Fiordland crested penguins on Taumaka I. (the largest of the Open Bay Islands, Fig. 1) in most years between 1987 and 1996. The intensity of our monitoring varied considerably, ranging from daily monitoring for the entire breeding season, to occasional visits for a few days at critical times. My visit in 1995 (12-15 September) was timed to allow documentation of hatching success.

During the period 9-21 October 1995, I visited 9 sites across the species' range in order to take blood from chicks after they had formed creches (Fig. 1). Creches form at random locations in the breeding colonies and may or may not form at nest sites. Locations visited from south to north were: Codfish I., Coal I. (Preservation Inlet), Passage I. (Chalky Sound), an unnamed island in Dusky Sound, Johns Is and Breaksea I. (Breaksea Sound), Seymour I. and Rolla I. (Doubtful Sound), and Martins Bay. Taumaka I. is north of Martins Bay. While at each breeding site, I counted the number of chicks and recorded details of their development (size, creching, and moult). Some additional details about breeding were provided by colleagues who visited several of the sites earlier in the breeding season. Details of timing were inferred from their notes made at the time, as timing of breeding can be estimated reasonably accurately from descriptions of size of chicks, chick behaviour, and the relative occurrence of nests containing eggs and chicks in the colony.

RESULTS

Timing of breeding

A comparative estimate of the timing of hatching can be made from notes made on developmental stage of the chicks at each location (Table 1). Chicks begin to moult into juvenile plumage at about 8 weeks, and chicks beginning to moult were found in Preservation Inlet (10 October) and Dusky Sound (12 October). Chicks on Codfish I. (20 October) and in Chalky Sound (11 October) were large, and similar in size to the moulting chicks, although they were not yet moulting. Chicks in Breaksea (9 & 13 October) and Doubtful Sounds (15 & 17 October) were smaller, and similar in size to chicks in Martins Bay

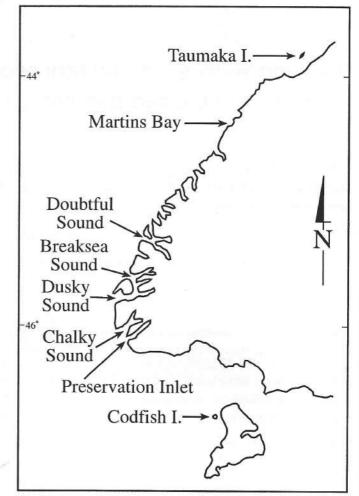


Fig. 1 The southwestern corner of South Island, New Zealand, showing locations mentioned in the text.

(21 October). The first egg hatched in Preservation Inlet on about 8 August (R. Russ, pers. comm.), in Martins Bay on about 27 August (C. Challies, pers. comm.), and on Taumaka I. on about 9 September (pers. obs.).

There is a clear trend of earlier breeding in the south and later breeding in the north, with the spread of peak breeding covering about 5 weeks.

Hatching success

All potential nest sites in the study colonies on Taumaka I. (Open Bay Is) can be checked using a combination of visual and acoustic cues. Any concealed sites that had not been confirmed as active were checked visually before I left the island (such checks usually involve disturbing more exposed nests, so are only undertaken when necessary). In 1995, there were a total of 25 nests active in the study colonies. I determined the contents for 17 and the number of chicks hatched for 15 (one contained 1 egg and 1 contained 2 eggs when I left the island). The other 8 nests were in inaccessible locations and the contents could not be checked, but there was no indication

Table 1 Estimated timing of breeding by Fiordland crested penguins (*Eudyptes pachyrhynchus*) at various sites across the species range in 1995. The sites are listed from south to north. The value for timing is an arbitrary number that indicates relative placement in the timing order over a 5-week period; it does not indicate a timing unit such as weeks. Details in text.

Location	Latitude	Nesting habitat Tir	Timing	
Codfish I.	46°S 45'	Burrows, dugouts	3	
Preservation Inlet	46°S 03'	Cave	1	
Chalky Sound	46° S 0'	Burrows	2	
Dusky Sound	45° S 45'	Cave	1	
Breaksea Sound	45° S 34'	Site 1: burrows		
		Site 2: open nests, dugouts	4	
Doubtful Sound	45° S 15'	Burrows (2 sites)		
Martins Bay	44° S 15'	Caves & under boulders		
Taumaka I.	43° S 50'	Caves & under overhangs		

Table 2 Proportion of Fiordland crested penguin (*Eudyptes pachyrhynchus*) nests hatching 1 or 2 eggs; the proportion of nests hatching no eggs was not usually available and is not included here (1 nest and a likely 0 nests hatched 0 eggs in 1990 and 1995 respectively). Unk.=unknown.

No.(%) of nests hatching

Year	l egg	2 eggs	Unk.	Source
1969	12(32)	25(68)		Warham (1974)+
1970	8(17)	38(83)		Warham (1974) ⁺
1988	34(42)	47(58)		Phillipson (1992)#
1989	12(36)	21(64)		St Clair (1991)
1990	10(42)	14(58)	4	IGM
1995	0(0)	15(100)*	2*	IGM.

+Estimates based on the number of nests retaining 2 eggs from laying to a stated date in early September rather than to hatch *per se.* Other data in Warham (1974) suggest that failure or loss of one or both eggs was high late in incubation (>47%), indicating that the estimated proportion of nests hatching 2 eggs given here is high.

#Phillipson presented data based on survival of eggs rather than hatch rate for nests, thus these values reflect back-calculation using stated sample sizes.

*Of two nests not yet hatched when I left the island, 1 contained 1 egg and 1 contained 2 eggs, thus a more conservative estimate of the proportion of nests hatching two eggs is 96%.

that they were any different to the 17 nests that were monitored closely, as all hatched during the same period as the nests that were checked (indicated by peeping calls of small chicks). The 25 nests represent all nests likely to be active at the study site in 1995 based on records of nest locations for the previous three years, indicating that few if any nests failed completely in 1995. All 15 nests that hatched produced two chicks, and only 1 of 17 nests was clearly going to hatch only one chick. A 96-100% hatch rate of two eggs is unprecedented (Table 2).

Two chicks from one nest?

Two chicks can occur at one nest for the following reasons: i) creching, ii) adoption, and iii) survival of both siblings. Creches had formed in all the colonies visited in October. However, some nesting habitats limited the potential for chicks to locate each other, as some chicks in isolated burrows had to cross open ground in order to enter another burrow (burrows can contain one or more nests). At these sites, many chicks of creching age were standing alone on or near a nest.

I located 5 nests where one large and one small chick were standing together as a "pair" (Table 3). In each case, the smaller of the two chicks was considerably larger than a 7-10 day-old chick (the age by which most nests have lost the smaller chick), and was at about minimum size for creching. I discount the Codfish I. pair because they were close to a creche of 4 chicks, and the Martin's Bay pair because of a second nest in the cave that had clearly been active but contained no chick. However, three of the pairs were isolated from all other chicks in the colony by being in burrows (2 pairs) or in a dugout under a tree (1 pair). These pairs were in locations where chicks would have to leave the burrow and travel across several metres of open ground to reach another burrow containing a chick in order to form a creche. Such movements are possible, but unlikely for burrow-living chicks early in the creching period (pers. obs.)

For the isolated nests, it is likely that the two chicks were both raised in the nest at which they were found. Although not definitive, these observations suggest that about 12% of nests produced two chicks on the Johns (2 of 16) and Passage Is (1 of 9) in 1995. It is worth noting that at all other visited locations, colony topography and nest distribution meant that nests producing two chicks were undetectable even if they existed, because there were few or no isolated nests.

DISCUSSION

Unusually high hatching success, as indicated by the 1995 data for Taumaka I., does not necessarily predict higher per capita nest production. The cause of brood reduction in a nest that hatches two chicks is either that the female does not feed the smaller chick (in which case it dies in 3-6 days), or apparently that she cannot provide enough food for two chicks once they are 7-10 days old (males provide no food until chicks are about 3 weeks old) (Warham 1974; Phillipson 1992). Unusually good hatching success may indicate that birds were more

Location	Nesting habitat	Total no. chicks	No. "pairs"	Creche or vacant nest nearby?
Codfish I.	Burrows; dugouts	>20	1	Yes
Passage I., Chalky Sd	Mostly burrows	10	1	No
Johns Is, Breaksea Sd	Mostly burrows	18	2	No
Martins Bay	Cave	2	1	Yes

Table 3 Locations and nesting habitat of sites at which two chicks were found standing at a nest as a "pair".

effective incubators in that year, perhaps because they were more alert to egg-predators (such as weka *Gallirallus australis*, see St Clair & St Clair 1992).

More important is what happens after hatching. Although most brood reduction occurs when the two chicks are <10 days old, Warham (1974) estimated one sibling pair to be 19 days and Phillipson (1992) recorded survival of both chicks to >12 days in 11 of 49 nests, with maximum survival of 21, 22 and 30 days. [Some of Phillipson's nests were manipulated with the prediction that the survival of both chicks would be extended, perhaps explaining these unusually long periods of survival.] Phillipson (pers. comm.) monitored one unmanipulated nest (of 114 nests in total) that fledged two chicks, indicating that such success may be very rare, but it is not impossible. Such a result may be of little interest if it happens to an occasional pair. But if survival of two chicks happens occasionally on a population-wide basis, it may help to explain the maintenance of the twoegg/one-chick brood reduction system. The likely mechanism is that food is unusually readily available in rare years, allowing the female to keep both chicks alive for three weeks after which the additional support of the male could result in both chicks surviving. Clearly, these comments have little bearing on the problem of why some species lay two eggs, but reject the smaller egg early in incubation.

A corollary of this hypothesis is that "good" years should occur very rarely for those *Eudyptes* species that never hatch both eggs. More technically, species that sometimes hatch two eggs should experience greater resource variability than species that hatch only one egg.

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