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Asynchronous hatching and variation in breeding success of the Lesser Black-backed Gull (*Larus fuscus*)

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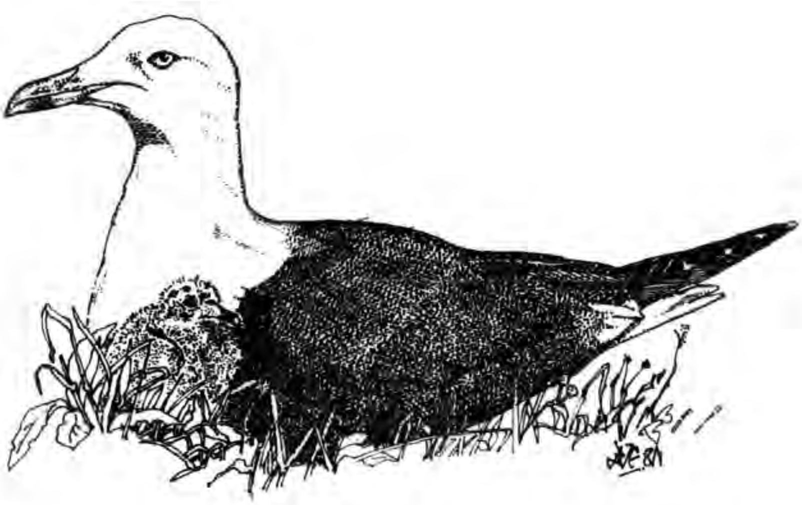
Being a dissertation as part of the requirements for the examination for the Master of Science Degree (by advanced course) in Ecology, University of Durham.



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CONTENTS

CHAPTER 1

Introduction

Gulls are colonial breeders and the onset of breeding, as measured by the date on which birds lay the first egg of the clutch has received much attention in studies of avian biology. Both external and internal factors affect the variation found in the date of laying. Parsons (1975a) suggested that day-length was likely to be the most important environmental cue co-ordinating the endogenous events prior to egg laying. Other factors affecting the date of laying in seabirds have been recorded. These include the relative roles of age in the Kittiwake *Rissa tridactyla* (Coulson and White 1960), mutual stimulation in the Herring Gull *Larus argentatus*, Lesser Black-backed Gull *Larus fuscus* (MacRoberts and MacRoberts 1972) and Common Tern *Sterna hirundo* (Nisbet 1973), interference between colony members in the Glaucous-winged Gull *Larus glaucescens* (Hunt and Hunt 1975), and differences in the birds' responses to such stimuli (Coulson and White 1960, Thomas 1980).

Pattern of laying in the Lesser Black-backed Gull approximates to a normal distribution and is found to be synchronous within small groups of the colony (Brown 1967). This is the case for most other colonial nesting species, e.g. the Herring Gull (Parsons 1975a), the Kittiwake (Coulson and White 1960), the Black-headed Gull *Larus ridibundus* (Patterson 1965) and the Shag *Phalacrocorax aristotelis* (Potts 1966). One of the advantages of synchrony is thought to be as a useful combat against external predators which take a constant supply of chicks throughout the season (Lack 1954). This occurs in the Herring Gull by swamping of the predators (Parsons 1971a, 1975a) and in the Black-headed Gull by mobbing of the predators (Krunk 1964, Patterson 1965) during the synchronous period.

However Davis and Dunn (1976) found that the breeding success of the Lesser Black-backed Gull colony at Skokholm was already declining during the peak laying and attributed this to the increasing inter-neighbour predation occurring at this time. They point out that the increase in several gull colonies has generally led to increased nesting densities with characteristically little expansion of colony area and that this will probably facilitate and intensify any inter-neighbour predatory effect.

Several studies have shown that hatching success and chick survival is correlated to egg size and that there is a seasonal decline in egg size as the season progresses (Parsons 1972, Nisbett 1973). Factors affecting egg size include the position of the egg in the laying sequence, the breeding experience and age of the female and the possibility that a component of egg size is inherited (Coulson 1963, Parsons 1976, Davis 1975). Studies have shown that egg size increased amongst older birds but since the older, more experienced birds tend to lay earlier in the season it is difficult to distinguish between the relative importance of age and egg size to breeding success. In his study of the Kittiwake Thomas (1980) suggests that "while the relationship between egg size and success is independent of female breeding age, its effect upon hatching success is more marked in pairs containing older birds, whilst its effect upon fledging success is only apparent in pairs containing first breeding females."

Likewise, clutch size has been shown to decline through the breeding season even amongst birds of the same age (Coulson and White 1961, Parsons 1975a). Parsons reasons that perhaps young and late-laying birds have insufficient time for maximum development and functioning of their reproductive system but that the disadvantage of producing smaller and fewer eggs are offset by the advantage of synchronised laying since chicks hatching during the peak of the season in his study area were the most successful. Day-length may be linked to the determination of clutch size, circumstantial evidence for which is the more rapid decline in clutch size in northern colonies where the increase in day-length is also more rapid (Parsons 1975a, Thomas 1980).

The usual clutch size for Herring and Lesser Black-backed Gulls is three. In most cases the first laid egg hatches first and the rest in sequence. These will be referred to as the a-egg and a-chick, the b-egg and b-chick and so on. The last egg of the clutch is characteristically smaller than those laid in clutches of 2 and 3 and the eggs from the clutches of one (Parsons 1970, 1972). Factors involved in the reduction in size of the last egg of a clutch probably include the physiological changes associated with the termination of laying, the follicle producing the egg being susceptible to the depressive influence of incubation (Parsons 1972, Paludan 1951). Incubation begins after the second egg is laid in clutches of three and after the first egg is laid in clutches of one and two (Parsons 1972). At the onset of incubation the development of the c-egg lags behind the b-egg by 32 hours, but this is reduced to 18-24 hours at hatching; usually the b-egg hatches up to 12 hours after the a-egg and the c-egg is chipping for another day before hatching (Parsons 1971b). Asynchronous hatching has been found to be an important factor determining the fate of the chick. Studies on the Herring Gull show that the last chick to hatch in broods of 3 suffers a significantly higher mortality than its siblings (Parsons 1970, 1971b, Davis 1975).

To separate the effects of small egg size and hatching sequence upon chick survival in the Herring Gull, Parsons (1975b) carried out a series of egg exchange experiments. Eggs were transferred from nest to nest, so that the larger a-eggs hatched last whilst the smaller c-eggs hatched first. He showed that c-chicks hatching first survived markedly better than those hatching last but the survival was still less than that of the a-chick. Similarly, a-chicks hatching last survived better than c-chicks hatching last. He suggests that while asynchrony at hatching is accountable for most of the poorer survival of the c-chick under normal conditions, the small but significant difference between a- and c-yolks shown during his study may account for the remaining differential mortality. Parsons also found that although the size of the a- and b-eggs was not significantly different, the size of the b-yolk was significantly larger than either the a- or c-yolk. However, no studies were carried out to compare the mortality of a- and b-chicks hatching at the same time, which could indicate whether the larger b-yolk confers an advantage on the b-chick.

The aim of this study was to determine the relative importance of egg size and sequence of hatching upon chick survival for the Lesser Black-backed Gulls in the mixed Lesser Black-backed/Herring Gull colony at Rockcliffe marsh, Carlisle. Eggs were transferred so that clutches of 3 a-eggs, 3 b-eggs and 3 c-eggs would hatch in the sequence of a 'normal' a-, b- and c-egg clutch. These experiments would also determine whether the larger b-yolk confers an advantage on the b-chick.

However, these aims had to be revised when extensive flooding of the marsh occurred between 1 - 3 June, washing out all but a few hundred nests of the colony. Since data on the surviving clutches was not detailed enough for any egg transfer experiments, they were all performed on the clutches laid after the flood. Re-laying was highly synchronous and the peak occurred 11 days after the last day of the flood. Parsons found that a reduction in egg size occurs between first and repeat clutches and showed that this mainly results from a smaller a-egg rather than an exaggerated seasonal effect. The result is that the difference in size between the first two and last egg is less marked in re-laid clutches and this may influence the egg's probability of producing chicks (Lundberg and Vaisanen 1979).

The present study aimed to determine the relative importance of egg size, sequence of hatching and nesting density to the fate of the a-, b- and c-chicks respectively in the re-laid clutches of 1, 2 and 3.

CHAPTER TWO

Study Area

2.1 The Marsh

Rockcliffe Marsh lies at the head of the Solway Firth about 7 miles N.W. of Carlisle and 3km from Rockcliffe Village (Nat. Grid Ref. NY325635). The marsh is formed from silt deposits from the rivers Esk and Eden, flanking the North and South edges of the marsh respectively.

The marsh is owned by Castletown Estates and is managed as a nature reserve by Cumbria Naturalists' Trust during the breeding season.

The 800 hectares of mature saltmarsh grades, at the edges, into less mature, 'new', marsh and eventually to sand in the river channels. Surface water drains from the marsh by means of channels or creeks which intersect the marsh at numerous points. The main vegetation of the marsh is *Festuca rubra* which is grazed in winter by geese and in the summer by cattle (850 head in 1981).

The Herring and Lesser Black-backed Gull colony is situated at the Point of the marsh (Fig. 2), approximately 5km from the Esk Boathouse, covering both mature and 'new' marsh to an area of about 300 hectares. About 2,500 pairs of Lesser Black-backed and Herring Gulls in a ratio of 4 : 1 respectively breed in the colony. The nesting density is fairly low with most nests being 5 - 15 metres apart.

The cattle do not spread out as far as the gull colony to graze until well into June, and so the vegetation of fescue grass, *Carex* spp., *Juncus* spp. and scurvy grass, *Cochlearia officinalis* (in the creeks) grows to 30 - 40cm on the mature marsh. The vegetation of the 'new' marsh, consisting of common saltmarsh grass, *Puccinellia maritima,* thrift, *Armeria maritima* and sea milkwort, *Glaux maritima,* is generally much shorter (<15cm).

The study area was a section through the colony, including some of the new marsh at the point (Fig. 2)

2.2 The Gull Population

The gull colony is occupied almost exclusively by gulls with a few skylark, oystercatcher and mallard nests being sparsely scattered through it (total less than 30).

The distribution of gulls is non-homogeneous. Large areas within the colony are empty of nests, usually because they are on slightly lower-lying ground and, as such, prone to waterlogging and flooding.

The ratio of Lesser Black-backed Gull to Herring Gull also differs between the old and new marsh. More Herring Gulls nest in the shorter vegetation around the edge of the colony, giving rise to a ratio of 3 : 1 on the new marsh compared with 4 : 1 on the old.

FIG: 1 Geographical location of Rockcliffe Marsh

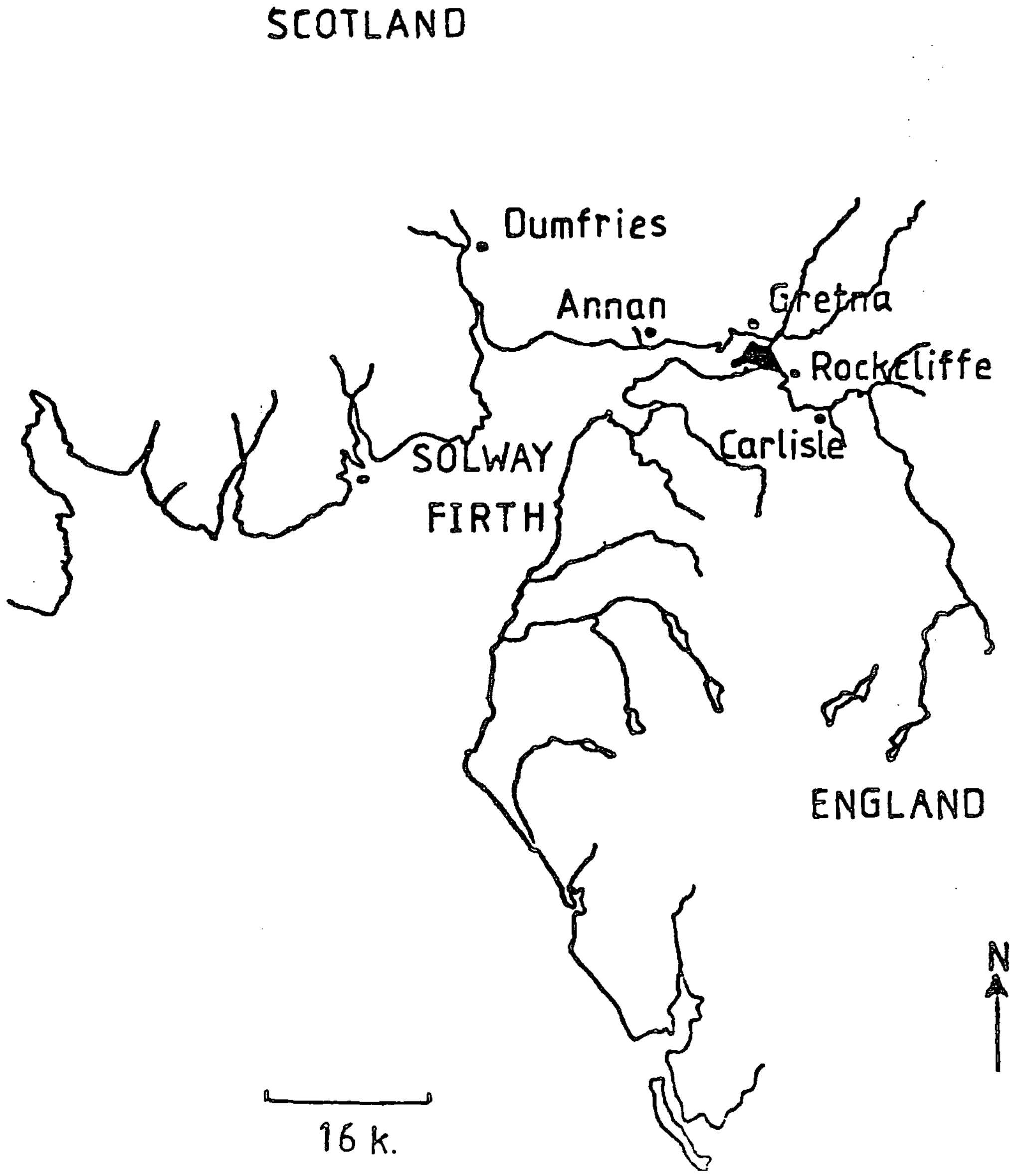


FIG: 2 Map of Rockcliffe Marsh, showing position of the Herring and Lesser Black-backed Gull colony and the study area

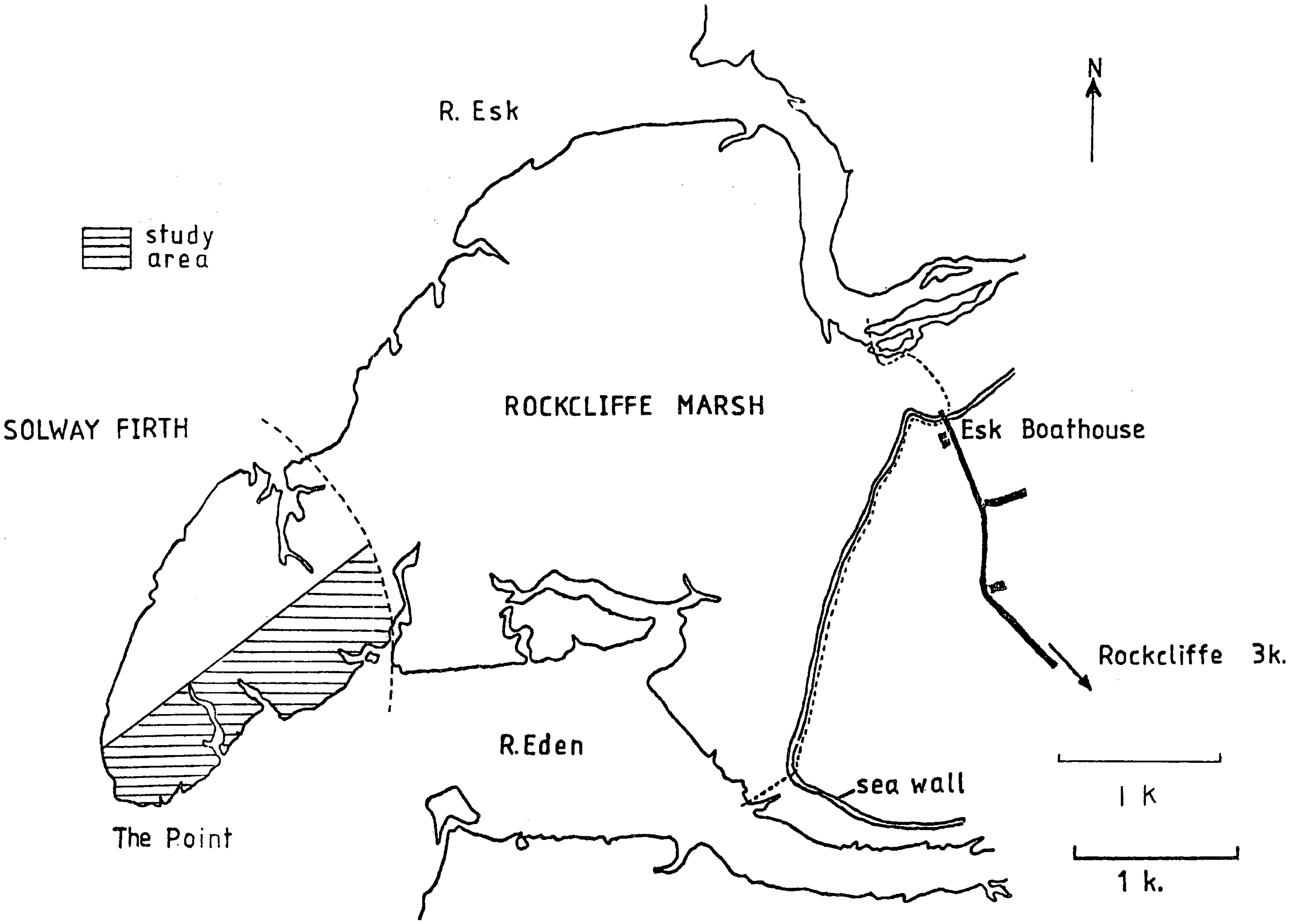


Plate 1 : a) The Marsh in May

b) The colony during the flood

CHAPTER 3

Methods

3.1.
Marking nests and eggs

Nests were marked with wooden stakes (300x25x7mm) sharpened to a point at one end and numbered at the other by a black waterproof ink pen. The nest was marked as soon as the first egg was found and this, and later eggs, were individually marked according to the sequence of laying. Thus the first or a-egg (nomenclature cf. Paludan 1951) was labelled number one, b-egg number two and c-egg number three (Plate 2a.) This increased the accuracy of clutch size measurements. If a solitary unmarked egg is found in a nest which previously contained a marked first egg, it signifies that the first egg was robbed and a second egg laid. Had the first egg been unmarked, no such conclusion could be drawn. On those occasions when nests with 2 eggs were found or when the second and third egg had been laid before refinding the same nest, the eggs were labelled 1,1, and 2,2, respectively.

The lengths and breadths of Lesser Black-backed Gull eggs were measured to 0.01cm using Vernier calipers. From these measurements the volume and shape index of each egg was calculated using the following formulae:

$$\text{Volume cm}^3 \text{ (V)} = K.L.b^2$$

L = length cm

b = breadth cm

K = a constant 0.476 (Harris 1964)

$$\text{Shape Index (S.I.)} = \frac{100b}{L} \quad \text{(Coulson 1963)}$$

Plate 2 : a) Method of marking nests and eggs

b) Photograph of (approx.) 5-day old chick

3.2.
Marking newly hatched chicks

The chicks were marked on hatching by soft plastic rings numbered according to the nest number and sequence of laying of the egg from which it hatched. If the sequence was not known, the chicks were labelled A, B or C. The rings were cut from insulating tubing which had the same internal diameter as the monel ring (11mm diameter, size 6). These could be slipped over the leg and temporarily held in place with a staple pinching one edge together (Fig. 3.) These could later be cut off and replaced by the monel and darvic rings. If left, the staple quickly rusted and would be pulled apart by the growing leg. The tube would then open to the full diameter without injury or constriction to the bird's leg.

3.3.
Estimation of nesting density and inter-nest distances

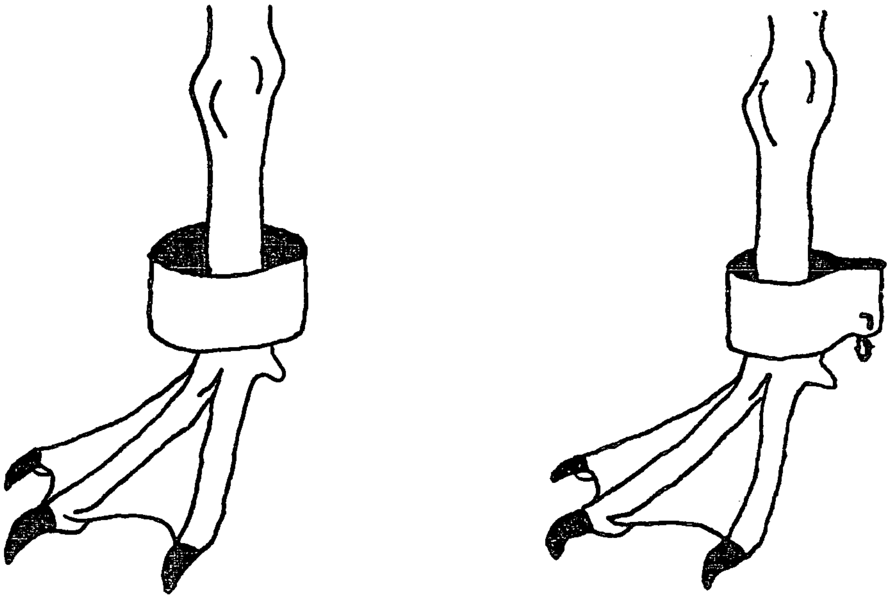
Half the colony was divided into 10 areas ranging from 0.02km^2 to 0.036km^2. Each area was subdivided into a series of 20m^2 squares by placing bamboo canes at 20m intervals. The nests in each square were mapped onto graph paper, each 2cm^2 of the graph paper corresponding to each 20m^2 square of the grid. The nests were estimated to be within 0.5 metres of their real position and thus the accuracy of their position on the graph paper is estimated as ±0.05cm. The nearest neighbour distance for each nest was then calculated from the map to an accuracy of ±1m.

3.4.
Identification of birds on the nest

A hide was set up on a 2 metre platform at the edge of each grid. From the hide most of the nest stakes and corresponding nesting birds could be identified as either a Lesser Black-backed or Herring Gull with the aid of a telescope. A total of 33% of the birds were identified in this way before the flood. After the flood, the much longer length of the grass

FIG: 3 Method of marking chicks

Method of ringing chicks using stapled insulating tube.



obscured many of the stakes from viewpoint and the above method of identification was more difficult. Fortunately the birds had started to moult by this time and some of the nesting birds could be identified from flight feathers found in the nest. 72% of the birds were identified as either Lesser Black-backed or Herring Gulls using the original method and a further 3% were identified from flight feathers found in the nest.

3. 5.

Transfer experiments

Eggs were transferred between nests so that clutches of 3 a-eggs, 3 b-eggs or 3 c-eggs laid within 2-day intervals of each other would hatch in the sequence of a 'normal' a-, b- and c-egg clutch. This was usually achieved by six interchanges of the a-, b- and c-eggs involved in the transfer (see Fig. 4.) . The volumes of the a-eggs were similar for each clutch involved in the mutual transfer and were within ±5cc of each other; this was also found for the b- and c-eggs respectively and while two of the clutches (X and Y) were at a similar stage of chipping and hatching the other one (Z) was approximately one day behind in its development. The result was that each altered nest contained eggs of similar volume but which hatched in the sequence of a 'normal' a-, b- and c-egg clutch.

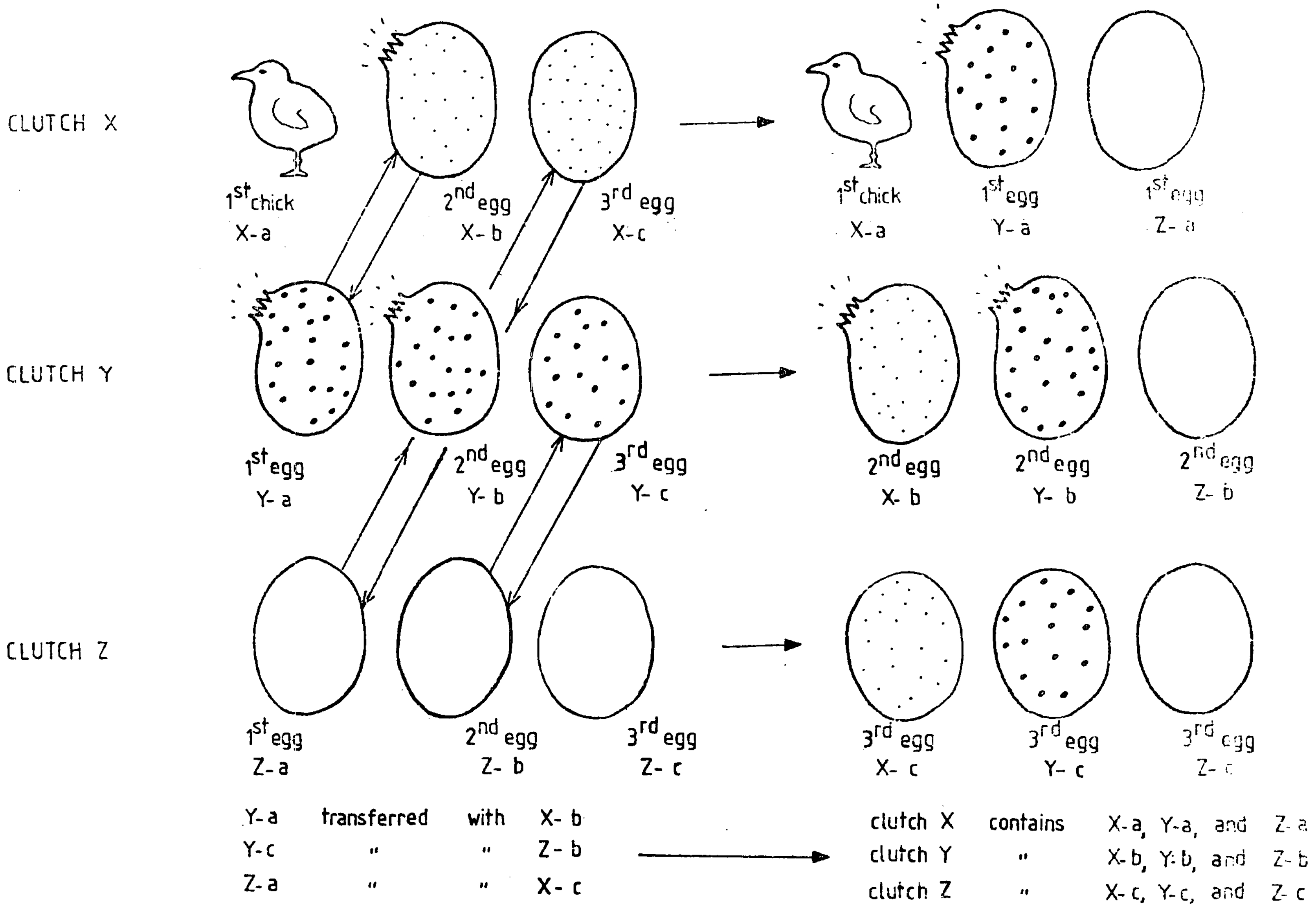
However, the difficulty in finding nests where all 3 eggs are hatching, and are of the appropriate size and state of chipping meant that some of the transfers involved transferring chicks of 1-2 days old, but there is no evidence that this adversely affected their survival. 35 nests were found suitable for the appropriate transfer.

3. 6.

Estimation of fledging success : mark and recapture

Chick survival up to fledging in the study area was estimated from the simple index used by Lincoln:

FIG: 4 Transfer experiment - to investigate differential mortality between first, second and third chicks of a brood



$$N = \frac{an}{r}$$

N = the estimate of the number of individuals in population (N)

n = the total number of individuals in the second sample

a = the estimate of the number of individuals marked on day 1 that are available for recapture in day 2

r = the number of arrivals captured on the second day that have been marked on the first.

The assumptions underlying the Lincoln index have been fully listed and explained in Southwood (1978). Three separate searches of the area were carried out between 29 July and 3 August when all the chicks were at least 14 days old. The first two searches were of equal intensity (253 and 245 chicks being caught on each search respectively) and were used in the Lincoln index equation to give an estimate of 433 chicks fledged. The actual number of chicks found, including the number of new chicks found on the third search was 385 which is 89% of the estimated number of fledged chicks. Thus in the analysis of the factors affecting chick survival up to fledging it should be noted that only 89% of the estimated number of chicks surviving are available for analysis.

Paynter (1949), Paludan (1951), Brown (1967), Kadlec *et al.* (1968, 1969) and Parsons (1971) all agree that over half of the chick mortality occurs in the first week of life. A search of the study area was therefore made on 22 July and 23 July when all the chicks were at least 7 days old. However, strong winds and heavy rain prevented a second search from being carried out at this time and thus an estimate for the total number of chicks surviving up to 7 days old is unavailable.

3.7.
Growth of Chicks

Chicks were weighed using a Pesola balance with an accuracy of ±5gm. The same chick was weighed at least twice during the first 10 days of its life so that its growth rate could be calculated and an average growth rate for the a-, b- and c-chicks estimated. (Plate 2.b.)

CHAPTER 4

Fate of Eggs and Hatching Success

4.1 Egg size and shape

A total of 77 Lesser Black-backed Gull clutches of three eggs were measured before the flood and, as far as could be detected, none of these were re-laid clutches. After the flood a total of 208 Lesser Black-backed Gull clutches of three were measured, all of which were re-laid clutches. Length, breadth, egg volume and shape index were measured and calculated as outlined in the methods of Chapter 3.

The mean egg volume and shape index for the a-, b- and c-eggs laid before (first-laid clutches) and after (re-laid clutches) the flood are compared in Table 1. In first-laid clutches the volumes of the a- and b-eggs were not significantly different but both were significantly larger than the volume for the c-egg ($P<0.001$). Shape indices for the a-, b- and c-eggs were not significantly different. Conversely all the egg volumes of the re-laid clutches were significantly different from one another ($P<0.001$) and the a- and b-eggs had a significantly larger shape index than that of the c-egg ($P<0.02$).

A comparison of the individual eggs in the first laid and re-laid clutches show that in each case a significant decrease in egg volume ($P<0.001$) and increase in shape index occurs ($P<0.001$). The difference in size between the first-laid and repeat clutches is mainly the result of a smaller a-egg. These results are compared with those found by Parsons (1971) for the Herring Gull (Table 2). Parsons found that the volume of the c-egg remains more or less constant at 68 ± 6cc (± one standard deviation) whereas in this study a decrease of 3cc occurred.

Table 1. Mean egg dimensions of clutches of three laid before and after the flood on Rockcliffe marsh ± one standard error

	First-laid clutches			Re-laid clutches		
	Volume	Shape index	Sample size	Volume	Shape index	Sample size
a-egg	75.69 ± 0.78	70.39 ± 0.39	77	70.22 ± 0.37	72.26 ± 0.19	208
b-egg	76.02 ± 0.74	70.47 ± 0.32	51	72.62 ± 0.39	72.28 ± 0.23	193
c-egg	70.68 ± 0.83	70.40 ± 0.46	50	67.54 ± 0.39	71.58 ± 0.24	193

Table 2. Decrease in the volumes of the a-, b- and c-eggs from re-laid clutches

	Volume decrease cc	
	This study	Parsons (1971)
a-egg	5.5	4.5
b-egg	3.4	3.2
c-egg	3.1	0.7

Eggs were grouped according to egg volume and laying sequence and the percentage hatching was recorded (Table 3) in the re-laid clutches. In contrast to the results found in previous studies of wild birds (Parsons 1970, Thomas 1980, Lundberg and Vaisanen 1979, Davis 1975, Barrett 1978, Lloyd 1979, Nisbet 1978, Schiffesli 1973 and SyroechKovsky 1975) hatching success was not correlated with egg size (χ^2_2 = 4.09 PNS). However there was a trend for hatching success to increase with egg size and when the hatching success from the smallest egg volumes was compared to that from the largest egg volumes, then the difference is significant (χ^2_1 = 4.07 $P<0.05$).

4.2 Laying sequence and hatching success

Amongst clutches of three and clutches of two where only one egg hatches, there is a significant decline in hatching success with laying sequence (Table 4). Similar results have been found for the Ring-billed Gull (Chardine 1978) and the Kittiwake (Thomas 1980) although Parsons (1971) could find no difference in the hatching success of the a-, b- and c-eggs for the Herring Gull. An explanation for at least part of the variation observed can be offered in those studies where egg size has been correlated to hatching success. However in this study no such correlation was found and other explanations must be looked for. Perhaps part of the explanation lies in a differential fertility between eggs in relation to order of laying (Section 4.3). Thomas (1980) discusses the possible effects to the hatching success of eggs with the change-over of adults from incubation to 'parental' behaviour after a chick appears in the nest. Any marked change in the behaviour of the adult after the first chick hatches could result in chilling or damage to those eggs which remain.

Table 3. Comparing Egg Volume with Hatching Success in the re-laid clutches of three

		Egg volume cc					
		<68	68-72	>72	Total	χ^2_2	P
a-egg	Number laid	75	62	71	208		
	Number hatched	55	51	53	159	1.69	N.S.
	% hatching success	73.3	82.3	74.6	76.4		
b-egg	Number laid	44	46	103	193		
	Number hatched	32	33	88	153	5.12	N.S.
	% hatching success	72.7	71.7	85.4	79.3		
c-egg	Number laid	104	50	38	192		
	Number hatched	71	35	27	133	0.12	N.S.
	% hatching success	68.3	70.0	71.0	69.3		
All eggs	Number laid	223	158	212	593		
	Number hatched	158	119	168	445	4.65	N.S.
	% hatching success	70.8	75.3	79.2	75.0		

	Volume	<68	>72	χ^2_1	P
All eggs	Hatched	158	168	4.08	<0.05
	Not hatched	65	44		

Table 4. Hatching success of eggs in relation to order of laying

THREE EGG CLUTCHES

				Significance of difference		
	No. laid	No. hatched	% hatching	a- and b-egg	a- and c-egg	b- and c-egg
a-egg	376	285	75.8	χ^2_1 = 0.016	χ^2_1 = 12.06	=
b-egg	374	282	75.4	N.S.	$P<0.001$	$P<0.001$
c-egg	371	238	64.1			

THREE EGG CLUTCHES IN WHICH ONE OR TWO EGGS HATCH

a-egg	227	125	55.1	χ^2_1 = 1.72	χ^2_1 = 14.35	χ^2_1 = 6.49
b-egg	223	109	48.9	N.S.	$P<0.001$	$P<0.05$
c-egg	182	66	36.3			

TWO EGG CLUTCHES

	No. laid	No. hatched	% hatching	Significance of difference
a-egg	130	99	76.2	χ^2_1 = 3.64 N.S.
b-egg	130	85	65.4	

TWO EGG CLUTCHES IN WHICH ONLY ONE EGG HATCHES

a-egg	45	20	44.4	χ^2_1 = 9.83 $P<0.01$
b-egg	31	6	19.4	

4.3 Variation in percentage egg predation and egg infertility with laying sequence

The disappearance of eggs from nests during the laying and incubation periods was noted as having been predated. In clutches of three the c-egg suffered a significantly higher percentage predation than either the a- or b-egg (Table 5). This result contrasts with those found by Parsons (1971) and Dighton (1973) but help towards explaining why the c-egg is less successful at hatching than either the a- or b-egg in clutches of three (refer to section 4.2).

Unhatched eggs left in the nest were recorded as infertile. The last laid egg in clutches of three and two was found to be significantly less fertile ($P<0.05$) than the egg laid immediately before it. This supports the suggestion made in section 4.2 of differential fertility between eggs in relation to order of laying as one of the reasons for the variation observed in hatching success with laying sequence.

4.4 Nesting density and amount of cover at the nest site

Nesting density was divided into four categories A, B, C and D, based on nearest neighbour distances. A were nests with nearest neighbours less than 6m distance, B nests with nearest neighbour between 6-9m distance, C nests with nearest neighbour between 9-12m distance and D included all nests with nearest neighbour over 12m distance. Assessment of the amount of cover was based on the height of vegetation in the area. Areas 6, 7 and 8 all had relatively short grass and were termed 'no-cover' areas compared to areas 1-4, 9 and 10 which were termed 'cover' areas(fig. 5)

Hatching success for the a-egg was highest at density C in the no-cover areas (Table 7), although this was not significant. However when density C is compared with density D, then the difference is significant ($P<0.05$). This is an unexpected result since the most common nesting

Table 5. Predation of eggs in relation to order of laying

THREE EGG CLUTCHES

				Significance of difference		
	No. laid	No. predated	% predation	a- and b-egg	a- and c-egg	b- and c-egg
a-egg	376	64	17.0	$\chi^2_1 = 0.20$	$\chi^2_1 = 9.22$	$\chi^2_1 = 6.59$
b-egg	372	68	18.3	N.S.	$P<0.01$	$P<0.05$
c-egg	371	92	24.8			

TWO EGG CLUTCHES

	No. laid	No. predated	% predation	Significance of difference
a-egg	130	29	22.3	$\chi^2_1 = 0.52$ N.S.
b-egg	130	34	26.2	

Table 6. Infertility of eggs in relation to order of laying

THREE EGG CLUTCHES

				Significance of difference		
	No. laid	No. infertile	% Infertility	a- and b-egg	a- and c-egg	b- and c-egg
a-egg	376	25	6.6	$\chi^2_1 = 0.80$	$\chi^2_1 = 1.62$	$\chi^2_1 = 4.61$
b-egg	372	19	5.1	N.S.	N.S.	$P<0.05$
c-egg	371	34	9.2			

TWO EGG CLUTCHES

				Significance of difference	
a-egg	130	2	1.5	$\chi^2_1 = 5.59$	$P<0.05$
b-egg	130	10	7.7		

FIG: 5 Map of Rockcliffe Marsh showing the position of grids 1-10 and the areas of long (cover) and short (no-cover) grass

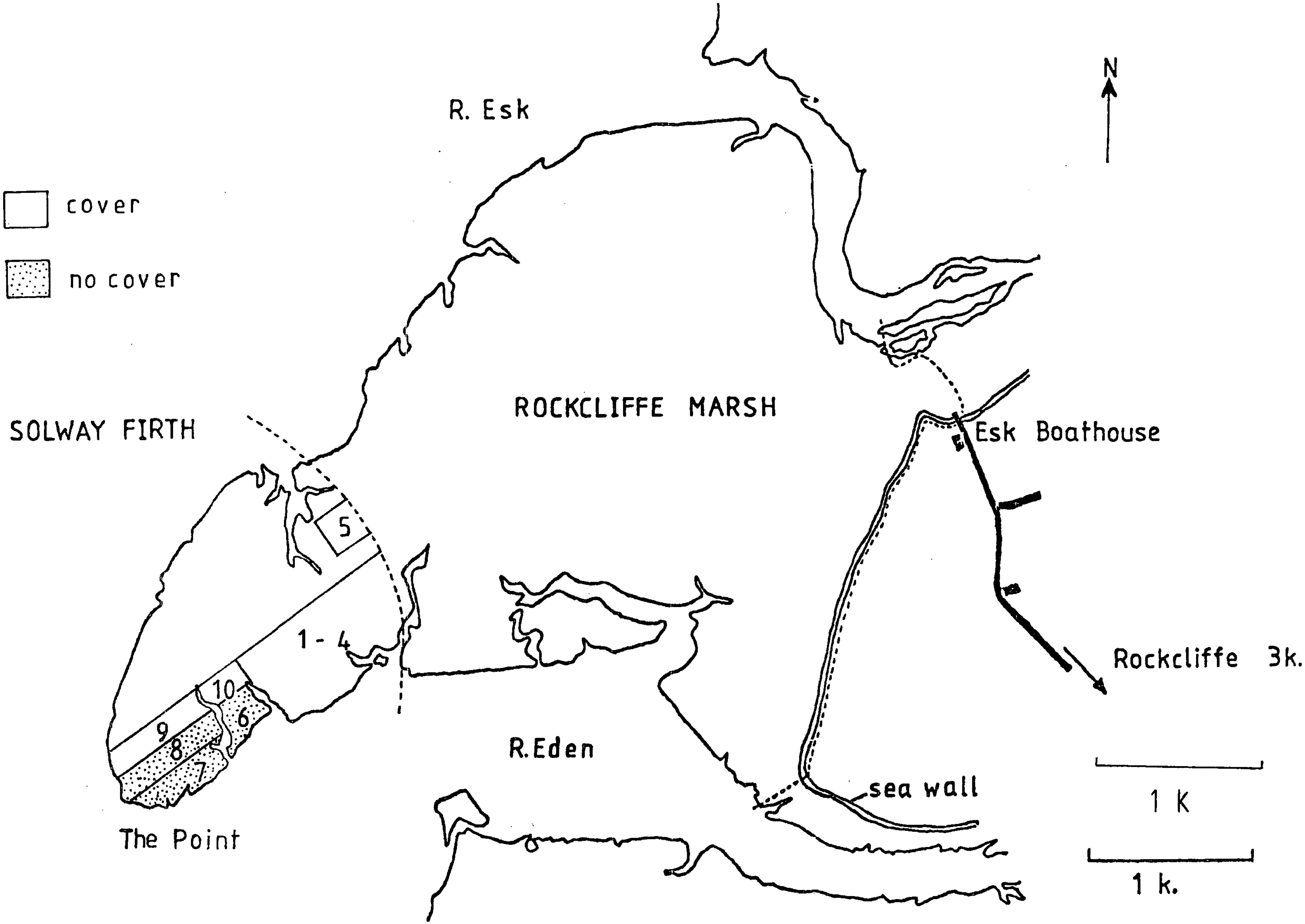


Table 7. Hatching success compared with density in cover and no-cover areas

		Cover						No-cover					
		A	B	C	D	χ^2_3	P	A	B	C	D	χ^2_3	P
	No. laid	36	72	70	100			67	108	38	35		
a-egg	No. hatched	28	61	56	83	1.05	N.S.	46	73	30	19	5.1	N.S.
	% hatched	77.8	84.7	80.0	83.0			68.6	67.6	78.9	54.3		
	No. laid	35	66	66	87	1.60	N.S.	65	104	37	34		
b-egg	No. hatched	25	54	53	69			48	61	27	20	1.29	N.S.
	% hatched	71.4	81.8	80.3	79.3			73.8	58.6	72.9	58.8		
	No. laid	21	45	46	67	0.12	N.S.	53	81	28	28		
c-egg	No. hatched	11	31	30	45			38	50	18	15	2.85	N.S.
	% hatched	52.4	68.9	65.2	67.2			71.7	61.7	64.3	53.6		

densities (A and B) are therefore not the densities in which maximum hatching success occurs for the a-egg. One source of this variation may lie in the different predation pressures occurring at high and low densities. Nests at low densities will be more liable to have their eggs predated by predators other than neighbouring nesting birds since there can be little group defence against such predators. This was found to be the case for the a-egg in no-cover areas ($P<0.05$) and when the A, B and C densities are combined, the difference in percentage predation is also significant for the c-egg (Table 8). On the other hand, birds nesting at high densities will suffer a greater amount of conspecific predation. In cover areas the c-egg is preyed upon significantly more times at high than low densities (Table 8, $P<0.05$).

The results indicate that high nesting density may have evolved partly to offset the disadvantages of laying eggs on ground with little or no vegetation in which to hide the eggs from being preyed upon. However this is offset in areas of cover by a larger conspecific predation pressure at the higher nesting densities.

Tests of homogeneity on the hatching success for the eggs of clutches of 3 and 2 in the cover and no-cover areas show that the decline in hatching success with laying sequence is only significant in the cover areas (Table 9). When the a-, b- and c-eggs are compared for hatching success between cover and no-cover, then for clutches of 3 the a- and b-egg have a significantly higher hatching success in the cover areas ($P<0.05$), whereas the hatching success of the c-egg does not differ between the two areas (Table 9). For clutches of 2, the a-egg has a significantly higher hatching success in the cover areas ($P<0.001$) while the hatching success of the b-egg does not differ between cover and no-cover. Some of this variation is accounted for by the different predation rates in the cover and no-cover areas (Table 10). In cover areas, the a-egg of 3-egg clutches

Table 8. Percentage of eggs predated compared with density in cover and no-cover areas

		COVER						NO-COVER					
		A <6m	B 6-9m	C 9-12m	D >12m	χ^2_3	P	A <6m	B 6-9m	C 9-12m	D >12m	χ^2	P
	No. laid	36	72	70	100			67	108	38	35		
a-egg	No. predated	8	8	10	12	2.56	N.S.	14	27	7	16	9.2	<0.05
	% predation	22.2	11.1	14.3	12.0			20.9	25.0	18.4	45.7		
	No. laid	35	66	66	87			65	104	37	34		
b-egg	No. predated	8	7	10	16	3.03	N.S.	14	24	8	11	1.6	N.S.
	% predation	22.8	10.6	15.1	18.4			21.5	23.1	21.6	32.3		
	No. laid	21	45	46	67			53	81	28	28		
c-egg	No. predated	10	7	9	11	10.8	<0.05	12	21	7	13	5.8	N.S.
	% predation	47.6	15.5	19.5	16.4			22.6	25.9	25.0	46.0		

		NO-COVER			
		A, B and C	vs D	χ^2	P
	No. laid	162	28		
c-egg	No. predated	40	15	5.6	<0.05
	% predation	24.7	46.0		

		COVER			
		B, C and D	vs A	χ^2	P
	No. laid	242	36		
a-egg	No. predated	30	8	2.6	N.S.
	% predation	12.4	22.2		
	No. laid	219	35		
b-egg	No. predated	33	8	1.3	N.S.
	% predation	15.1	22.8		

Table 9. Hatching success compared between cover and no-cover for clutches of two and three

			No. laid	No. hatched	% hatched	χ^2_1	P
Clutch 3	a-egg	Cover	183	149	81.4	5.9	<0.05
		No-cover	191	135	70.7		
	b-egg	Cover	181	146	80.7	3.86	<0.05
		No-cover	189	136	71.9		
	c-egg	Cover	179	117	65.4	0.11	N.S.
		No-cover	190	121	63.7		

			No. laid	No. hatched	% hatched	χ^2_1	P
Clutch 2	a-egg	Cover	79	69	87.3	13.88	<0.001
		No-cover	51	30	58.8		
	b-egg	Cover	79	55	69.6	1.6	N.S.
		No-cover	51	30	58.8		

Table 10. Percentage predation compared between cover and no-cover for clutches of two and three

			No. laid	No. predated	% predation	χ^2_1	P
Clutch 3	a-egg	Cover	183	22	12.0	4.1	<0.05
		No-cover	191	41	21.5		
	b-egg	Cover	181	26	14.4	2.9	N.S.
		No-cover	189	40	21.2		
	c-egg	Cover	179	37	20.7	2.6	N.S.
		No-cover	190	53	27.9		
	a-egg	Cover	79	10	12.6	10.8	<0.01
		No-cover	51	19	37.2		
	b-egg	Cover	79	15	19.0	5.3	<0.05
		No-cover	51	19	37.2		

and both eggs of 2-egg clutches all have a significantly lower percentage predation than in the no-cover areas.

The results suggest that the c-egg is under a constant predation pressure which is unaffected by whether the nest is conspicuous (no-cover) or concealed (cover) and that this is different to the predation pressure on the a- and b-eggs since these are affected by whether the nest is in a conspicuous or concealed position. One speculative explanation for these results is that the a- and b-eggs are more likely to be predated during the laying period whereas the c-egg is more likely to be predated during the asynchronous hatching of the eggs. During the laying period the nest is often left unguarded and in areas where there is little or no cover the eggs will be conspicuous and much more likely to be preyed upon than those eggs in nests which are concealed in the surrounding vegetation. The change-over from laying to incubation behaviour may be more rapid in those birds which are older, more experienced, have an established pair status, and a greater individual fitness. One reason why only the a-egg of 3-egg clutches, whereas both the a- and b-egg of 2-egg clutches had a significantly higher percentage predation in the no-cover areas, could be that those birds laying 3-egg clutches are older and more experienced than those birds laying 2-egg clutches. In contrast, the change-over of adults from incubation to 'parental' behaviour after a chick appears in the nest could result in chilling or damage to those eggs which remain. This threat will be highest for the c-egg in clutches of 3 and will remain unaffected by whether the nest is in a cover or no-cover area; in this study, such eggs would have been recorded as having been predated.

There is no appreciable difference in the hatching success for the a-, b- and c-egg of 3-egg clutches in the no-cover areas and this result is comparable to that found by Parsons (1971) for the Herring Gull (refer to section 4.2 and Table 11).

Table 11. Hatching success of eggs in relation to order of laying in no-cover areas compared to the results of Parsons (1971)

This study

	No. laid	No. hatched	% hatched	χ^2_2	P
a-egg	191	135	70.7		
b-egg	189	136	71.9	3.5	N.S.
c-egg	190	121	63.7		

Parsons (1971)

	No. laid	No. hatched	% hatched	χ^2_2	P
a-egg	449	349	77.7		
b-egg	445	351	78.9	0.47	N.S.
c-egg	443	341	77.0		

CHAPTER 5

Fledging Success

5.1 Laying sequence and post-hatching mortality

It is known that most of the pre-fledging mortality in the Herring Gull occurs soon after hatching and over half within the first week of life (Paynter 1949, Harris 1964, Kadlec and Drury 1968, Parsons 1975b and Davis 1975). Therefore in this study the mortality of the chicks was divided into that which occurred within 5 days of hatching (post-hatching) and mortality after this period (pre-fledging). Table 12 shows the percentage mortality found from broods of three for the Lesser Black-backed Gull and compares them with those found by Parsons (1968) and Dighton (1973) for the Herring Gull and mixed Lesser Black-backed/Herring Gull respectively. The third chick suffered a significantly higher post-hatching mortality than its siblings ($P<0.01$), but this was not apparent after the first 5 days of its life. One difference between this study and those of Parsons and Dighton is that in this study the differential post-hatching mortality is completed within 5 days as opposed to 7 days.

When more than one chick of the brood died there was a trend, although not significant, for the b-chick also to show a greater mortality than the a-chick (Table 13). A comparison of these results to those found by Parsons (1975b) also shows that the overall mortality of the Herring Gull in the first week of its life is 31.9% compared to 46.9% for the Lesser Black-backed Gull in this study and that this difference is attributable to the significantly higher mortality ($P<0.001$) of the a- and b-chicks in this study.

In those clutches of 3 in which only two eggs hatch per nest no significant differences were detected in mortality between siblings (Table 14a). However if the mortality of the b-chick is compared between

Table 12. Mortality of chicks from broods of three according to the sequence of hatching

		Total dead chicks	Number of dead chicks (Percentage in parenthesis)			Significance of difference between the a-, b- and c-chick		
			a-chick	b-chick	c-chick	a- and b-chick	a- and c-chick	b- and c-chick
Post-hatching	This study (Lesser Black-backed Gull) (0-5 days old)	192	44 (35.2)	57 (45.3)	91 (62.5)	$\chi^2_2 = 2.99$ P N.S.	$\chi^2_2 = 19.8$ P<0.01	$\chi^2_2 = 7.25$ P<0.01
	Parsons (Herring Gull) (0-7 days old)	267	(20.6)	(21.7)	(57.7)		P<0.001	
	Dighton (mixed Lesser Black-backed/Herring Gull colony) (0-7 days old)	138	48 (29.4)	39 (22.1)	51 (45.5)	$\chi^2_2 = 0.093$ P N.S.	$\chi^2_2 = 7.46$ P<0.01	$\chi^2_2 = 8.47$ P<0.01
Pre-fledging	This study (Lesser Black-backed Gull) (after 5 days old)	81	31 (38.3)	27 (40.3)	23 (41.8)	$\chi^2_2 = 0.027$ P N.S.	$\chi^2_2 = 0.074$ P N.S.	$\chi^2_2 = 0.012$ P N.S.
	Parsons (Herring Gull) (after 7 days old)	82	(28.0)	(35.4)	(36.6)		P N.S.	

Table 13. Laying sequence and post-hatching mortality in broods of three chicks (mortality within 5 days of hatching

(Percentage in parenthesis)

This study (1981)

No. chicks dying in brood	No. nests	a-chick		b-chick		c-chick
Nil (all survived)	28	28		28		28
One chick	60	8		11	***	41
Two chicks	38	20(52.6)		26(68.4)	*	30(78.9)
Three chicks	26	26		26		26
Total no. chicks hatched		152		152		152
Total no. died		54		63	***	97
% mortality		35.5		41.4		63.8

Parsons (1971)

No. chicks dying in brood						
Nil (all survived)	90	90		90		90
One chick	130	18		11	***	101
Two chicks	40	18	*	28	***	34
Three chicks	19	19		19		19
Total no. chicks hatched		279		279		279
Total no. died		55		58	***	154
% mortality		19.7		20.8		55.2

Significant differences between a-chick and other chicks in the hatching sequence : * $P<0.05$ *** $P<0.001$

Table 14. Hatching sequence and post-hatching mortality (within 5 days of hatching) when only two Lesser Black-backed Gull chicks hatched per nest

(a)

	No. nests	No. dying	Percentage Mortality	Significance of diff.	
				χ^2_1	P
a-chick	50	27	54.0	0.009	N.S.
b-chick	49	26	53.1		
(c-egg failed to hatch)					
a-chick	15	9	60.0	0.056	N.S.
c-chick	14	9	64.3		
(b-egg failed to hatch)					
b-chick	27	8	29.6	0.92	N.S.
c-chick	26	11	42.3		
(c-egg failed to hatch)					

(b)

b-chick (nests where c-egg failed to hatch)	49	26	53.1	3.86	<0.05
b-chick (nests where a-egg failed to hatch)	8	19	29.6		

those nests where either the a- or c-egg fail to hatch, then its mortality is significantly smaller in nests where the a-egg fails to hatch than in those nests where the c-egg fails to hatch (Table 14b). This would indicate that asynchronous hatching is an important factor contributing to the differential mortalities of the a-, b- and c-chicks.

Egg size was not found to affect chick survival in this study (Table 15).

5.2 Nesting density and amount of cover at the nest

The fledging success of the a-, b- and c-chicks does not differ between densities A, B, C or D in the cover or no-cover areas (Tables 16 and 17). However if data for the first and last chick to hatch from clutches of 2 and 3 are combined, then the fledging success is significantly higher at densities C and C and D respectively in areas of no-cover (Table 18, Fig. 6). In cover areas the situation is reversed: the survival of the first and last chicks is not influenced by nesting density but the mid-chick suffers a significantly lower fledging success at density A when density A is compared with the combined densities of B, C and D (Table 18, Fig. 6).

It can be concluded that there was a trend, though not significant, for the overall fledging success of chicks to be highest at density C in the no-cover areas. When the data of densities A, B and D are combined, the difference in fledging success between them and density C is significant ($P<0.05$) (Table 19). Explanations for this trend may be connected to the different chick predation pressures occurring at high and low densities and in cover and no-cover areas. These are similar to the different egg predation pressures which have been fully described in Section 4.4.

Table 15. Comparing chick mortality within a week of hatching and calculated egg volume

		Egg volume cc						
		68	68-72	72-76	76	Total	X_3^2	P
	No. hatched	41	37	24	14	102		
a-egg	No. died	18	17	12	5	47	0.76	N.S.
	% mortality	43.9	46.0	50.0	64.3	46.1		
	No. hatched	23	23	30	32	108		
b-egg	No. died	11	10	15	14	50	0.34	N.S.
	% mortality	47.8	43.5	50.0	43.7	46.3		
	No. hatched	48	26	16	5	95		
c-egg	No. died	28	17	11	5	61	3.67	N.S.
	% mortality	58.3	65.4	68.8	100.0	64.2		
	No. hatched	112	86	70	51	319		
Total	No. died	57	44	38	24	163	0.15	N.S.
	% mortality	50.9	51.2	54.3	47.0	51.1		

Table 16. Fledging success of the a-, b- and c-chicks from clutches of 2 and 3 in densities A, B, C and D. NO-COVER

CLUTCH SIZE 3

	Density	No. Hatched	No. Fledged	% Fledged	χ^2_3	P
a-chick	A<6m	24	8	33.3		
	B 6-9m	39	12	30.8		
	C 9-12m	18	8	44.4		N.S.
	D>12m	9	3	33.3		
b-chick	A<6m	29	10	34.5		
	B 6-9m	40	15	37.5		N.S.
	C 9-12m	18	6	33.3		
	D>12m	14	5	35.7		
c-chick	A<6m	27	4	14.8		
	B 6-9m	38	5	13.1		N.S.
	C 9-12m	16	5	31.2		
	D>12m	10	3	30.0		

CLUTCH SIZE 2

	Density	No. Hatched	No. Fledged	% Fledged	χ^2_3	P
a-chick	A<6m	7	1	14.3		
	B 6-9m	15	5	33.3		
	C 9-12m	5	4	80.0		N.S.
	D>12m	3	0	0.0		
b-chick	A<6m	7	1	14.3		
	B 6-9m	16	3	18.7		N.S.
	C 9-12m	5	2	40.0		
	D>12m	2	1	50.0		

Table 17. Fledging success of the a-, b- and c-chicks from clutches of 2 and 3 in densities A, B, C and D. COVER

CLUTCH SIZE 3

	Density	No. Hatched	No. Fledged	% Fledged	χ^2_3	P
a-chick	A<6m	15	6	40.0		N.S.
	B 6-9m	34	16	47.1		
	C 9-12m	25	11	44.0		
	D>12m	44	12	27.3		
b-chick	A<6m	14	2	14.3	A	<0.05
	B 6-9m	32	15	46.9	vs	
	C 9-12m	29	14	48.3	B C & D	
	D>12m	40	13	32.5	$\chi^2_1 = 3.88$	
c-chick	A<6m	11	1	9.1		N.S.
	B 6-9m	26	7	26.9		
	C 9-12m	29	8	27.6		
	D>12m	45	14	31.1		

CLUTCH SIZE 2

	Density	No. Hatched	No. Fledged	% Fledged	χ^2_3	P
	A<6m	9	4	44.4		N.S.
	B 6-9m	18	7	38.9		
	C 9-12m	17	6	35.3		
	D>12m	21	7	33.3		
b-chick	A<6m	7	5	71.4		N.S.
	B 6-9m	14	4	28.6		
	C 9-12m	12	3	25.0		
	D>12m	18	5	27.8		

Table 18. Fledging success of the first and last chick to hatch from clutches of 2 and 3 in densities A, B, C and D

FIRST CHICK TO HATCH (NO-COVER)

	A <6m	B 6-9m	C 9-12m	D >12m	χ^2_3	P	A, B and D vs C
No. hatched	31	54	23	12			$\chi^2_1 = 4.1 \quad P<0.05$
No. fledged	9	17	12	3		N.S.	
% fledged	29.0	31.5	52.2	25.0			

LAST CHICK TO HATCH (NO-COVER)

							A and B vs C and D
No. hatched	34	54	21	12			$\chi^2_1 = 5.19 \quad P<0.05$
No. fledged	5	8	7	4		N.S.	
% fledged	14.7	14.8	33.3	33.3			

MID CHICK TO HATCH (COVER)

							A vs B, C and D
No. hatched	14	32	29	40			$\chi^2_1 = 3.88 \quad P<0.05$
No. fledged	2	15	14	13		N.S.	
% fledged	14.3	46.9	48.3	32.5			

FIG: 6 Fledging success of the a-, b- and c-chicks between densities A, B, C and D in the cover and no-cover areas

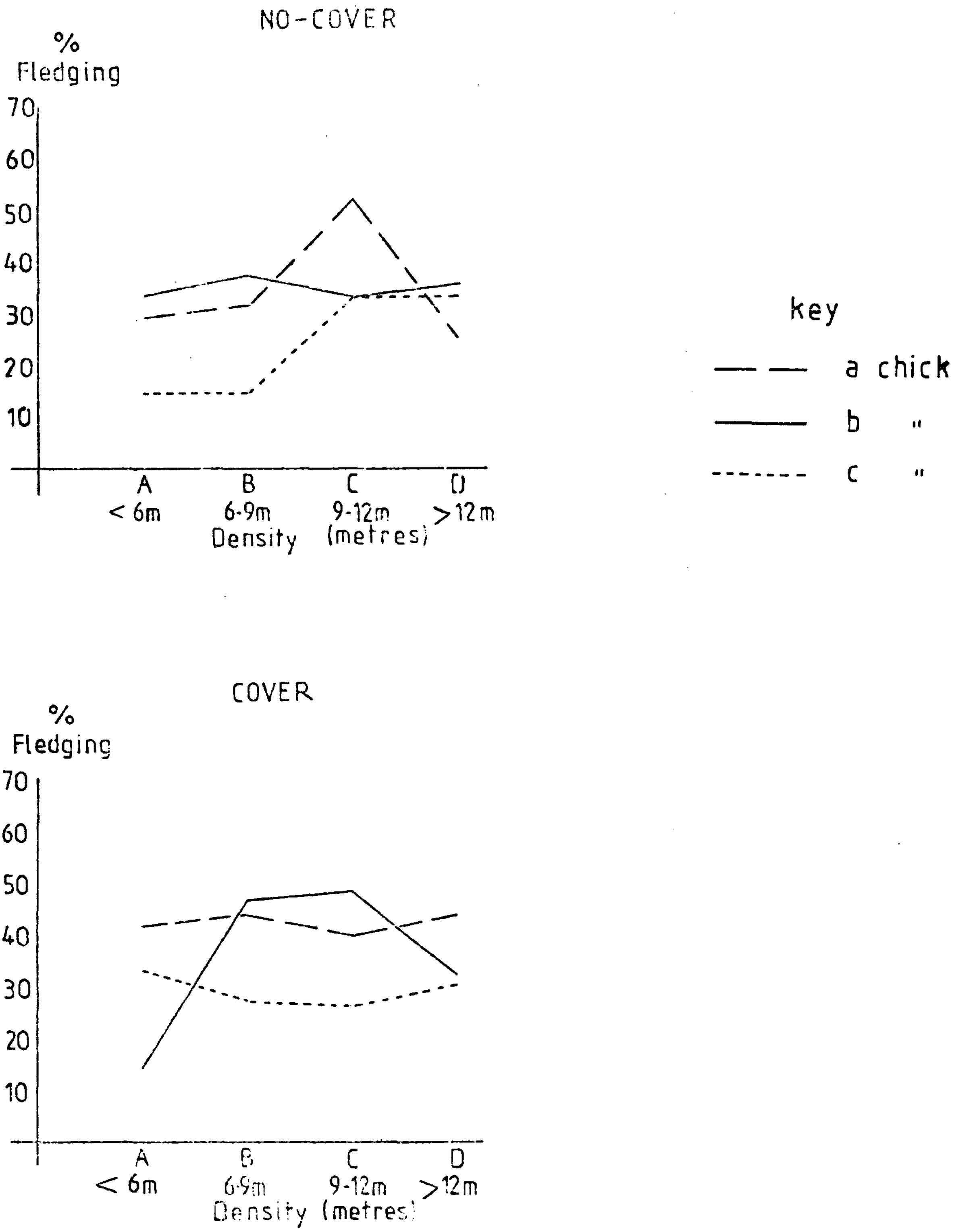


Table 19. Overall fledging success from densities A, B, C and D in the cover and no-cover areas

COVER

	A	B	C	D
	<6m	619m	9-12m	>12m
No. chicks hatched	65	144	146	201
No. chicks fledged	22	58	58	70
% chicks fledged	34	40	39	35

NO-COVER

No. chicks hatched	101	158	68	41
No. chicks fledged	28	43	29	13
% chicks fledged	28	27	43	32

Significance : A vs C $\chi^2_1 = 4.05$ $P<0.05$

B vs C $\chi^2_1 = 4.28$ $P<0.05$

D vs C $\chi^2_1 = 1.29$ P N.S.

5.3 Transfer experiment

Table 20 shows the post-hatching mortality (0-7 days old) of chicks from broods of 3 a-chicks, 3 b-chicks and 3 c-chicks. Firstly it should be pointed out that the chick hatching first in the sequence, whether it be an a-, b- or c-chick suffers a higher mortality than that of the 'normal' a-chick. This could be due to the adverse effects of handling some of the chicks during the first 1-2 days of their lives (see Section 3.4). However the results remain comparable since the chicks were all handled in a similar manner.

The results show that regardless of whether the chick is an a-, b- or c-chick the post-hatching mortality of those chicks hatching first and second is significantly lower ($P<0.05$) than that of the chick which is last to hatch in the order of hatching. There was no significant difference in the pre-fledging mortality of the a-, b- or c-chicks (Table 21). These results indicate that order of hatching is the predominant factor determining the post-hatching mortality of the chick and that egg size plays an unimportant role. In agreement with this study, Parsons' (1975) study on the Herring Gull showed that the sequence of hatching has a significant effect on the survival of the chick. However, Parsons also found that, even when hatching last, the a-chick did not suffer as high a mortality as the normal c-chick or that the c-chick hatching first survive as well as its siblings. He concluded that much of the remaining differential mortality was attributable to egg size (Parsons 1970).

In this experiment egg size was not found to have any significant effect on the post-hatching mortality of the chicks. An explanation for this may be connected to the much smaller egg volumes of the a-, b- and c-eggs in a relaid Lesser Black-backed Gull clutch. The mean volume for

Table 20. Post-hatching mortality (o-7 days old) of chicks from broods of 3 a-eggs, 3 b-eggs and 3 c-eggs according to the sequence of hatching. (Post-hatching mortality of chicks hatching in a normal sequence in parenthesis)

	Hatching sequence	First	Second	Third	Total
Broods of	Total no. hatching	11	11	11	33
3	Total no. dead	6	2	8	16
a-chicks	% mortality	54.5	18.2	72.7	48.5(40.8)
Broods of	Total no. hatching	11	11	9	31
3	Total no. dead	6	6	7	19
b-chicks	% mortality	54.7	54.7	77.8	61.3(57.2)
Broods of	Total no. hatching	32	31	30	
3	Total no. dead	17	15 *	22	
		└────────	────────┘ *	└────┘	
c-chicks	% mortality	53.1	48.4	73.3	
		(40.8)	(57.2)	(73.3)	

Note: Significance of difference between chicks in second and third position : * P<0.05

Significance of difference between chicks in first and second position combined versus third position: └──────┘ ∘ └──┘ P<0.05

Table 21. Pre-fledging mortality of chicks from broods of 3 a-chicks, 3 b-chicks and 3 c-chicks according to the sequence of hatching

	Hatching sequence	First	Second	Third	Total
Broods of	Total no. pre-fledging	5	9	3	17
3	Total no. dead	5	3	0	8
a-chicks	% mortality	100	33.3	0.0	47.0
Broods of	Total no. pre-fledging	5	5	2	12
3	Total no. dead	3	2	2	7
b-chicks	% mortality	60.0	40.0	100	58.3
Broods of	Total no. pre-fledging	5	2	3	10
3	Total no. dead	4	1	2	7
c-chicks	% mortality	80.0	50.0	66.1	70.0
	Total no. pre-fledging	15	16	8	
	Total no. dead	12	6	4	
	% mortality	80.0	37.5	50.0	

the c-egg of a Herring Gull is 69.32cc ± 0.30 and in the relaid clutches of the Lesser Black-backed Gull all the eggs were within 3.3cc of this volume (Table 1). Also the volume difference between the largest and smallest eggs in a clutch of 3 is 8.6cc for the Herring Gull as opposed to 5.1cc in the relaid clutches of the Lesser Black-backed Gull. Thus although the mean egg volumes for the relaid Lesser Black-backed Gull clutches are all significantly different from one another, they are not considered to have any significant effect on the post-hatching survival of the chick.

5.4 Growth of chicks

A plot of the log of the mean chick weight against time gave an approximately straight line between days 2-7 (Fig. 7). Growth rates were therefore calculated for the a-, b- and c-chicks during this period of time (Table 22a). It was found that the c-chick had a significantly lower log growth rate ($P<0.05$) than any of the other chicks. The most likely explanation for this was that there were more zero and negative values for the growth rates of each c-chick in the calculation of its overall growth rate than there were for either of the a- or b-chicks.

The results indicate that one of the reasons for the higher mortality of the c-chick during the post-hatching period is that it is being selectively starved. It was observed that in those broods of 3 where 2 of the chicks were sturdy and the other one still very small, then the latter was invariably the c-chick.

In the transfer experiment, the growth rate was lower than expected for the a-chick in the first hatching position and for the a- and b-chick in the second hatching position (Table 23). This may be due to small sample sizes and the fact that some of the a- and b-chicks were handled during the first 1-2 days of their lives.

FIG: 7 Log of mean chick weight against time (days)

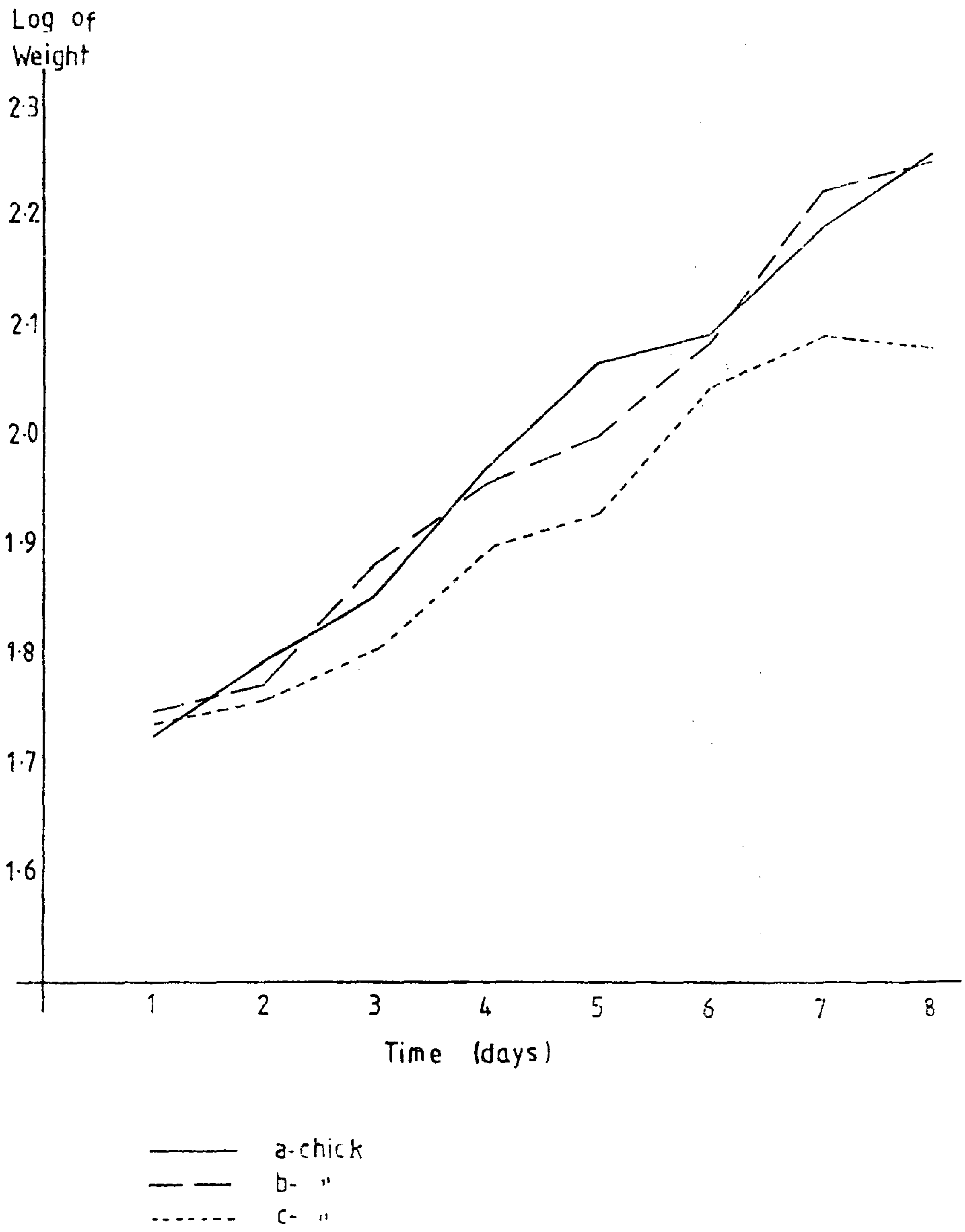


Table 22. Log of the mean growth rate of the a-, b- and c-chick

	Sample size	Mean growth rate	Standard deviation	Student d-test and significance			
				a- and b-chick	a- and c-chick	b- and c-chick	a- and b- vs c-chick
a-chick	32	0.435	0.173	d = 0.44	d = 2.22	d = 1.72	d = 2.49
				N.S.	$P<0.05$	N.S.	$P<0.05$
b-chick	37	0.410	0.293				
c-chick	32	0.259	0.414				
a- and b-chick	73	0.452	0.210				

Table 23. Log of the mean growth rate of the a-, b- and c-chicks in the transfer experiment

	Hatching sequence	First	Second	Third
	Sample size	7	10	5
a-chicks	Mean growth rate	0.283	0.375	0.478
	Standard deviation	0.526	0.401	0.129
	Sample size	6	5	4
b-chicks	Mean growth rate	0.491	0.244	0.466
	Standard deviation	0.122	0.436	0.107
	Sample size	10	9	8
c-chicks	Mean growth rate	0.544	0.441	0.552
	Standard deviation	0.093	0.199	0.121

CHAPTER 6

Discussion

The last chick to hatch in broods of three in Herring Gulls has been shown to suffer a higher mortality than its siblings (Parsons 1970, 1971; Davis 1975) and a similar decline in the survival of chicks in relation to hatching sequence has been reported in Arctic Terns, Black-headed Gulls, Snow Geese and the South Polar Skua (Lemetyinen 1972, Lundberg and Vaisanen 1979, SyroechKovsky 1975, Procter 1975). In this study it was found that the c-egg was significantly smaller than either the a- or b-eggs in the relaid clutches of the Lesser Black-backed Gull and that asynchrony of hatching occurred. There was no significant difference between the percentage of first-laid and re-laid clutches of 3 for the Lesser Black-backed Gull (75.0% and 70.0% respectively) whereas a significant decline occurred for the Herring Gull (58.0% and 40.3% respectively). This indicates that the Lesser Black-backed Gull can continue putting its energy reserves into egg production as the season progresses whereas the Herring Gull cannot, and that the Lesser Black-backed Gull is therefore better adapted to breeding later in the season. One explanation for this could be connected to the ability of the Lesser Black-backed Gull to lay smaller viable c-eggs than the Herring Gull. In contrast to the results found by Parsons (1971) for the Herring Gull, a reduction of 3.3cc, as opposed to 0.7cc, took place in the mean volume of the c-egg from the relaid clutches of 3 for the Lesser Black-backed Gull.

A significant decline in hatching success with laying sequence was found to occur in clutches of 3 and in clutches of 2 when only one egg hatched. An explanation for at least part of this variation can be offered in those studies in which egg size has been positively correlated to hatching success. However in this study no such correlation was found and other explanations must be looked for. Hatching success of the a- and b-egg was shown to be directly influenced by whether the nest was in a cover or no-cover area. The a- and b-eggs had a significantly higher hatching success than the c-egg in the cover areas, whereas in the no-cover areas the hatching success of the eggs was not significantly different from one another or from the c-egg in the cover areas. This supports the suggestion that hatching success was influenced by factors other than variation in egg size. The percentage predation of the a-egg from clutches of 3 and both the a- and b-eggs from clutches of 2 was significantly lower in the cover areas than in the no-cover areas. An explanation of the results may therefore be connected to the different predation pressures on the a-, b- and c-eggs . It was suggested (refer to Section 4.4) that the a- and b-eggs were more vulnerable to being predated during the laying period and that this was influenced by whether the nest was in a conspicuous (no-cover) or concealed (cover) position. On the other hand, the c-egg was more vulnerable to being predated during the hatching period and this was not affected by whether the nest was in a concealed or conspicuous position. Asynchrony of laying, amount of vegetation at the nesting site and the resultant predation pressures could therefore be important factors contributing to the decline in hatching success with laying sequence. Other factors affecting hatching success may include the differential fertility between eggs in relation to order of laying (refer to Section 4.3).

Egg size has been shown to be positively correlated with hatching success and chick survival in various species of wild birds (Davis 1975, Lloyd 1979, Lundberg and Vaisanen 1979, Nisbet 1978, Parsons 1970, Schifferli 1973, SyroechKovsky 1975 and Thomas 1980). However in this study, egg size had no significant effect on either hatching or fledging success of the Lesser Black-backed Gull. This may be explained by the fact that data for hatching and fledging success was only available for relaid clutches and all eggs laid in the relaid clutch of a Lesser Black-backed Gull had a significantly smaller mean egg volume and larger shape index than those laid in the first clutch (refer to Section 4.1).

Post-hatching mortality of the third chick was significantly higher than either the first or second chick in broods of three. Similar results have been found for the Herring Gull, Arctic Tern, Black-headed Gull, Snow Goose and the South Polar Skua (Parsons 1970, 1971, Davis 1975, Lemmetyinen 1972, Lundberg and Vaisanen 1979, SyroechKovsky 1975, Procter 1975). Parsons (1975b) showed that both order of hatching and egg size affects the survival of the c-chick in Herring Gulls. This chick emerges from a smaller egg, has a smaller yolk reserve at hatching and faces greater competition from its older siblings during the first few days after hatching. However, in this study small egg size of the c-egg was not shown to have any effect on the post-hatching survival of the chick. This was further substantiated by the results of the transfer experiment which showed that, regardless of whether the chick hatched from an a-, b- or c-egg, the post-hatching mortality of those chicks hatching first and second was significantly lower ($P<0.05$) than that of the chick which is last to hatch in the hatching sequence. Measurement of chick growth-rates between the first 2-7 days of their lives showed that the c-chick had a significantly lower growth rate than either the a- or b-chick. An explanation for this was connected to the selective starvation of the c-chick (refer to Section 5.4).

Hatching asynchrony is regarded as an adaptation to an unpredictable food supply reducing the brood size to the availability of food without jeopardising the survival of the older young (Lack 1954). When food is plentiful, all young are reared, but when food is scarce, the late-hatched chick is selectively starved and dies before it can consume food better fed to the sturdier young more likely to survive (O'Conner 1978, Procter 1975). In this study the fledging success of chicks from broods of 1, 2 and 3 did not significantly differ and this indicates that food was not in short supply. Also 70.3% of the chick mortality occurred within the first 5 days of the chick's life when their food demands were still relatively small. These two results suggest that food availability was not a limiting factor in this study. However, asynchronous hatching and selective starvation have both been shown to contribute to the higher mortality of the third chick and only 6% of the birds laying clutches of 3 reared 3 chicks to fledging. Parsons (1975b) suggested that for the Herring Gull inadequate parental behaviour may have contributed to the mortalities noted during his experiment. This may also be true for the Lesser Black-backed Gull in this study. Even if there was no shortage of food available to the parents, inexperienced breeders may provide insufficient food for their young. Under these circumstances, asynchronous hatching and selective starvation would still be important in reducing the brood size to the numbers that an individual can manage. Alternatively, experienced breeders may adopt the process of selective starvation as a defence mechanism against a high predation pressure. It is known that unfed chicks are more active and wander further from the parents than recently fed chicks (Hunt and Hunt 1976). Thus a predator is more likely to attack the selectively starved c-chick from a brood of three.

SUMMARY

1. Various aspects of the breeding success of re-laid clutches of the Lesser Black-backed Gull were studied on Rockcliffe Marsh, Cumbria. The study aimed to determine the relative importance of egg size, sequence of hatching and nesting density to the fate of the a-, b- and c-chicks respectively in the re-laid clutches of 1, 2 and 3.

2. In first-laid clutches the volumes of the a- and b-eggs were not significantly different but were both a significant 7% larger than the volume of the c-egg. There was a significant reduction of at least 4% between the egg volumes of first-laid and re-laid clutches. In the repeat clutches the volumes of the a-, b- and c-eggs were all significantly different from one another, the b-egg being the largest and the c-egg the smallest.

3. In both clutches of 3 and clutches of 2 where only one egg hatched, a significant decline in hatching success with laying sequence occurred, Hatching success was not correlated with egg size although there was a trend for hatching success to increase with egg size.

4. The last laid egg in clutches of 2 and 3 was found to be significantly less fertile* ($P<0.05$) than the egg laid immediately before it.

5. In clutches of 3 the c-egg had a significantly higher percentage predation than either the a- or b-egg.

6. Division of the colony into cover and no-cover areas showed that the decline in hatching success with laying sequence was only significant in the cover areas. In the cover areas the a-egg from clutches of 3 and both the a- and b-eggs from clutches of 2 had a significantly lower percentage predation than in the no-cover areas.

* Measured by number of eggs left unhatched in a nest.

7. It was postulated that the a- abd b-eggs were more likely to be predated during the laying period whereas the c-egg was more likely to be predated during the hatching period. The predation of the a- and b-egg alters according to whether the nest is in a cover or no-cover position, being greater in the no-cover area, whereas the predation of the c-egg remains unaltered by whether the nest is in a cover or no-cover area.

8. Hatching success of the a-egg was shown to be highest at density C (9-12m) in the no-cover areas, but this was not significant.

9. In broods of 3 the third chick had a significantly higher post-hatching mortality than its siblings but this was not apparent after the first 5 days of life.

10. A transfer experiment was carried out to evaluate the importance of egg size and sequence of hatching in the differential mortality of the third chick. The results showed that, regardless of whether the chick hatched from an a-, b- or c-egg, the post-hatching mortality (0-7 days) of the chicks which hatched first and second was significantly lower ($P<0.05$) than of the chick which hatched last in the hatching sequence. No relationship was found between egg size and post-hatching mortality.

11. Measurement of chick growth rates between days 2-7 showed that the c-chick had a significantly lower growth rate than either the a- or b-chick from broods of 3. This was due to the larger number of zero and negative growth rates for the c-chicks in the calculation of its overall growth rate. It was suggested that selective starvation of the c-chick occurred.

12. There was a trend, though not significant, for the overall fledging success of chicks to be highest at density C (9-12m) in the no-cover areas.

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