Short Communications

An Experimental Manipulation of Clutch Size in the Little Penguin *Eudyptula minor*

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The evolution of clutch size in birds is determined by either the optimal number of offspring that the parents can rear (Lack 1954) or the amount of energy that the female can assimilate to produce the eggs (Lack 1966). The relative significance of these hypotheses can be investigated by comparing the fledging and post-fledging successes of the young of parents with artificially enlarged clutches to those of parents with usual clutch size. If the parents are capable of successfully raising more offspring to maturity than they usually have, it would give support to the latter proposal.

Artificially enlarged clutches and broods have been used to examine the significance of these factors in single-egg clutches in the Procellariiformes and Pelecaniformes (Rice & Kenyon 1962; Nelson 1964; Plumb 1965; Harris 1966; Norman & Gottsch 1969; Jarvis 1974; Lloyd 1977). There are no published experimental manipulations of clutch size in the Sphenisciformes. The clutch of the Little Penguin is two (Reilly & Cullen 1981) and thus both experimental clutch reduction and enlargement are possible. In October 1980, clutches of one, two and three eggs were artificially established in a population of Little Penguins at Summerland Reserve on Phillip Island in southern Victoria and the successes of each recorded until the chicks went to sea.

Methods

Three adjacent burrows of similar depth and aspect and containing newly-laid eggs were selected in each of ten locations of similar distance from the sea, vegetation type and cover. During the third week of incubation, the three clutches of two eggs in the adjacent burrows were re-arranged into clutches of one, two and three eggs so that no burrow contained any of its original eggs. This ensured that the disturbance of having the eggs changed was comparable in the control clutch (c/2) and the experimental clutches (c/1 and c/3). Each burrow was visited weekly, the contents recorded and chicks weighed.

The hatching success was taken as the number of young hatched per eggs incubated, the fledging success as the proportion of chicks leaving the burrows and egg success as the proportion of eggs producing fledged young. The chances of survival of the young in their first year after leaving the burrow were estimated from banding and recovery data. The probability of an individual

being recovered alive more than one year later was tabulated against the weight class of that individual at banding age (*c.* 40-50 days). This relationship was established by Reilly & Cullen (1982) and their information was supplemented with another 109 recoveries. From this relationship, the probabilities of survival were estimated from weights of chicks at banding age in this study. Comparative data were also collected from fifteen pairs at Summerland Reserve where the two eggs were not rearranged and visits were made at four-weekly intervals. This study area was described by Reilly & Cullen (1979). The *G*-tests used in this analysis to estimate goodness of fit are described in Sokal & Rohlf (1969).

Results

The hatching success was independent of clutch size (Table 1) ($G = 1.18$, *d.f.* 2, $P > 0.05$). The causes of failure to hatch are shown in Table 2. The desertion, disappearance and shifting out of the nest of eggs occurred in the first week of the experiment and accounted for 68% of the failure of eggs to hatch. The fledging and egg successes were independent of clutch size in this experiment (Table 1) (fledging success: $G = 0.12$, *d.f.* 2, $P > 0.05$; egg success: $G = 0.17$, *d.f.* 2, $P > 0.05$). The post-fledging survival of young was estimated from their weights at banding (Table 4) and summed for each category of clutch size. The estimated survival per banded chick was greater in c/2 than c/1 and c/3 (Table 1). The estimated number of young surviving per pair increased with clutch size but not in proportion to the number of eggs in the clutch (Table 1). The development of chicks was divided into three consecutive periods of 20 days (Table 3). The mean increases in weight decreased with increasing clutch size in the first 40 days and were similar in the final 20 days. The mean brood sizes of c/2 and c/3 declined throughout the study. The sample sizes in these three periods were small and statistical testing was not feasible.

The chances of survival of chicks after leaving the colony in relation to their weights at banding age are shown in Table 4. The chances of survival through the first year increase with weight at banding except for the final weight class (1300-1499 g) in which the chance of survival declined. The production of young per pair in c/1, as

TABLE 1 Breeding parameters of Little Penguins with clutches of one, two and three eggs.

	Clutch Size		
	c/1	c/2	c/3
Number of eggs	10	20	30
Hatching success	70%	50%	53%
Fledging success	43%	50%	44%
Egg success	30%	25%	23%
Mean weight ($\pm$ s.d.) of young at banding age (g)	956.7 $\pm$ 133.2	964.0 $\pm$ 105.7	935.71 $\pm$ 197.6
Number of young leaving the natal area per pair (egg success x clutch size)	0.30	0.50	0.69
Estimated number of young surviving per pair	0.16	0.32	0.38
Estimated survival per banded chick	0.52	0.63	0.54

TABLE 2 Fate of eggs of Little Penguins (numbers of burrows in brackets) in clutches of different size.

	Clutch Size		
	c/1	c/2	c/3
Deserted	1(1)	4(2)	3(1)
Shifted out of nest	—	—	6(4)
Disappeared	2(2)	1(1)	2(2)
Incubated but failed to hatch	—	5(3)	3(2)
Hatched	7(7)	10(6)	16(9)
Total eggs	10	20	30

TABLE 3 The mean increase in weight during the development of chicks from clutches of different size. The mean brood size is given in brackets and the data are grouped in periods of 20 days.

	Mean increase in weight (g)		
Period (days)	c/1	c/2	c/3
0-19	425(1)	325(1.6)	275(1.6)
20-39	525(1)	440(1.2)	400(1.4)
40-59	203(1)	183(1)	205(1.3)
Total (0-59)	1153	948	880

TABLE 4 The survival of chicks through their first year in relation to their weights at banding.

Weight at banding (g)	Survived at least one year	Total	% Survival
< 699	1	12	8.3
700-899	21	58	36.2
900-1099	36	55	65.4
1100-1299	46	54	85.1
1300-1499	4	7	57.1
Total	108	186	58.0%

estimated by the likelihood of being subsequently recovered alive at the natal colony, was half that of c/2 and c/3 (Table 1). The majority of young that died before going to sea were found near their natal burrows without signs of predation, thus presumably died of starvation. The hatching success of the less disturbed two-egg clutches in the adjacent Summerland Reserve was 62% and was not significantly different from that of the three experimental clutch sizes ($G = 1.56$, $d.f.$ 3, $P > 0.05$). The fledging success of the clutches in the Reserve (57%) was not significantly different from that of three experimental clutch sizes ($G = 0.88$, $d.f.$ 3, $P > 0.05$). The egg success in the Reserve was 35% and was significantly greater than that of the experimental c/2 and c/3 ($G = 9.58$, $d.f.$ 2, 0.01 $> P > 0.005$). The mean weight of chicks at banding in the Reserve was 981 g and the estimated production of young surviving per pair was 0.25.

Discussion

In those manipulative studies of clutch and brood sizes in seabirds where the clutch or brood size has been experimentally enlarged, clutches or broods usually consist of birds unaffected by the introduction of foreign eggs or young into their nests during the experiment and thus may be inadequate as control clutches or broods if disturbance affects survival. In this study, the less disturbed c/2 in Summerland Reserve, did not have a significantly different hatching success from the experimental c/2 ($G = 0.71$, $d.f.$ 1, $P > 0.05$), but it is inappropriate to extrapolate such results to other species.

Although Little Penguins have been recorded incubating three eggs (Reilly & Balmford 1975), possibly from two females, it is an extremely rare event. A small number (0.005%) of burrows examined on Phillip Island in 1980 contained birds sitting on two eggs and an egg-like stone.

I did not determine if these pairs had a lower hatching success but this does suggest that some birds were undeterred by an enlarged clutch. Although two pairs successfully hatched three eggs in this study, six eggs in four burrows of c/3 were shifted out of the nest (Table 2) suggesting a response in some birds to the enlarged clutch size. Despite this, the hatching successes of c/2 and c/3 were not significantly different.

Rice & Kenyon (1962) added one egg to the nests of the Laysan Albatross *Diomedea immutabilis* containing the usual clutch of one and all the eggs failed to hatch. Norman & Gottsch (1969) recorded hatching successes of 35% and 20% in enlarged clutches of the Short-tailed Shearwater *Puffinus tenuirostris* on Green and Phillip Islands compared to hatching success of 80% in undisturbed clutches of usual size (one egg) on Green Island. The proportion of young hatching in nests with an added second egg was as high as in nests with the usual one egg in the North Atlantic Gannet *Sula bassana* (Nelson 1964). Thus, the ability to incubate enlarged clutches successfully varies greatly between species and is likely to be related to the size of the brood patch, method of incubation (Lloyd 1977) and the size of the egg relative to the adult (Norman & Gottsch 1969).

The increasing inability of parents to provide sufficient food with increasing brood size is reflected in the slower growth in the larger broods throughout their development (Table 3) and the lower weights of young at fledging rather than in the fledging and egg successes (Table 1). Towards the end of the development of chicks, the brood sizes of c/2 and c/3 approached that of c/1 and the changes in weight correspondingly became similar (Table 3). At banding age, the weights of chicks also were similar so that the estimated survival of chicks was independent of clutch size.

The major difference between the three clutches sizes was in the number of young produced per pair and, because of similar chances of survival, the number of young surviving the first year per pair. The c/2 produced twice as many surviving offspring as the c/1. The c/3 produced more surviving offspring than c/1 or c/2 but the number per pair (0.38) was lower than expected in proportion to c/1 (0.16 x 3 = 0.48) or c/2 (0.32 x 1.5 = 0.48). Hence, the production of young per egg laid was reduced in c/3 and the costs per offspring, at least to the female parent, would be greater had she actually laid three eggs.

The production of young was less in reduced clutches but greater in enlarged clutches, which suggests that, under the conditions of this experiment, clutches of three eggs would produce more surviving offspring than the usual clutch of two eggs. Therefore, the results tend to support Lack's (1966) hypothesis of clutch size being determined by the amount of energy that the female can assimilate to produce the eggs. However, the costs of the increased parental investment of enlarged clutches were not measured and it was noteworthy that the costs per offspring surviving the first year were higher for the female in enlarged clutches. The availability of food during the experiment may not have been typical and the repetition of the experiment in several breeding seasons could provide data under different feeding regimes.

Acknowledgements

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