Aspects of the breeding biology of Herring and Lesser Black-backed Gulls (Larus argentatus and L. fuscus) on Rockcliffe Marah, Cumbria

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Aspects of the breeding biology of Herring and Lesser Black-backed Gulls (*Larus argentatus* and *L. fuscus*) on Rockcliffe Marsh, Cumbria

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CHAPTER ONE

Introduction

The breeding habits of birds have evolved through natural selection with the result that the birds concerned produce, on average, the greatest possible number of surviving young. The environmental factors which may exert selection pressure on bird populations are i) the availability of food for the young and, to a lesser extent, for the laying female, and ii) predation on eggs, young and adults (Lack 1968). These factors will influence the two basic parameters of breeding habit, namely where to breed and when to breed.

Gulls are colonial breeders. Predation pressure is thought to be an important factor in the evolution of the colonial habit (Krunk 1964, Tinbergen 1967). Collective alarm signalling and mobbing of predators affords a pair considerably more protection than if they were nesting solitarily.

In gulls, as in most animals of temperate regions, breeding is confined to a breeding season and this may be considered as a necessary adaptation to a restricted food supply (Lack 1954). Seasonal decline in egg size and clutch size has been recorded in a number of birds including the Kittiwake, ***Rissa tridactyla*** (Coulson and White 1961, 1963), the Shag, ***Phalacrocorax aristotelis*** (Coulson, Potts and Horobin 1969) and the Herring Gull, ***Larus argentatus*** (Parsons 1972) and this has been interpreted as a reflection of the decreased chances of raising young as the season progresses, due to diminishing food supplies (Perrins 1970). Perrins concludes that, if food is limiting, there is an overwhelming advantage in breeding early.

Several studies have shown a seasonal decline in breeding success in various species, including the Lesser Black-backed Gull, ***Larus fuscus*** (Brown 1967, Davis and Dunn 1976), the Herring Gull (Paynter 1949, Kadlec ***et al.*** 1969, Nisbet and Drury 1972, Burger and Shisler 1980) and the Kittiwake (Coulson and White 1958), but the role of food availability in this decline is questionable.

There is considerable evidence to suggest that gull populations are not, at least at present, being limited by their food supply. The numbers of European seabird species have increased over the last half century, the numbers of both Herring and Lesser Black-backed Gulls in Britain doubling in the last twenty years (Harris 1964). The causes are thought to be increased fish waste and human rubbish (Hickling 1967) contributing to low first year and adult mortalities, especially in the winter months (Harris 1963).

The survival of chicks from supplemented broods of the Glaucous-winged Gull, *Larus glaucescens* (Vermeer 1963) and Herring and Lesser Black-backed Gull (Harris and Plumb 1965) indicates that food is not a factor limiting the number of chicks raised. The lack of correlation between brood size and fledging success (Brown 1967, Parsons 1975) also supports this view. Parsons (1975) delayed clutches by egg removal and found that chicks hatching at the peak of normal and delayed hatching fared equally well, and that late layers, within a group, irrespective of season, did worst.

On this evidence, seasonal variation in breeding success is unlikely to be the result of limited food availability. Seasonal changes in the age and experience of breeding birds offer a more plausible explanation.

Studies on the Kittiwake (Coulson and White 1963) and the Shag (Coulson, Potts and Horobin 1969) have shown that younger birds tend to lay later and produce smaller eggs in smaller numbers. They may also occupy inferior nest sites on the edge of the colony (Coulson 1968) and consequently be exposed to greater egg and chick losses than older birds nesting in the centre of the colony. Breeding experience is also important. In the Kittiwake (Coulson and White 1958) and the Gannet, *Sula bassana* (Nelson 1966), younger less experienced birds may raise fewer chicks due to inadequate incubation and care of the young.

Breeding in colonial birds is often highly synchronous with small subcolonies showing the most synchrony (Burger and Shisler 1980, Davis and Dunn 1976, Parsons 1976). Some studies have shown that synchronised layers, irrespective of season, achieve the highest breeding success (Patterson 1965, Nisbet 1975, Parsons 1976, Ryder and Ryder 1981).

The advantage of synchronous egg laying and hatching is thought to lie in decreased losses to predators during peak laying and hatching periods. In all the studies cited above, egg and chick loss was thought to be primarily due to either a predator of another species or a cannibalistic conspecific. However, synchronisation only decreases losses to predators if the predation rate remains constant throughout the season. Nisbet (1975) was able to show that the biomass of prey taken was roughly constant throughout the season, resulting in the lowest proportion of chicks being taken from those hatching at the mid-season peak. Parsons (1975) also recorded a constant number of chicks taken in one season by cannibalistic Herring Gulls, despite fluctuating numbers being available to them.

However, if predation pressure is not constant, then synchrony may not be selected for. A second type of predation can be distinguished; that due to neighbour interference (Hunt and Hunt 1976). This may involve egg stealing and/or chick mortalities due to territorial aggression by neighbouring gulls.

Intraspecific predation in gulls has frequently been identified as a major cause of egg or chick loss (Paynter 1949, Harris 1964, Brown 1967, Vermeer 1970, Parsons 1975), but in most cases the predatory habit has been attributed to birds lacking breeding status (Tinbergen 1953). More recent studies (Davis and Dunn 1976, Burger 1980) have indicated that aggressive encounters between two neighbours are frequently responsible for egg losses. Davis and Dunn further observed that, in the majority of cases, the aggressors were all adult conspecifics which had lost their own clutches shortly beforehand. Egg predation rate was not uniform, but increased to a maximum during the peak egg laying period. They suggest that gulls which have lost their eggs or chicks are predisposed to steal those of their neighbours and that this leads to a spiral of increasing numbers of failed breeders and increasing egg loss as the season progresses.

Pecking of trespassing chicks by neighbouring adults had been shown to be a major cause of chick mortality in the Herring Gull (Tinbergen 1953) and in the Glaucous-winged Gull (Hunt and Hunt 1976). Hunt and Hunt also showed that incubating gulls were less aggressive than gulls in the chick stage and also that territory size increases during the chick stage. Increase of territory size during the chick stage has also been shown for Herring Gulls (Burger 1980). Hunt and Hunt suggest that these two factors will lead to an increase in chick mortalities due to territorial aggression during the peak hatching period.

Therefore, if neighbour interference is an important factor in egg and chick losses, early, rather than synchronous, breeding should be favoured. Davis and Dunn (1976) found that, although synchronous breeding was evident, the peak of breeding success preceded peak laying. They suggest that heavy losses due to neighbour interference may be a relatively recent phenomena associated with the high densities found in rapidly expanding gull colonies.

Studies to determine the effect of nesting density on breeding success have been both confusing and inconclusive, some finding no correlation between the two (Vermeer 1963, Patterson 1969, Dexheimer and Southern 1974, Ryder and Ryder 1981) and others finding a positive correlation between breeding success and low density (Butler and Trivelpiece 1980), median density (Parsons 1976) and high density (Harris 1980).

Clumping of nests in space, as in time, serves an anti-predator function and this is likely to be an important selective pressure leading to the evolution of the colonial habit. In the Gannet (Nelson 1978), the Herring Gull (Burger and Shisler 1980) and the Guillemot , *Uria aalge* (Birkhead 1977), it was found that an aggregation of nests resulted in earlier and more synchronous laying. Thus it appears that a causal relationship has evolved between spatial and temporal clumping. This is reflected in social stimulation being required for settling, territory acquisition, ovulation in the female and for copulation (MacRoberts and MacRoberts 1972).

However, as nesting density increases, territory size decreases and neighbour interference increases. External predation selects for high density breeding, whilst high levels of neighbour interference favours low density nesting. Thus, the opposing selection pressures of external predation and neighbour interference, on clumping in space and on clumping in time, are identical.

Hunt and Hunt (1976) have put forward a model to show how the balance between these two types of predation influence the optimum laying date and the optimum territory size. The model predicts that high density, synchronous breeding is favoured in cases where external predation is the most significant cause of egg and chick loss, whereas high levels of neighbour interference favour low density, early breeding. Vermeer (1970), in a comparative study on the California Gull, *Larus californicus* and the Ring-billed Gull, *Larus delawarensis*, found that the nests of the smaller Ring-billed Gulls showed a more clumped distribution than those of the California Gulls. He suggested that there is an inverse relationship between the size of gull species and the tendency to clump. The Hunt and Hunt model provides a functional explanation for this relationship. That is, in small gull species, where external predation is likely to be high and inter-neighbour aggression low, nesting is at a high density to facilitate predator defence. Conversely, larger gull species are potentially more dangerous as neighbours and have fewer external predators, so nests are more widely spaced. In support of this, Butler and Trivelpiece (1980) found that fledging success in the Greater Black-backed Gull, *Larus marinus*, was lower in high density areas, and they attributed this to observed increased levels of aggression in these areas, leading to high levels of chick mortalities due to neighbour interference. However, they also found that the majority of birds were nesting at these seemingly disadvantageous high densities, and one explanation they offer, similar to that advanced by Davis and Dunn (1976), is that this high level of neighbour interference is a recent phenomena associated with the rapid increase in gull numbers.

The evolution of cannibalism, with its potentially dispersive effect (Hamilton 1971), as a response to increasing density, although very difficult to examine, can be seen as a means of applying a density dependent brake to the expansion of the population such that the threshold density resulting in heavy losses due to neighbour interference is not reached. It may be that the recent, rapid expansion of gull populations has outstripped the slower process of selection for cannibalistic behaviour, and that heavy losses due to neighbour interference can be likened to the "shock disease" recorded in some overcrowded mammals (Barnet 1964).

Another important parameter in breeding habit is choice of nest site. Areas are rarely uniform with regard to the amount of cover afforded chicks by the vegetation. Brown (1967), in a study on a mixed colony of Herring and Lesser Black-backed Gulls, found that Lesser Black-backed nests in "cover" (i.e. beside clumps of marram or bracken) were more successful than "no cover" nests, irrespective of season. He also found that eggs from "cover" nests had highest chick survival at the mid-season hatching peak, whereas those from "no cover" nests did best early in the season. Hunt and Hunt (1976), interpreting these results in the light of their model, consider that open nests will be more vulnerable to neighbour interference while, in dense cover, visually orientated neighbours will be less important than nocturnal mammalian predators relying on scent. In Brown's study, the majority of Herring Gulls were nesting (by his definition) in cover, and they showed a higher chick survival than the Lesser Black-backed Gulls, and also a mid-season optimum for laying date. However, no assessment of the effects of nesting density or synchrony on breeding success was made in this study. Hosey and Goodridge (1980), in a more recent study of the same colony, used a different measure of cover, that of vegetation height. They found that the majority of Herring Gulls were nesting at lower densities in shorter vegetation, whilst the Lesser Black-backed Gulls were nesting at higher densities in taller vegetation. This difference in nesting density could be interpreted in terms of the Hunt and Hunt model. Unfortunately, in this study, no determinations of breeding success were made.

The present study was carried out on a large, mixed colony of Herring and Lesser Black-backed Gulls on Rockcliffe Marsh, Cumbria. The aim of the study was to investigate the relative importance of laying date, synchrony of laying, nesting density, amount of cover and position in the colony to overall breeding success of both species. In addition, areas with different ratios of the two gull types were to be compared to find out if there were differences in egg and chick losses, which might be explained in terms of the above factors and the balance of predation pressures.

These aims had to be modified when, in June, exceptionally high tides covered the marsh, washing out most of the nests. A small group of nests on the edge of the colony survived the flooding. Over half of the birds relaid 11-12 days later, but this included only a small proportion of the Herring Gulls (approximately 30%), and so the possibilities for comparative work on areas differing in Herring/Lesser Black-backed ratio were reduced. However, the relaid clutches were highly synchronous, being synchronised by physiological rather than environmental cues, and gave rise to a delayed hatching peak four weeks later than normal. Using comparisons with the nests surviving the flood and results from other colonies of similar size and composition, it was possible to assess the effect of this increased synchrony and delayed hatching peak on breeding success.

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.

Figure 1 : Geographical location of Rockcliffe Marsh

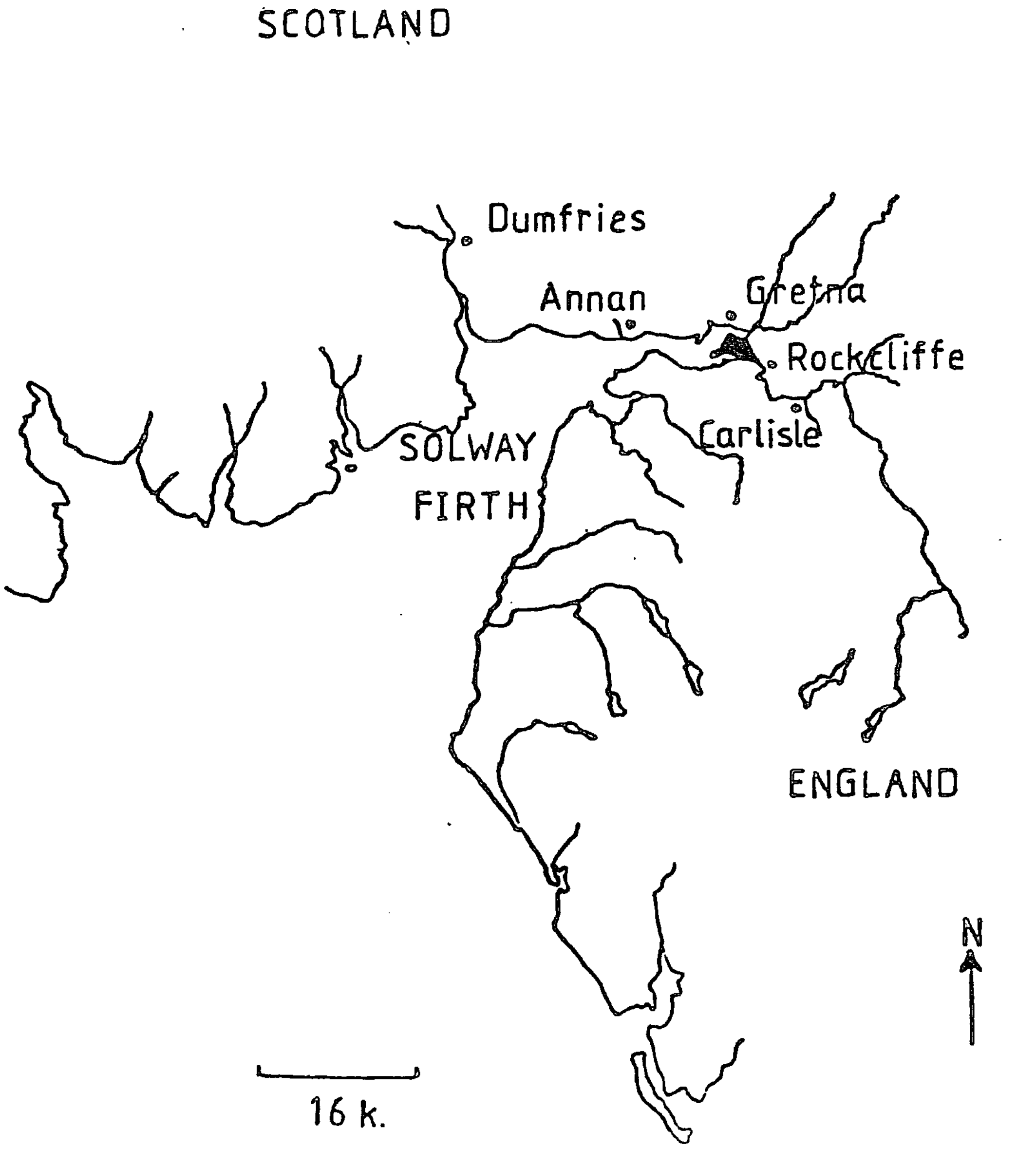
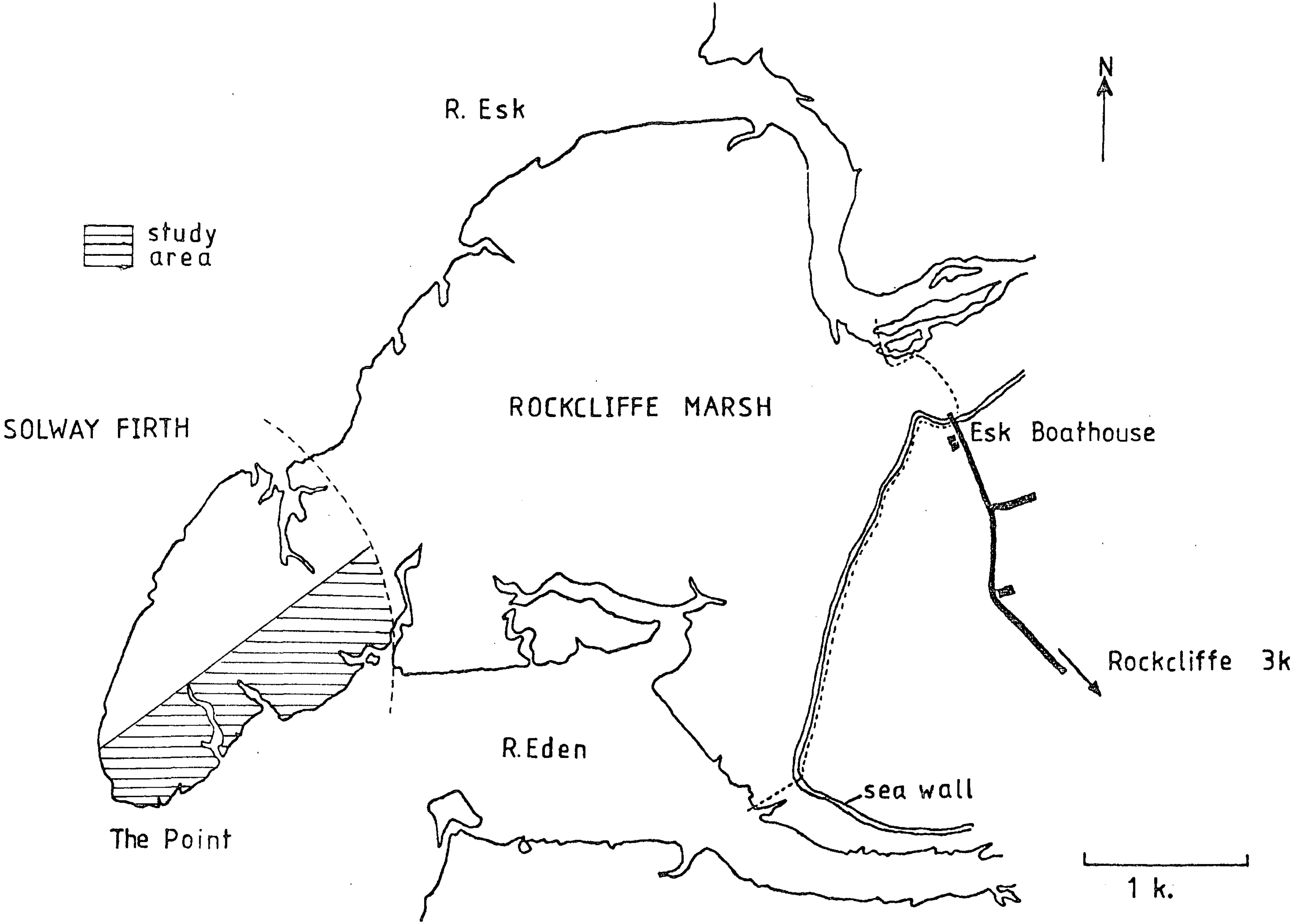


Plate 1 : a) The Marsh in May b) The colony during the flood.

a)

b)

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


R. Esk
study area
SOLWAY FIRTH
ROCKCLIFFE MARSH
Esk Boathouse
Rockcliffe 3k.
R.Eden
sea wall
The Point
N
1 k.

CHAPTER THREE

Methods

3.1 Marking nests and eggs

Nests were marked with wooden stakes (30 x 2.5 x 1cm) sharpened to a point at one end and numbered at the other with black waterproof ink. The stakes were placed about 20cm from the nest, such that the number was clearly visible above the surrounding vegetation. There was no evidence that the stakes caused any disturbance to the nesting birds.

Eggs were marked with black waterproof ink, according to the sequence of laying, the first or a-egg bearing the number 1, b-egg the number 2 and c-egg the number 3 (Plate **2**) Eggs were marked, usually within 2 days after laying so that accurate records of egg losses could be kept.

3.2 Egg Measurements

All eggs measured were clutches of 3 laid by Lesser Black-backed Gulls. A total of 80 first clutches and 150 relaid clutches were measured.

The maximum length and breadth of each egg was measured using Vernier calipers, measuring to the nearest 0.01cm. The volume and shape index of each egg was calculated using the following formulae:

$$\text{Volume} = k.\ell.b^2$$

where ℓ is the length of the egg in cm
b is the breadth of the egg in cm
and k is a constant for a particular species.
Here the value used was k = 0.476 (Harris 1964)

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

3.3 Estimating density and nearest nest distances

The positions of the nests in over half the colony were mapped by dividing the area up into 20m grid squares demarcated by conspicuous

Plate 2 : Method of marking nests and eggs.

bamboo canes. The gridding was completed in a series of continuous sections, each section being designated with a grid number i.e. grid 1, grid 2 and so on. The group of nests which survived the flooding were not within this gridded area, and so a separate grid (designated grid 5) was completed to map the positions of these nests (Fig. 3).

The positions of nests within each grid square were mapped on graph paper to a scale of 1cm = 10m, using the canes placed at the corners of each square as reference points. It was estimated that the true nest position was within 0.5m of the mapped position. Inter-nest distances were then calculated from these maps to an accuracy of ± 1cm. or m?

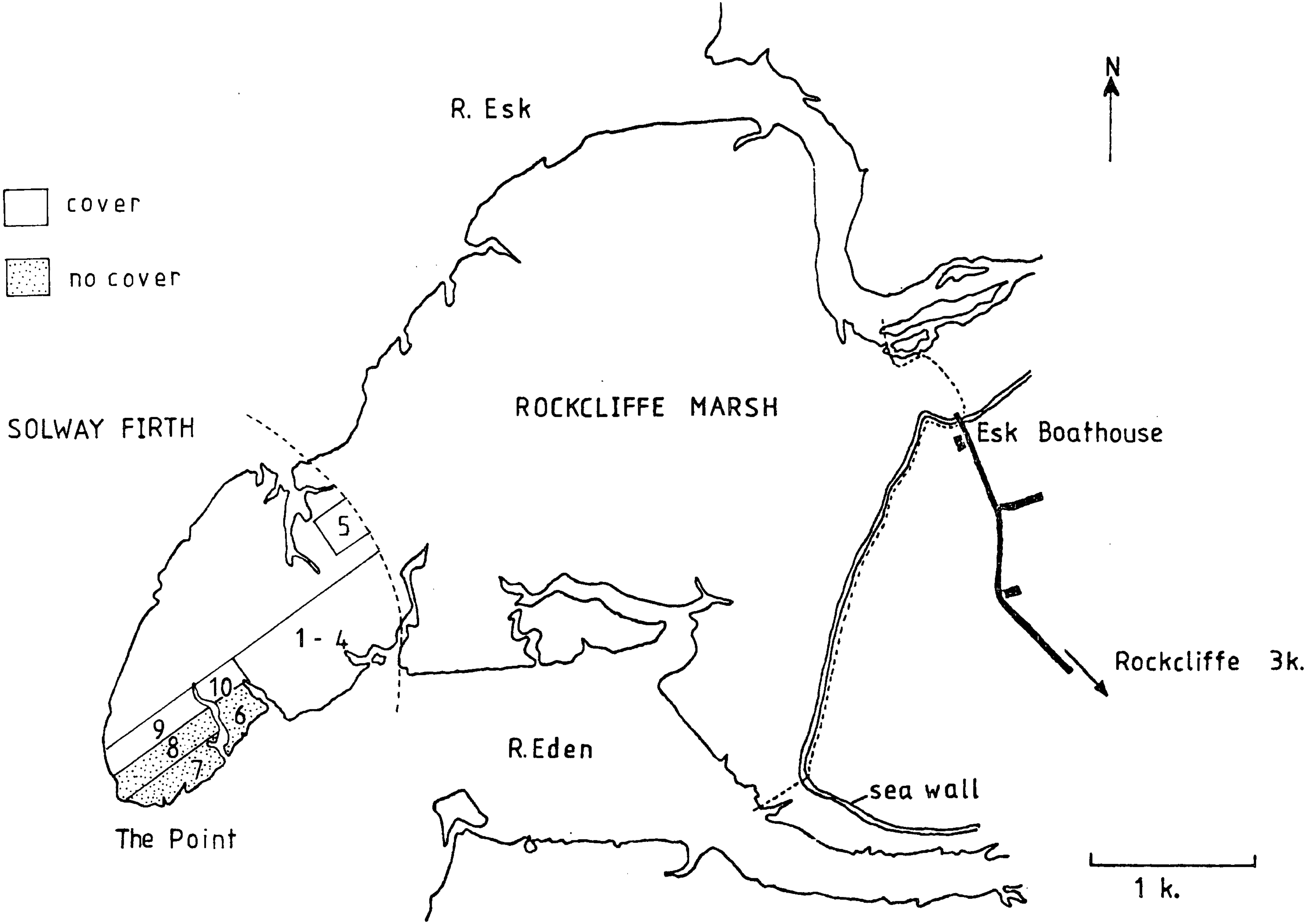
3.4 Identification of Gull species

The nests, eggs and young chicks of the Herring Gull and the Lesser Black-backed Gull are indistinguishable and it was necessary to identify the sitting bird on the nest. Observations were made, of the mapped area, from a hide raised 2m off the ground on a scaffolding platform. The nest markers were positioned so that the numbers were visible from the hide.

Unfortunately, the flooding occurred before the birds in grids 4 and 6-10 had been identified and therefore the specific identity of the parent birds is only known for 23% of first clutches.

Of the relaid clutches, 72% were identified using the above method. Difficulties with identification were due to the position of the nest, height of vegetation or abandonment by parent birds. Later in the season (mid-July) identifications for a further 3% of relaid clutches were made from primary feathers found around the nest due to moulting. Nests of known identity were also identified in this way (N = 30) and the method was found to be 98% reliable. Further checks on identity were possible when parent birds defended their nests, and especially their chicks, by swooping on anybody getting too close.

Figure 3 : Map of Rockcliffe Marsh showing the position of grids 1 - 10 and the areas of long (cover) and short (no cover) vegetation.



R. Esk
N
cover
no cover
ROCKCLIFFE MARSH
SOLWAY FIRTH
Esk Boathouse
5
1 - 4
10
6
9
8
7
Rockcliffe 3k.
R.Eden
sea wall
The Point
1 k.

3.5 Marking newly hatched chicks

Chicks were marked on hatching with a leg-ring, numbered according to the nest number and sequence of laying of the egg from which it hatched. Thus first chicks were numbered 1, second chicks 2 and so on. If the laying and/or hatching sequence was not known, the chicks were marked A, B or C.

Chicks hatched from c-eggs (third chicks) were ringed on the left leg, all other chicks being ringed on the right leg.

The rings were made from 10mm sections of 10mm diameter black plastic tubing, which were covered with white tape. The ring was slipped over the chick's leg and the diameter of the ring was reduced with one end of a staple (Fig. 4). The rusting of the staple, combined with the tension due to the growth of the leg, ensured that the staple dropped out after one or two weeks, allowing the ring to open to its full diameter (equal to that of a metal ring). Some of the plastic rings were replaced with metal rings when chicks were, on average, 14 days old, the others remaining on the chicks without any danger of constriction or injury.

The rings were marked with a red, waterproof ink, fine-pointed, felt-tip pen. Figures were clearly visible for the duration of the study period even on regurgitated rings.

3.6 Estimating fledging success; Mark Recapture technique

Several studies have shown that most chick mortality in Herring and Lesser Black-backed Gulls occurs in the first week of life (Paynter 1949, Paludan 1951, Brown 1967, Parsons 1975). On this basis, in the present study, survival to 14 days or more was equated with fledging success.

From 3-4 days old, chicks start to leave the nest and tend to hide in clumps of vegetation or in creeks, and therefore only a proportion of chicks present is likely to be found in any one search. Since all chicks were individually identified by ring number, a series of searches or

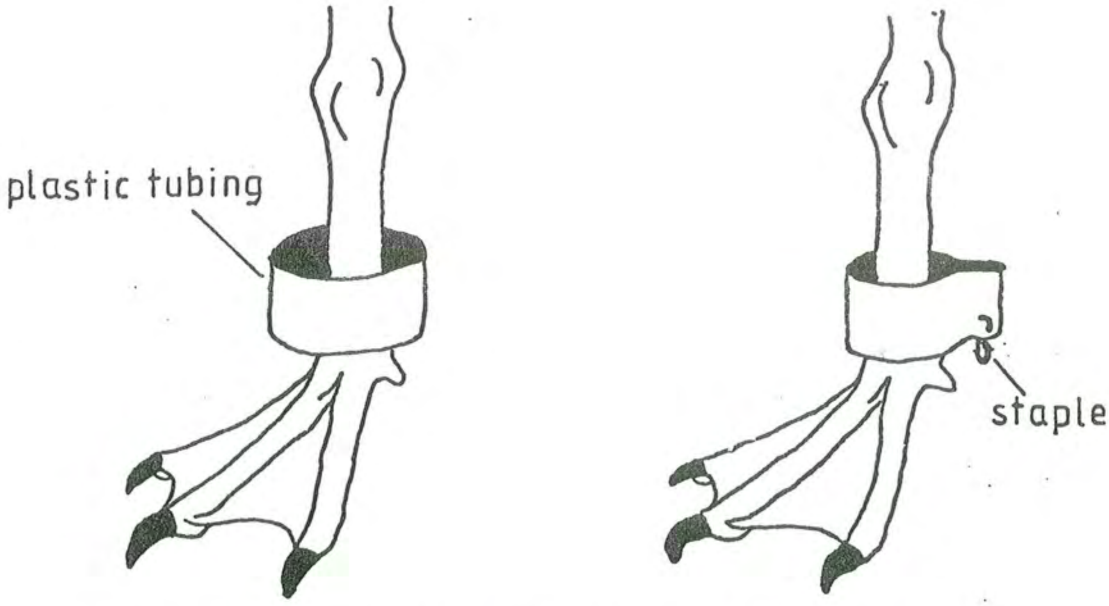


Figure 4 : Method of marking chicks and photograph of (approx) 5 day old chick.

recaptures can be used to give:

a) a total for the number of chicks found

b) an estimate of the total number of chicks present based on the Lincoln Index.

Comparison of a) and b) gives an estimate of the number of chicks which escaped recapture. The Lincoln Index, in this case, is given by the formula:

$$N = \frac{an}{r} \qquad \text{(i)}$$

where N is the estimate of the total population
n is the total found on the 2nd recapture
a is the total found on the 1st recapture
r is the total found on both 1st and 2nd recaptures

Bailey (1952) has suggested that with small samples, where the value of r is small (<20), a less biased estimate is given if 1 is added to n and r, i.e.:

$$N = \frac{a(n + 1)}{t + 1} \qquad \text{(ii)}$$

This method is based on what is referred to as "direct sampling" in which the size of n is predetermined and approximately equal to a, i.e. the numbers recaptured on each occasion should be approximately equal. If this condition is satisfied, then the variance of the estimate is given by:

$$\text{Var } N = \frac{a^2 n(N - r)}{r^3} \qquad \text{(iii)}$$

and for $r<20$

$$\text{Var } N = \frac{a^2 = (n + 1)(n - r)}{(r + 1)^2(r + 2)} \qquad \text{(iv) (Southwood 1978)}$$

In all recaptures, areas were searched maximally, with the result that approximately equal numbers were found on each occasion.

As slightly different methods were used with those clutches which survived the flood (Grid 5) compared with the relaid clutches, these will be discussed separately.

a) Relays: Survival of chicks was followed from hatching, nests being visited at least once every 2 days for the first 10 days after hatching. All chicks found dead were recorded. A total of 3 recaptures were carried out when all the chicks from the relaid clutches were at least 14 days old. The Lincoln Index and the variance of the estimate was calculated from (i) and (iii), using data from the first two recaptures, since the third recapture was at a lower catching intensity.

Comparison of the estimated total with the observed total indicated that 89% of chicks had been found. In subsequent analyses, fledging success was defined as the number of chicks known to have survived to 14 days. Since the number of chicks known to have survived is 89% of the estimated total, a value for fledging success calculated in this way will be a slight underestimate, although it will be offset by the small amount of mortality occurring between 14 days and fledging.

There were no differences in catching intensity between grids or between Lesser Black-backed and Herring Gull and therefore values for fledging success in different parts of the colony are comparable. The hatching of the relaid clutches was highly synchronous and therefore one pair of recaptures was sufficient to give an estimate of all chicks fledged.

b) Grid 5: Since these nests were hatching whilst the relays were at their peak of laying, regular visits were impossible.

Chicks were ringed as they hatched but their survival was not followed in the same detail as that of the relays. The first laying in Grid 5 was less synchronous than that of the relays and, therefore, a series of pairs of recaptures at staggered intervals would have been necessary to obtain a good estimate of fledging success.

A total of 3 recaptures was carried out, the first two when 20% of the chick population could have been over 14 days old. A Lincoln Index and variance was calculated for this section of the population, using (ii) and (iv) because of small sample size, and this indicated that all available chicks had been found. The third recapture was carried out 14 days later, by which time a further 76% of chicks could have been over 14 days old. All but one of the less than 14 day old chicks found on the first and second recaptures were found on the third, and therefore a Lincoln Index could be calculated from the first and second recaptures for these chicks as well.

Comparing these two estimated subtotals with the observed total indicated that 93% of chicks had been found. As with the relays, fledging success in Grid 5, in subsequent analyses, was defined as the number of chicks known to have survived to at least 14 days, and again this will be a slight underestimate.

3.7 Assessment of nest cover

Cover was defined in terms of the height of the vegetation using two categories: tall (>20cm) and short (<20cm). On this basis the study area was divided into 2 sections - a 'cover' area (Grids 1-5, 9-10) where nests were relatively concealed, and a 'no cover' area (Grids 6-8) where nests were relatively conspicuous (Fig. 3). The difference in vegetation height was apparent from the beginning of May onwards, i.e. after most breeding pairs had established territories and built nests.

CHAPTER FOUR

Onset and Pattern of Laying

4.1 The Laying period

Normal Laying

The first eggs were found on 23 April and laying continued until the flood on 1 June. The laying dates of the a-eggs of each clutch were divided up into 7-day periods. The cumulative percentages of clutches laid by Lesser Black-backed and Herring Gulls (Table 1) both indicate that most of the laying occurred in week 4.

The mean laying dates for the Herring Gull and the Lesser Black-backed Gull are shown in Table 2 together with mean laying dates from other colonies for comparison.

Mean laying dates in Table 2 indicate that Herring Gulls tend to lay earlier than Lesser Black-backed Gulls. The difference in mean laying dates for the two species at Rockcliffe, whilst being significant ($p<0.001$), is less than that which has been recorded for single species colonies. Earlier breeding of Lesser Black-backed Gulls at Rockcliffe may be a consequence of their being in a mixed colony.

The synchrony of laying as measured by the standard deviation of laying dates and by the percentage of clutches laid in the peak laying week was less for Herring Gulls than for Lesser Black-backed Gulls (Table 3).

Repeat Clutches

The time taken to relay was slightly less in Lesser Black-backed Gulls than in Herring Gulls (Table 4).

Table 1 : Cumulative percentages of normal clutches laid by Lesser Black-backed and Herring Gulls

Laying period (week)	1	2	3	4	5	6	7	Total no. of nests
	up to 29 April	30 April-6 May	7 May-13 May	14 May-20 May	21 May-27 May	28 May-3 June	4 June-10 June	
Lesser Black-backed Gull	-	0.7	23.5	83.9	97.4	98.7	100	296
Herring Gull	4.9	6.5	37	88.2	96.4	100	-	121

Table 2 : Mean laying dates for various gull colonies

	Study Area	Mean laying date	Year	Authority
Herring Gull	Skover Island, Wales	5 May	1962	Harris (1964)
	Isle of May	18 May	1966-69	Parsons (1971)
	Rockcliffe Marsh	12 May	1981	This study
Lesser Black-backed Gull	Skokholm Island	21,23 May	1969,1970	Davis and Dunn (1976)
	Rockcliffe Marsh	14 May	1981	This study

Table 3 : Synchrony of laying in Lesser Black-backed and Herring Gull

	Lesser Black-backed	Herring
Total no. of nests	296	121
Standard deviation of laying dates	5.1 days	6.7 days
% of clutches laid in peak laying week	60.4	51.2

Table 4 : Mean laying dates and standard deviations for repeat clutches

	Lesser Black-backed	Herring
Total no. of nests	548	72
Mean laying date	12 June	13 June
Standard deviation	2.55 days	3.37 days
Average time to relay (± 1 S.E.)	11± .11 days	12± .39 days

The relaying period was relatively brief, 99% of relaid clutches being laid in 14 days (Table 5).

The repeat clutches were highly synchronous compared with the first clutches and, again, Lesser Black-backed Gulls showed greater synchrony of laying dates than Herring Gulls (compare standard deviations in Tables 3 and 4).

Ability to Relay

Lesser Black-backed and Herring Gulls differ markedly in their ability to relay following loss of the clutch. It was estimated that 79% of Lesser Black-backed Gulls relaid compared with 29% of Herring Gulls. In all birds, the ability to relay decreases as the season advances. Parsons (1971) investigated the relationship between ability to relay and the number of days between normal laying and loss of the clutch in Herring Gulls. In this study, clutches were lost 18 days after the mean laying date for Herring Gulls. The comparable percentage for Herring Gulls relaying at this stage of the season, from Parsons' study, is 38%. The smaller percentage recorded in this study may be due to the additional stresses involved in rebuilding nests. There are no comparable figures available for relaying in Lesser Black-backed Gulls.

4.2 Timing and spacing of nests

Distribution of first clutches

The distribution of nests throughout the study area was analysed by calculating the coefficient of dispersion which, for a random distribution, is unity.

$$\text{Coefficient of Dispersion} = \frac{\text{Variance}}{\text{Mean}}$$

Table 5 : Pattern of laying in repeat clutches : cumulative %s

Laying period (week)	8 (11 - 17 June)	9 (18 - 24 June)	10 (after 24 June)	Total no. of nests
Lesser Black-backed Gull	87.8	99.1	100	548
Herring Gull	74	99	100	72

The 0.05 probability level of significant difference from a random distribution is given by unity $\pm\ 2 \times \frac{2}{N-1}$. Values for the coefficient of dispersion greater than the upper limit are indicative of a clumped distribution, whilst values less than the lower limit is evidence of a uniform distribution. The sampling unit used was a grid square i.e. $400m^2$. Average nesting density and coefficients of dispersion were calculated for different parts of the colony (Table 6).

In areas of high nesting density (Grids 6, 7, 8) the distribution of nests is clumped. This is, in part, a reflection of gulls being aggregated in the more suitable nesting sites and avoiding areas which are less suitable, such as slightly lower areas of ground prone to waterlogging, large mud patches, creeks etc. At higher densities, nests are more concentrated in the suitable areas and so the "definition" of the avoided areas is increased.

Grids 6, 7 and 8, in addition to having the highest nesting densities, are areas of short vegetation (categorised 'no cover') and it may be that the clumped distributions in these areas are the result of nest spacing being more important in these areas, compared with areas where nesting cover is greater. Nesting cover, its relationship with density and the effect of both factors on breeding success, are discussed in Chapters 6, 7 and 8.

Timing of first clutches

Several studies have demonstrated higher synchrony of laying in small subcolonies than in the colony as a whole (Parsons 1975, Davis and Dunn 1976, Burger and Shisler 1980). Analysis of variance on laying dates failed to give any evidence of greater synchrony within small sub-areas. However, the pattern of laying was not uniform throughout the colony.

Table 6 : Nesting density and coefficients of dispersion in first clutches

Grid No.	No. of samples	Density nest m^{-2}	Coefficient of Dispersion	Limits for random distribution ($p<0.05$)	Distribution R = Random C = Clumped
1	80	2.25×10^{-3}	1.27	1 ± .318	R
2	74	2.8×10^{-3}	1.32	1 ± .33	R
3	101	2.87×10^{-3}	1.36	1 ± .28	C
4	90	3.65×10^{-3}	1.14	1 ± .29	R
5	77	5.29×10^{-3}	1.98	1 ± .32	C
6	68	6.84×10^{-3}	1.82	1 ± .35	C
7	61	5.4×10^{-3}	2.07	1 ± .37	C
8	70	4.23×10^{-3}	1.34	1 ± .34	C/R
9 & 10	65	2.98×10^{-3}	0.97	1 ± .35	R

Laying began at The Point and as the season advanced progressively more laying took place inland from there. If the study area is divided into 3 sections, called for convenience A, B and C (Fig. 5), this spread of laying can be seen in the percentage of laying taking place in each section through the season (Table 7).

Small variations in synchrony of laying, as measured by standard deviation of laying dates, were found in different parts of the colony, but no connection was found between synchrony and nesting density.

Distribution of repeat clutches

Coefficients of dispersion calculated for the distribution of repeat clutches (Table 8) show a similar pattern to those of the first clutches i.e. random or clumped distributions.

Nearest neighbour distances were also calculated for the repeat clutches. Nearest neighbour distance can be used as an indicator of territory size. Burger (1980) has suggested that the second nearest neighbour distance, in a direction different from that of the first nearest neighbour, gives a better correlation with territory size, in that it includes more information about the relative positions of nests.

In an attempt to obtain a closer measure of territory size, a tesselation* was performed on the nest distribution of repeat clutches (Fig. 6 a), b)). The tesselation draws a polygon around each point, the boundaries of which are defined by the mid-points of lines joining a point to its nearest points (Fig. 7). The area of each polygon or tile, since it includes more information about overall nest distribution, should give a better measure of territory size than the first nearest neighbour distance. The problems with this technique are:

i) there are no means of defining the avoided areas i.e. the "holes" within the distribution, and ii) where the edge of the distribution is

*A Dirichlet tesselation was constructed using a computer programme written by Green and Sibson (1978).

Figure 5 : Map of Rockcliffe Marsh showing the positions of sections A, B, C to illustrate the pattern of laying throughout the colony.

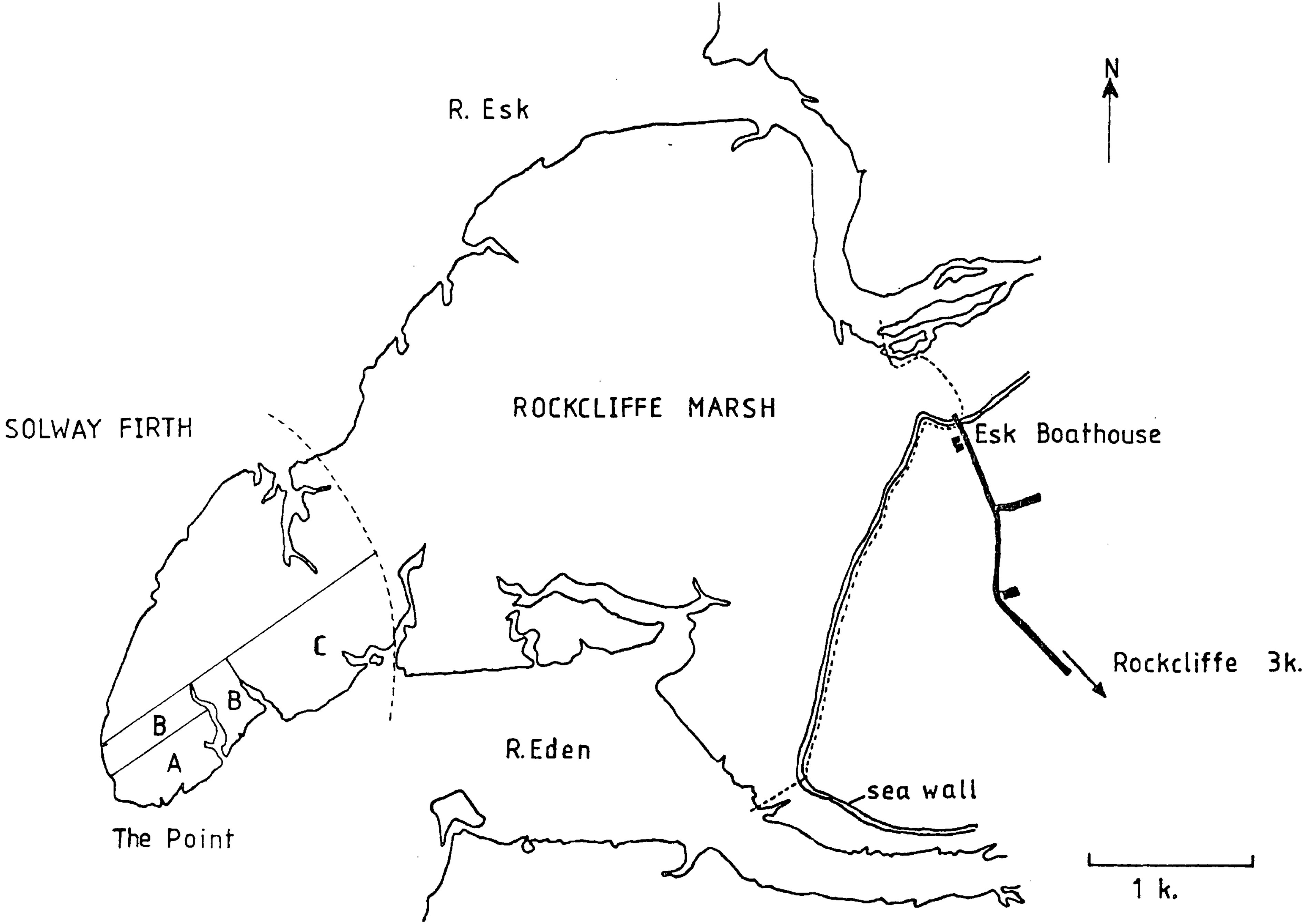

R. Esk
N
ROCKCLIFFE MARSH
SOLWAY FIRTH
Esk Boathouse
C
B
B
A
Rockcliffe 3k.
R.Eden
sea wall
The Point
1 k.

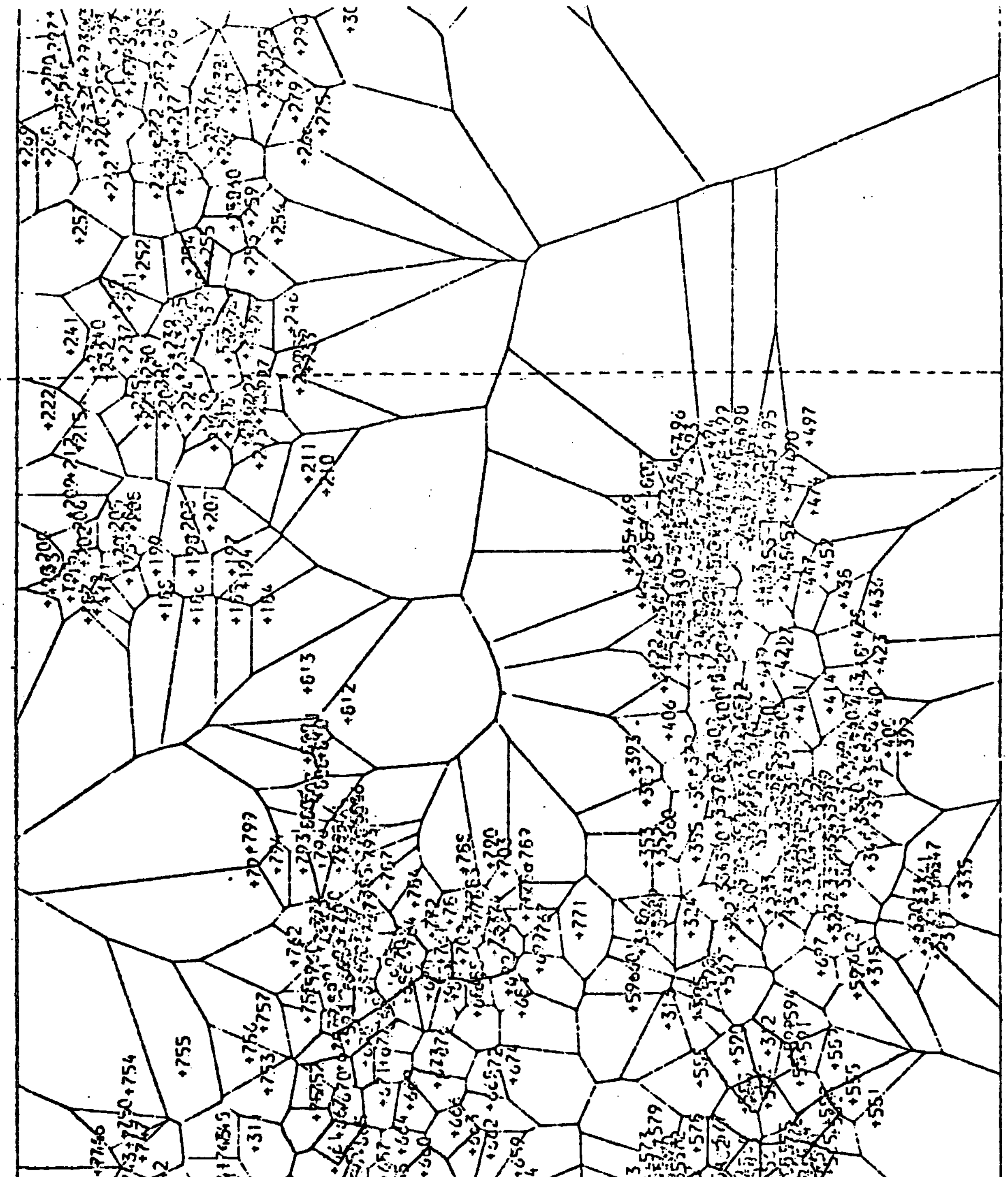
Table 7 : Percentage of laying through the season in 3 parts of the colony

Laying Period	No. of Nests	% laying A	% laying B	% laying C
up to 6 May	103	50.5	44	6
7 - 13 May	261	39.5	21	40
14 - 20 May	464	15	33	52
21 - 27 May	69	22	17	61
Mean laying date (±1 S.E.)		7 May (± .5 days)	10 May (± .5 days)	13 May (± .3 days)

Table 8 : Nesting density and coefficients of dispersion in repeat clutches

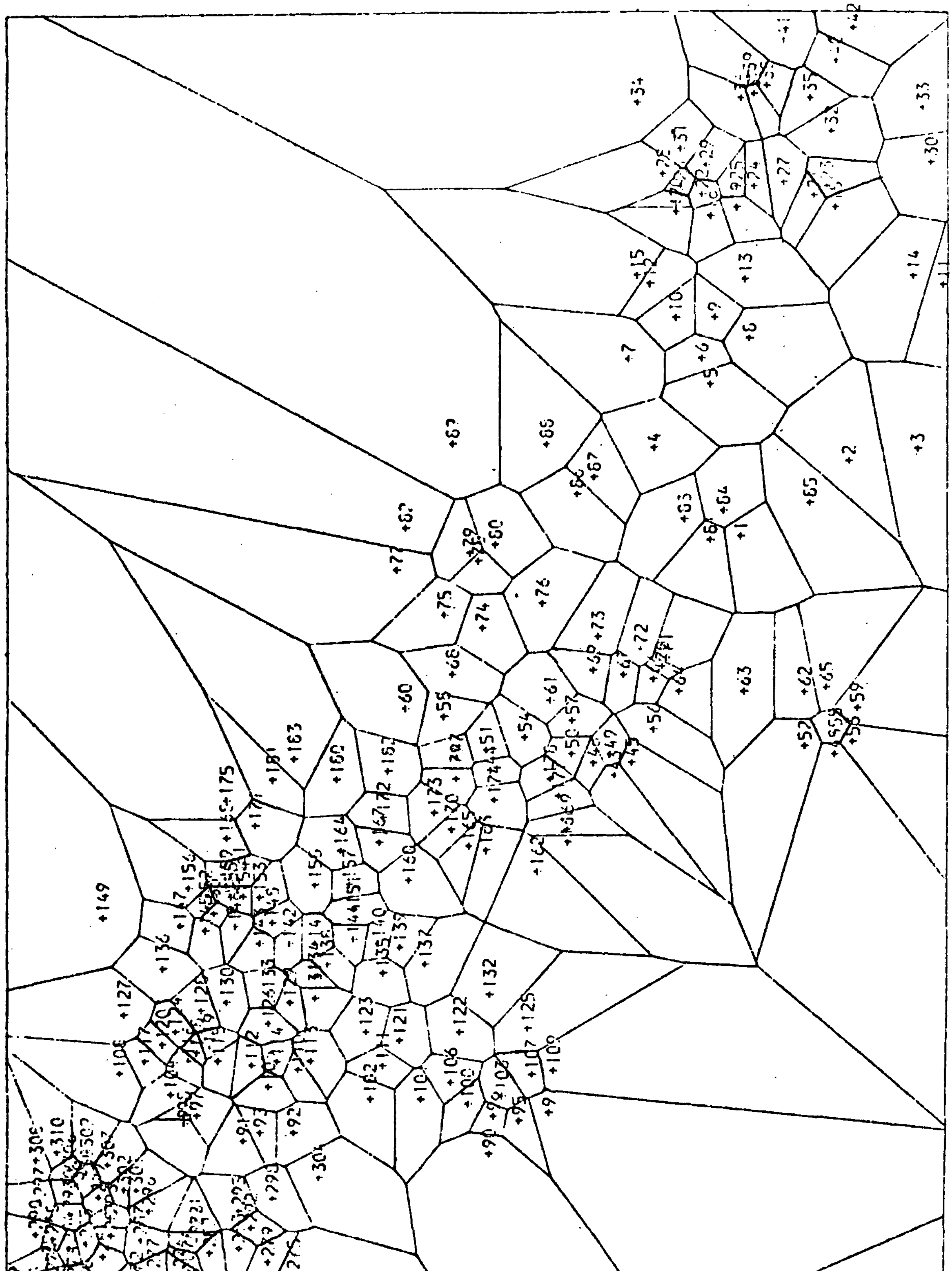
Grid No.	No. of samples	Density nests m^{-2}	Coefficient of Dispersion	Limits for random distribution	Distribution R = Random C = Clumped
1	80	1.16×10^{-3}	1.28	1 ± .318	R
2	82	1.4×10^{-3}	0.93	1 ± .314	R
3	102	2.25×10^{-3}	1.18	1 ± .28	R
4	90	3.55×10^{-3}	1.53	1 ± .29	C
6	69	6.48×10^{-3}	1.18	1 ± .35	R
7	68	4×10^{-3}	1.80	1 ± .35	C
8	70	3.62×10^{-3}	1.19	1 ± .34	R
9 & 10	80	3.22×10^{-3}	1.39	1 ± .32	C

Figure 6 a) and b) Result of tesselation on distribution of repeat clutches of all birds within the study area.



6a)

overlap with Fig. 6b
(see overleaf)



6b)

irregular and difficult to define, as in most biological situations, the tile areas for edge points are meaningless. In an attempt to overcome these problems, a maximum distance from a nest site to the edge of its territory can be defined. A circle of this set radius is drawn around the nest site and any boundaries further from the nest than this set distance will result in the tile area being truncated (Fig. 7). A truncation circle of 15m radius was used and in subsequent analyses, only non-truncated areas were used.

The relationship between nearest neighbour distance and non-truncated area is shown in Fig. 8. The range of nearest neighbour distances for all nests is 2 - 44m. This is reduced to 2 - 16m when only those nests with non-truncated areas are used. Therefore nests with nearest neighbour distances greater than 16m are not represented in analyses using non-truncated areas.

Both average nearest neighbour distance and average tile area were greater for Herring Gull than for Lesser Black-backed Gull (Table 9).

Since the greatest difference in density is between cover and no cover areas, nearest neighbour distance and tile area were calculated separately for these areas (Table 10).

Differences between Lesser Black-backed Gull and Herring Gull were not significant, but in both species 'no cover' nests had significantly lower nearest neighbour distances and tile areas than 'cover' nests.

Figure 7 : Example of tesselation showing "edge effect" and truncation circle.

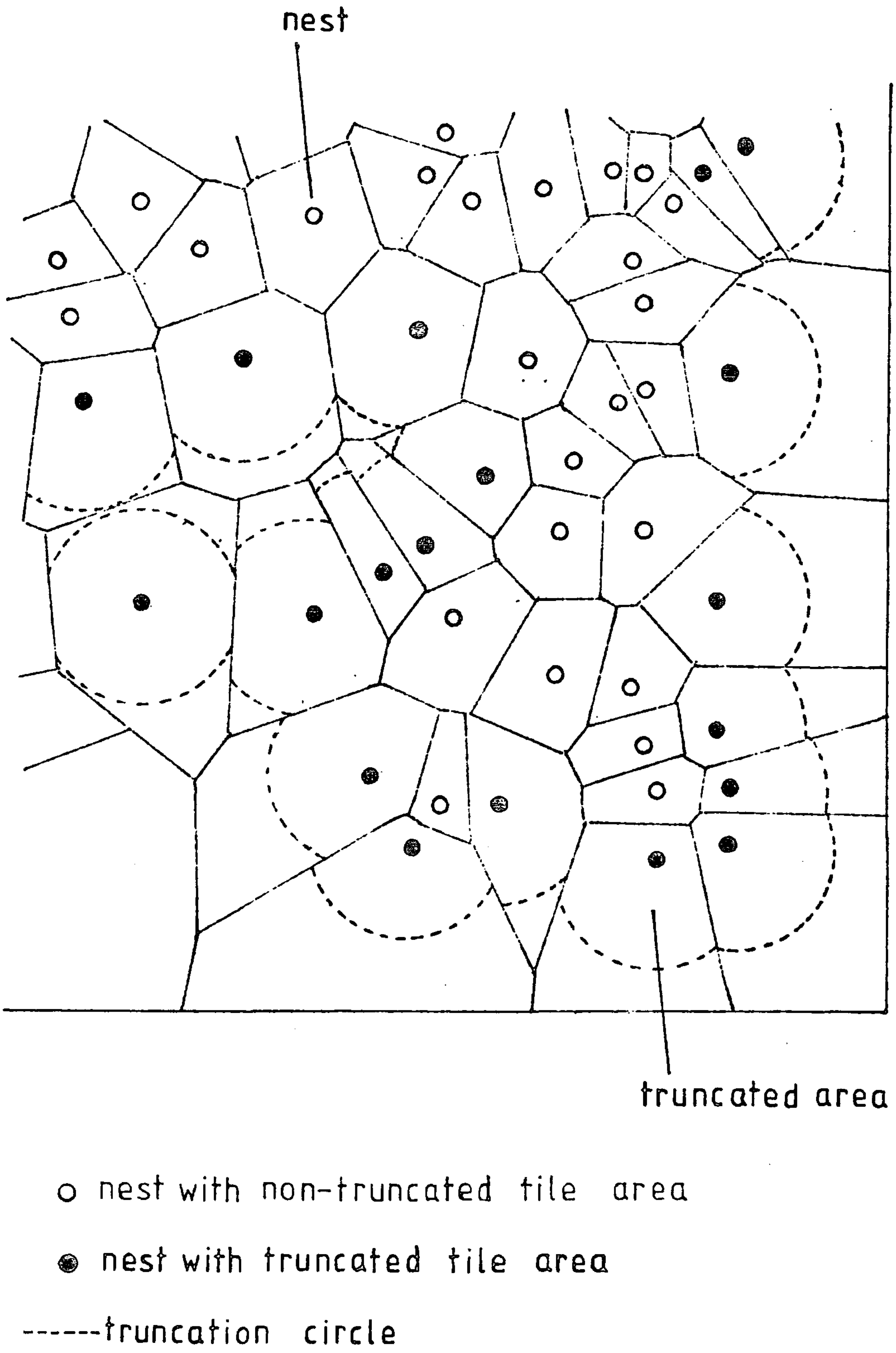
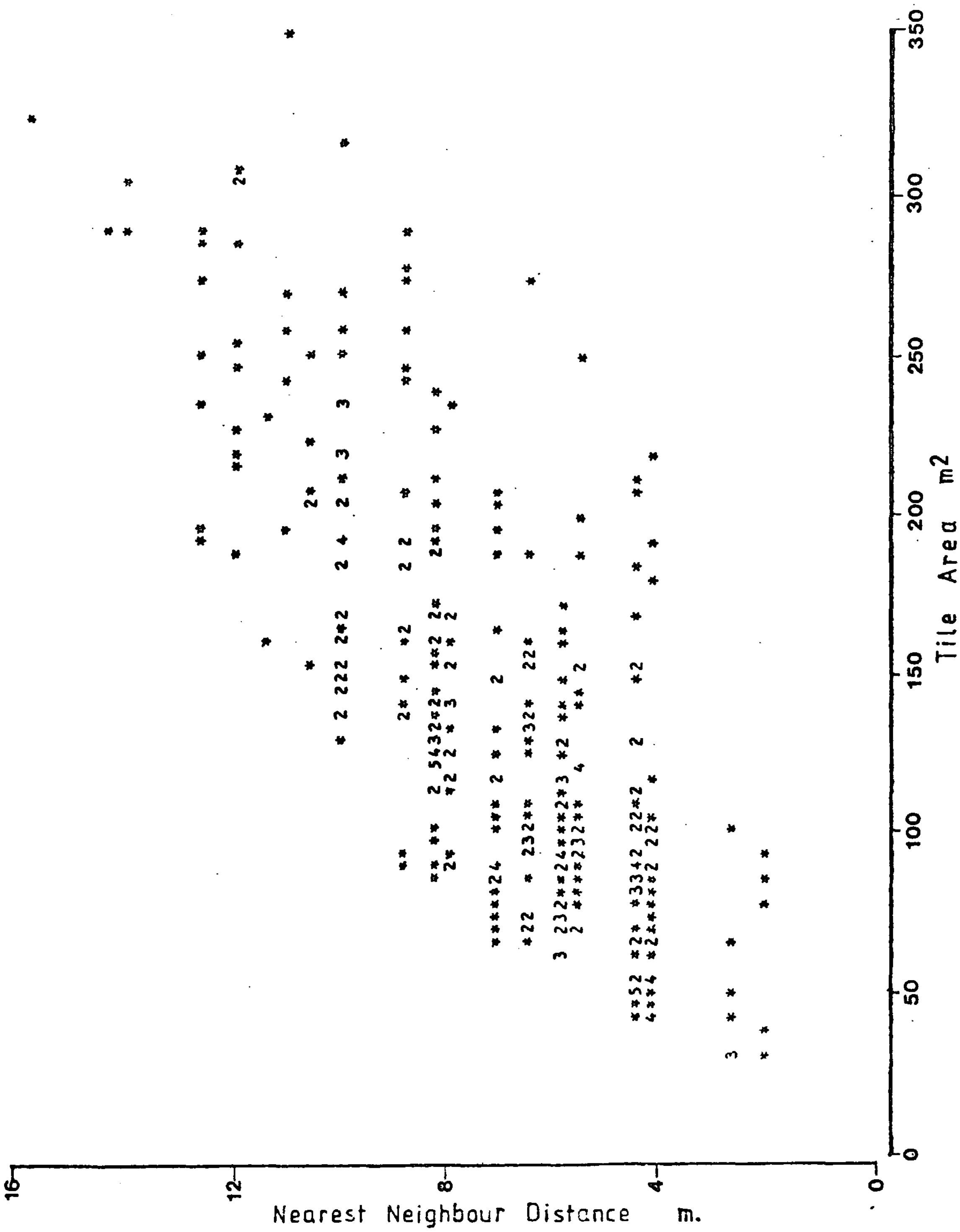


Figure 8 : Graph showing the relationship between nearest neighbour distance and tile area



Nearest Neighbour Distance m.
0
4
8
12
16
Tile Area m2
0
50
100
150
200
250
300
350

Table 9 : Average nearest neighbour distance and average tile area

(no. of nests shown in brackets; all values ± 1 S.E.)

	Lesser Black-backed Gull		Herring Gull		
Average nearest neighbour distance in metres	9.7 ± .22	(543)	10.4 ± .54	(71)	N.S.
Average tile area (m^2)	132 ± 4	(239)	162 ± 14	(21)	p 0.05

Table 10 : Nearest neighbour distance and tile area in 'cover' and 'no cover' areas

(No. of nests shown in brackets; all values ± 1 S.E.)

		Cover		No Cover		
Average nearest neighbour distance (m)	LBB	11.35 ± .35	(288)	7.84 ± .22	(255)	p<0.001
	H	12.14 ± 1	(29)	9.28 ± .5	(42)	p<0.05
Average tile area (m^2)	LBB	159 ± 7	(80)	118 ± 5	(59)	p<0.001
	H	169 ± 17	(7)	158 ± 19	(14)	N.S.

CHAPTER FIVE

Clutch size and total egg volume

5.1 Clutch size in Lesser Black-backed and Herring Gull

Clutch sizes of Lesser Black-backed and Herring Gull are shown in Table 11 together with values from other colonies for comparison. The mean clutch size in Lesser Black-backed Gulls at Rockcliffe is comparable to that from other colonies but the value for the Herring Gull is low; the nearest value (2.56) being recorded by Brown (1967), also from a mixed colony.

Both normal and repeat clutches laid by Lesser Black-backed Gulls were on average larger than those of Herring Gulls (Table 13). In normal clutches, Lesser Black-backed Gulls lay significantly more clutches of 3 ($p<0.001$) and significantly less clutches of 2 ($p<0.001$) than Herring Gulls. These differences remain in the relaid clutches with the addition that Herring Gulls lay significantly more clutches of 1 ($p<0.01$).

5.2 Seasonal variation in clutch size

There was a decline in clutch size through the season in normal and in repeat clutches, in both gull species (Table 12). The decrease from the beginning to the end of the laying period for the Herring Gull was greater and began earlier than that for the Lesser Black-backed Gull in both normal and repeat layings.

5.3 Variation with relaying

The repeat clutches of both Lesser Black-backed Gulls and Herring Gulls were on average smaller than first clutches (Table 13). Coulson and White (1961) showed that in the Kittiwake, the seasonal reduction in clutch

Table 11 : Comparison of mean clutch size for Lesser Black-backed and Herring Gull from various studies

(a) Lesser Black-backed Gull

Study Area	Mean clutch size	Year	Authority
Walney	2.76	1967	Brown (1967)
Skokholm	2.71, 2.67	1970,1972	Davis and Dunn (1976)
Rockcliffe (excluding repeat clutches)	2.67	1981	This study

(b) Herring Gull

Study Area	Mean clutch size	Year	Authority
Skomer	2.76	1964	Harris (1964)
Walney	2.56	1967	Brown (1967)
Isle of May	2.73	1971	Parsons (1971)
Rockcliffe (excluding repeat clutches)	2.46	1981	This study

Table 12 : Seasonal variation in clutch size in Lesser Black-backed and Herring Gull

a) Lesser Black-backed Gull

Laying period (week)		Percentage $c/_1$	$c/_2$	$c/_3$	Mean Clutch size	Number of nests
normal clutches	(3	4.4	13.2	82.4	2.78	68
	(4	5.9	17.8	76.3	2.70	169
	(5	12.5	20	67.5	2.55	40
repeat clutches	(8	2.7	22.9	74.4	2.72	480
	(9	14.5	38.7	46.8	2.32	62

Significance: normal clurches; N.S.
repeat clutches; week 8 vs 9, $c/_3$ vs $c/_1$ and $c/_2$ $\chi^2_1 = 20.4$ $p<0.001$

b) Herring Gull

Laying period (week)		Percentage $c/_1$	$c/_2$	$c/_3$	Mean Clutch size	Number of nests
normal clutches	(3	5.4	78.9	75.7	2.70	37
	(4	5.0	38.3	56.7	2.52	60
	(5	30.0	30.0	40.0	2.10	10
repeat clutches	(8	17	39.6	43.4	2.28	53
	(9	27.8	38.9	33.3	2.06	18

Significance: normal clutches; week 3 vs 5, $c/_3$ vs $c/_1$ and $c/_2$ $\chi^2_1 = 4.6$ $p<0.05$

Table 13 : Variation in clutch size with relaying in Lesser Black-backed and Herring Gull

a) Lesser Black-backed Gull

Clutch	Percentage $c/_1$	$c/_2$	$c/_3$	Mean Clutch size	Number of Nests
Normal	8.4	16.4	75.2	2.67	286
Repeat	4.2	25.0	70.7	2.66	547

Significance: $c/_1$ $\chi^2_1 = 6.18$ $p<0.01$

$c/_2$ $\chi^2_1 = 8.09$ $p<0.01$, $c/_3$ N.S.

b) Herring Gull

Clutch	Percentage $c/_1$	$c/_2$	$c/_3$	Mean Clutch size	Number of Nests
Normal	11.8	30.3	58	2.46	119
Repeat	19.4	40.3	40.3	2.21	72

Significance: $c/_3$ $\chi^2_1 = 5.6$ $p<0.05$ $c/_1$ and $c/_2$ N.S.

size was not solely a result of older birds breeding earlier, but that the time of laying also influenced clutch size. Since relaid clutches include those of older birds laying late in the season, a comparison of maximum clutch size in normal and repeat clutches should give an indication of the relative importance of age and time of laying, in determining clutch size.

In Lesser Black-backed Gulls, clutches laid at the start of the relaying period were not significantly smaller than those laid at the beginning of the season (Table 12). This indicates that variation in age is the primary factor influencing clutch size in Lesser Black-backed Gulls. However, in Herring Gulls the seasonal decline in clutch size was maintained in the repeat clutches, and therefore time of laying seems to be of primary importance in determining clutch size in Herring Gulls. It has been suggested (Coulson *et al.* 1969) that late laying birds have insufficient time for the maximum development and functioning of the reproductive system. This could explain the lowering of clutch size in late laying Herring Gulls, although apparently Lesser Black-backed Gulls are not affected in the same way.

5.4 Variation in total egg volume with relaying

Repeat clutches of 3 laid by Lesser Black-backed Gulls showed an average decrease in total egg volume of 11.99cc or 5.4%. Parsons gives figures for the Herring Gull showing the decrease in total egg volume of repeat clutches, at various intervals between normal and repeat clutches (Table 14).

In this study, the interval between normal and repeat clutches was approximately 26 days.

Table 14 : Decrease in clutch volume for clutches of 3 during relaying according to the interval between laying of first and repeat clutches (from Parsons 1971)

Interval between clutches	No. of clutches	Decrease in total egg volume cc	%
17 days	17	8.5	3.7
25 days	15	12.8	5.5
38 days	11	20.5	8.8

The % decrease observed for the Lesser Black-backed Gull is very comparable with that of the Herring Gull. Decrease of clutch size and decrease of egg size can be thought of as alternative strategies for reducing investment in egg production. Unfortunately no measurements of Herring Gull eggs were made but, if a similar decrease in total egg volume is assumed to that obtained in Parsons' study, then it is apparent that Lesser Black-backed Gulls are able to sustain a higher clutch size than Herring Gulls throughout the season, and that this difference in investment is not reduced by a differential decrease in egg size.

To summarise, at Rockcliffe, Lesser Black-backed Gulls are able to lay, on average, larger clutches than Herring Gulls and can maintain full egg production later into the season than Herring Gulls. Whilst there are differences in the diets of the two species, Herring Gulls tending to feed more offshore and Lesser Black-backed Gulls more inland, it is unlikely that food supply is limiting for either. Differences in laying performance are therefore more likely to be the result of physiological or behavioural differences between the two species.

Chapter 6

Breeding success

6.1 Factors affecting breeding success

Hatching and fledging success was followed in two groups of nests:
1) Grid 5; first clutches which survived the flood
2) Grids 1-4, 6-10; repeat clutches

In both groups it was possible to look at the effects of clutch size and laying date on breeding success. Investigation of seasonal variation was limited, for first clutches, by the truncation of the normal laying period by the flood, and the small number of nests (166) in Grid 5. Also, since only a small proportion (45%) of birds in Grid 5 were identified, all birds are grouped together in the analysis of the effects of clutch size and laying date on hatching and fledging success. The effects of cover and nesting density on breeding success were examined in repeat clutches only, since first clutches in Grid 5 were relatively few in number and lacked adequate variation in these factors. The effect of density was examined for Lesser Black-backed Gulls only since the number of Herring Gulls relaying was too low to permit such analysis.

6.2 Hatching success

First and repeat clutches

The results are shown in Table 15. In first clutches, hatching success of Lesser Black-backed Gulls was less than that of Herring Gulls. The high value for Herring Gulls is difficult to explain and may be an anomaly due to small sample size and the small proportion of Grid 5 nests which were identified. The overall hatching success (45%) for this group

Table 15 : Hatching success in normal and repeat clutches

a) Lesser Black-backed Gull

	Normal Clutch	Repeat Clutch
Number of nests	52	546
Number of eggs laid	134	1455
Number of eggs hatched	69	1034
% eggs hatching	51	71

Significance : $\chi^2_1 = 39.15$ $p<0.001$

b) Herring Gull

	Normal Clutch	Repeat Clutch
Number of nests	22	72
Number of eggs laid	50	159
Number of eggs hatched	38	77
% eggs hatching	76	48

Significance : $\chi^2_1 = 11.69$ $p<0.001$

of nests is probably a more reliable figure and its low value is likely to be due to heavy egg predation by large numbers of neighbouring birds which had lost their own clutches in the flood. Also, external predation may have been higher in this area since a small group of breeding birds will not be so effective at mobbing predators.

In the repeat clutches, Lesser Black-backed Gulls had higher success than Herring Gulls. Lower success for Herring Gulls is largely due to decreased clutch size, combined with lower hatching success of smaller clutches (see below).

Overall hatching success was higher in repeat clutches than in Grid 5. However, due to the special circumstances created by the flood, clutches in Grid 5 cannot be used as controls. Comparing hatching success in the repeat clutches with figures for hatching success of normal clutches from other colonies (Table 16) indicates that, in Lesser Black-backed Gulls no disadvantage is incurred in breeding late in the season. Indeed, the hatching success of repeat clutches is significantly higher than that of the normal clutches at Skokholm ($p<0.05$). It is possible that the highly synchronous laying of the repeat clutches may result in reduced egg losses to predators. Parsons (1975), similarly, found no decrease in hatching success in Herring Gulls when he experimentally delayed clutches, providing the delay was applied to a large group of nests at the same time. However, in this study the hatching success of repeat clutches in Herring Gulls was lower than that of both normal and repeat clutches recorded elsewhere ($p<0.001$). This may be a consequence of the relatively small numbers of Herring Gulls represented in the Rockcliffe colony in the repeat laying.

Variation in hatching success with clutch size

In both Grid 5 and repeat clutches, clutches of 3 had a higher hatching success than clutches of 2 or 1 (Table 17). The decrease in

Table 16 : Hatching success in Lesser Black-backed and Herring Gulls from various colonies

a) Lesser Black-backed Gull

Clutch	Study Area	% eggs hatched	Authority
Normal	Skokholm	65 (1970) 59 (1972)	Davis and Dunn 1976
Normal	Walney	72	Brown 1967
Repeat	Rockcliffe Marsh	71	This study

b) Herring Gull

Clutch	Study Area	% eggs hatched	Authority
Normal	Walney	65.7	Brown 1967
Normal	Isle of May	71.2	Parsons 1971
Repeat	Isle of May	66	Parsons 1971
Repeat	Rockcliffe Marsh	48	This study

Table 17 : Hatching success and clutch size in normal and repeat clutches

a) Normal clutches : All birds

Clutch size	1	2	3
Number of nests	27	59	80
Number of eggs laid	27	118	240
Number of eggs hatched	6	49	115
% eggs hatched	22	41	48

Significance : $^{c}/_{3}$ vs $^{c}/_{1}$ and $^{c}/_{2}$ $\chi^2_1 = 3.65$ N.S.

b) Repeat clutches : Lesser Black-backed (LBB) and Herring Gull (H)

Clutch size	1		2		2	
	LBB	H	LBB	H	LBB	H
Number of nests	23	14	138	29	385	29
Number of eggs laid	23	14	276	58	1155	87
Number of eggs hatched	13	3	191	20	830	54
% eggs hatched	56	21	69	36	72	62

Significance : LBB; N.S.

H; $^{c}/_{3}$ vs $^{c}/_{1}$ and $^{c}/_{2}$ $\chi^2_1 = 14.3$ $p<0.001$

hatching success was much more marked in the Herring Gull than in the Lesser Black-backed Gull, where the decrease was not significant. One explanation for lower hatching success in clutches of 1 and 2 is that younger birds tend to lay smaller clutches and that their lack of breeding experience leads to lower hatching success. However, since the timing of laying is of primary importance in determining clutch size in Herring Gulls, it is likely that poor hatching success in small clutches laid later in the season is attributable to a decrease in reproductive drive, poorer incubation and increased inattentiveness. Brown (1967) has also suggested that smaller clutches may present an inadequate stimulus to the bird, resulting in inadequate incubation.

In addition to egg losses being greater in smaller clutches, there may also be variation in egg losses within a given clutch size. The binomial expansion can be used to predict the numbers of clutches losing 0,1,2 etc eggs given a certain percent egg predation, assuming that all clutches are equally liable to egg predation and that the loss of one egg from a clutch does not affect the probability of another being lost. The expected numbers of clutches losing 0,1,2 etc eggs respectively can then be compared with the observed numbers as a test of wnether the above assumptions concerning egg predation are valid. The results of this analysis for Grid 5 (all birds) and for repeat clutches (Lesser Black-backed Gull only, since Herring Gull numbers were too small) are shown in Table 18.

In all cases, for clutches of both 2 and 3, there are more pairs losing no eggs and more pairs losing all their eggs than would be expected if the percent egg predation was constant in all clutches of a given size. Clearly some clutches are more prone to predation than others, as would be expected if there is a variation in breeding experience and nest site location amongst birds which affects their breeding success.

Table 18 : Variation in egg losses within clutches of 2 and 3

a) Grid 5 : All birds

Clutch size	2		Number of eggs lost 0	1	2	χ^2	d.f.	p
% eggs lost	59%	Obs.	20	10	29	24.6	2	<0.001
Number of nests	59	Exp.	10	28	21			

Clutch size	3		Number of eggs lost 0	1	2	3	χ^2	d.f.	p
% eggs lost	52%	Obs.	15	27	14	22	23.6	3	<0.001
Number of nests	78	Exp.	9	28	30	11			

b) Repeat Clutches : Lesser Black-backed Gull

Clutch size	2		Number of eggs lost 0	1	2	χ^2	d.f.	p
% eggs lost	31%	Obs.	79	31	27	31.4	2	<0.001
Number of nests	137	Exp.	65	59	13			

Clutch size	3		Number of eggs lost 0	1	2	3	χ^2	d.f.	p
% eggs lost	28%	Obs.	186	107	49	45	182.8	3	<0.001
Number of nests	387	Exp.	144	168	66	9			

In order to assess whether the loss of one egg from a clutch affects the probability of further eggs being lost, a similar analysis was carried out, omitting nests which lost no eggs, and using the ratios of clutches losing 0,1,2 and 3 eggs calculated from the binomial, to give the expected values (Table 19). In both normal and repeat clutches and the clutch sizes of both 2 and 3, there is a tendency to lose more than one egg and, in clutches of 3, to lose 3 rather than 2 eggs. This may be a function of the type of predation or a consequence of nest abandonment. Detailed observations of nests throughout the incubation period would be necessary to establish the exact causes of egg loss. Although this was not attempted in this study, abandoned nests in which all eggs were subsequently lost were observed, especially amongst repeat clutches.

Seasonal variation in hatching success

The results are shown in Table 20. In Grid 5, hatching success was higher for eggs laid from the time of peak laying onwards, compared to the start of laying. One interpretation of this is that egg predation was high at the start of the season due to losses to egg stealers and predation by neighbouring birds which had lost their own clutches. Also, if non-breeding birds are responsible for egg losses, that would explain higher levels at the start of the season.

In the repeat clutches of Lesser Black-backed Gulls, hatching success was greatest for eggs laid at the peak of laying, and showed a significant decrease in the later layers. No such seasonal effect was apparent in Herring Gulls for which a relatively small sample was available. Decreased egg losses at the peak of laying is indicative of a relatively constant predation rate and therefore losses to external predators, such as crows, are likely to be more important than egg stealing by neighbours.

Table 19 : Egg losses = effect of losing one egg on probability of losing another

a) Grid 5 : All birds

Clutch size	2		Number of eggs lost 1	2	χ^2	d.f.	p
% eggs lost	59%	Obs.	10	29	15.01	1	<0.001
Number of nests	39	Exp.	22	17			

Clutch size	3		Number of eggs lost 1	2	3	χ^2	d.f.	p
% eggs lost	52%	Obs.	27	14	22	20.69	2	<0.001
Number of nests	63	Exp.	26	27	10			

b) Repeat clutches : Lesser Black-backed Gull

Clutch size	2		Number of eggs lost 1	2	χ^2	d.f.	p
% eggs lost	31%	Obs.	31	27	34.9	1	<0.001
Number of nests	58	Exp.	48	10			

Clutch size	3		Number of eggs lost 1	2	3	χ^2	d.f.	p
% eggs lost	28%	Obs.	107	49	45	214	2	<0.001
Number of nests	387	Exp.	140	54	7			

Table 20 : Hatching success and laying date in normal and repeat clutches

a) Normal clutches : All birds

Laying period (week)	3	4	5
Number of nests	41	76	15
Number of eggs laid	94	188	36
Number of eggs hatched	34	108	22
% eggs hatched	36	57	61

Significance : week 3 vs 4 $\chi^2_1 = 6.6$ $p<0.05$

b) Repeat clutches : Lesser Black-backed (LBB) and Herring Gull (H)

Laying period (week)	8		9 and 10	
	LBB	H	LBB	H
Number of nests	477	53	67	19
Number of eggs laid	1301	120	154	38
Number of eggs hatched	953	58	81	19
% eggs hatched	73	48	53	50

Significance : LBB; $\chi^2_1 = 23.1$ $p<0.001$

H; N.S.

Effects of nest cover and nesting density on hatching success

In both Lesser Black-backed Gulls and Herring Gulls 'cover' nests had higher hatching success than 'no cover' nests, although the difference in the case of the Herring Gull was smaller and not significant (Table 21). Higher hatching success in cover nests could be due to decreased losses to predators and/or to neighbouring gulls.

The effect of nesting density on 'cover' and 'no cover' nests respectively was analysed by comparing hatching success with nearest neighbour distance (Table 22) and with tile area (Table 23).

In 'cover' nests nearest neighbour distance has no apparent effect on hatching success, whereas in 'no cover' nests hatching success is significantly lower in nests with nearest neighbour distances greater than 12m. Tile area appears to have no effect on hatching success, except 'cover' nests with the smallest tile areas show a lower hatching success, although this is based on a sample of only 10 nests. Nests with nearest neighbour distances greater than 16m are not represented in the 3 categories of non-truncated area used, and this may explain the apparent lack of effect of tile area on hatching success.

Summarising the effects of density and cover on hatching success;

i) cover nests hatch more eggs than 'no cover' nests irrespective of density

ii) in 'no cover' nests, wide nest spacing leads to lower hatching success, but in 'cover' nests, nesting density has no effect on hatching success.

Closer spacing of nests in no cover areas gives greater protection against external predators, such as crows, through mobbing, whereas protection is afforded by the vegetation in the 'cover' areas.

Table 21 : Hatching success in 'cover' and 'no cover' repeat clutches in Lesser Black-backed and Herring Gull

	Lesser Black-backed Gull		Herring Gull	
	Cover	No cover	Cover	No cover
Number of nests	287	254	29	42
Number of eggs laid	743	697	68	90
Number of eggs hatched	565	464	34	42
% eggs hatching	76	67	50	47

Significance : $\chi^2_1 = 15.8$ $p<0.001$ N.S.

Table 22 : Hatching success and nearest neighbour distance in 'cover' and 'no cover' repeat clutches in Lesser Black-backed Gulls

a) 'Cover' Nearest neighbour distance	A (<6m)	B (6-9m)	C (9-12m)	D (>12m)
Number of nests	37	75	73	102
Number of eggs laid	93	192	191	267
Number of eggs hatched	65	153	146	201
% eggs hatching	70	80	76	75

Significance = N.S.

b) 'No Cover' Nearest neighbour distance	A (<6m)	B (6-9m)	C (9-12m)	D (>12m)
Number of nests	68	112	39	35
Number of eggs laid	190	304	106	97
Number of eggs hatched	134	201	76	53
% eggs hatching	70	66	72	55

Significance : A vs D $\chi^2_1 = 7.14$ $p<0.01$

B vs D $\chi^2_1 = 4.17$ $p<0.05$

C vs D $\chi^2_1 = 6.36$ $p<0.05$

Table 23 : Hatching success and tile area in 'cover' and 'no cover' repeat clutches in Lesser Black-backed Gulls

a) 'Cover' Tile Area	A ($<88m^2$)	B ($88-184m^2$)	C ($>184m^2$)
Number of nests	10	41	29
Number of eggs laid	23	103	78
Number of eggs hatched	14	85	59
% eggs hatching	61	82	76

Significance = Avs B $\chi^2_1 = 5.2$ $p<0.05$

b) 'No Cover' Tile Area	A ($<88m^2$)	B ($88-184m^2$)	C ($>184m^2$)
Number of nests	51	85	22
Number of eggs laid	145	227	61
Number of eggs hatched	92	155	39
% eggs hatching	63	68	64

Significance = N.S.

Table 24 : Infertility in normal and repeat clutches (all birds)

	Normal Clutch	Repeat Clutch
Number of nests	166	832
Number of eggs laid	385	2044
Number of eggs infertile	10	127
% eggs infertile	2.6	6.2

Significance : $\chi^2_1 = 7.96$ p<0101

Table 25 : Infertility in repeat clutches of Lesser Black-backed and Herring Gulls

	Lesser Black-backed Gull	Herring Gull
Number of nests	546	72
Number of eggs laid	1455	159
Number of eggs infertile	92	18
% eggs infertile	6.3	11.3

Significance : $\chi^2_1 = 5.63$ $p<0.05$

6.3 Infertility

Eggs which failed to hatch were recorded as infertile, although they include those in which the embryo failed to develop fully. A higher percentage of infertile eggs were recorded in the repeat clutches than in the normal clutches (Table 24). A similar result was recorded by Parsons (1971) in the Herring Gull. He attributed this increased infertility to poor incubation or to a breakdown in normal pair beheaviour later in the season.

Infertility in repeat clutches was higher in Herring Gulls than in Lesser Black-backed Gulls (Table 25). Brown (1967) also recorded greater infertility in normal Herring Gull clutches compared with those of Lesser Black-backed Gulls.

6.4 Fledging success

Aspects of chick mortality

In both first and repeat clutches, most chick mortalities occurred in the first week of life (Table 26).

Table 26 : First and second week mortality

		% chicks dead				
		Week 1	Week 2	No. chicks hatched	χ^2_1	P
Grid 5:	LBB	59.0	22.7	68	17.7	<0.001
	H	72.9	16.2	37	24.1	<0.001
Repeat Clutches:	LBB	48.2	17.3	927	20.1	<0.001
	H	36.5	20.2	74	4.8	<0.005

A similar result has been recorded in several other studies on the Lesser Black-backed and Herring Gull (Paynter 1949, Paludan 1951, Brown 1967, Parsons 1975, Davis and Dunn 1976). Relatively few chicks were found dead whereas many simply disappeared without trace (Table 27).

Table 27 : Chick mortalities; numbers dead and disappeared (all birds)

	Grid 5	Repeat clutches
Total no. chicks dead/disappeared	143	743
No. chicks found dead	14	88
No. chicks disappeared	129	655
% chicks disappeared	90%	88%

It therefore seems likely that most of these chicks were eaten. There are few predators on the marsh, apart from carrion crows which were probably responsible for some egg predation. Stoats, mink, foxes and hedgehogs, although seen on or near the sea wall at the edge of the marsh, are thought unlikely to have home ranges large enough to include the gull colony. A sparrow hawk and short-eared owl were seen on the marsh, but they are unlikely to have been responsible for many chick mortalities. Thus it seems that conspecific predation is likely to be the most important cause of chick losses. A total of 10 regurgitated leg rings were found in nests of other gulls, but no other evidence of cannibalistic behaviour was found.

It might be expected that a greater proportion of the smaller, younger chicks would be eaten and therefore that more older chicks would be found dead. Higher numbers of less than 7 day old chicks were found dead (Table 28) but the differences were not significant.

Table 28 : Ages of chicks found dead (all birds)

	Age <7 days	Age 7-14 days	Total no. chicks hatched
Grid 5	10	4	170
Repeat clutches	49	39	1131

Fledging success in first and repeat clutches

Figures for fledging success, from various studies, are shown in Table 29. Fledging success in the first clutches in Grid 5 is clearly very low. The chicks hatching in Grid 5 lacked the protection of hatching in a large group and consequently suffered much higher predation. Also at the time of hatching in Grid 5, there were large numbers of birds in the colony, which had lost their clutches in the flood and were unable to relay. These birds may well have been responsible for much of the predation although no direct observations were made to substantiate this.

Table 29 : Fledging success in Lesser Black-backed and Herring Gulls from various colonies

a) Lesser Black-backed Gull

Study Area	No. of chicks hatched	% chicks fledged	Year	Authority
Walney	561	41	1967	Brown 1967
Skokholm	250	43	1970	Davis and Dunn 1976
,,	144	69	1972	,, ,,
Rockcliffe Marsh (first clutches)	68	20	1981	This study
Rockcliffe Marsh (repeat clutches)	927	34.5	1981	,, ,,

b) Herring Gull

Study Area	No. of chicks hatched	% chicks fledged	Year	Authority
Walney	230	52.6	1967	Brown 1967
Isle of May (normal clutches)	1966	50.8	1967	Parsons 1971
Isle of May (repeat clutches)	733	49.8	1967	Parsons 1971
Rockcliffe Marsh (first clutches)	37	11	1981	This study
Rockcliffe Marsh (repeat clutches)	74	43	1981	This study

Fledging success and clutch size

There were no differences in fledging success between clutches of 2 and 3 (Table 30). In Grid 5 (all birds) and in repeat clutches laid by Herring Gulls, no chicks fledged from clutches of one. However, the small numbers of clutches involved means that this not necessarily implies lower fledging success for clutches of 1.

Fledging success and brood size

No difference in fledging success was found for broods of 1, 2 and 3 in Grid 5 nor for repeat clutches laid by Lesser Black-backed Gulls (Table 31). In repeat clutches laid by Herring Gulls, broods of 2 had significantly higher fledging success than broods of 1 or 3 (Table 31). Lower success in broods of 3 may be indicative of limiting food supply or, more probably, a breakdown in normal parental behaviour making the rearing of 3 chicks more difficult later in the season. Similarly, it may be that a brood of one provides an inadequate stimulus, in the same way as has been suggested for clutches of one, and thus a single chick may receive inadequate parental care.

Although the percentage of chicks which fledged was similar for broods of 2 and 3, in repeat clutches laid by Lesser Black-backed Gulls there was variation in the numbers of chicks lost within a given brood size (Table 32). Expected values for numbers of nests losing 0, 1, 2 or 3 chicks were derived from the binomial expansion, in the same way as those for egg losses (see Chapter 6.2 and Table 18). Significantly more nests lose either no chicks or all their chicks than would be expected if all nests were equally prone to chick losses. The same analysis could not be done for first clutches or for repeat clutches laid by Herring Gulls because samples were too small.

Table 30 : Fledging success and clutch size in first and repeat clutches

a) First clutches : all birds

Clutch size	1	2	3
No. of nests	27	59	80
No. of chicks hatched	6	49	115
No. of chicks fledged	0	9	18
% chicks fledged	0	18	16

b) Repeat clutches : Lesser Black-backed (LBB) and Herring Gull (H)

Clutch size	1		2		3	
	LBB	H	LBB	H	LBB	H
No. of nests	13	3	104	7	260	21
No. of chicks hatched	13	3	189	20	725	51
No. of chicks fledged	4	0	62	11	254	11
% chicks fledged	31	0	33	55	35	41

Table 31 : Fledging success and brood size in first and repeat clutches

a) First clutches : all birds

Brood size	1	2	3
No. of nests	31	47	15
No. of chicks hatched	31	94	45
No. of chicks fledged	5	13	9
% chicks fledged	16	14	20

b) Repeat clutches : Lesser Black-backed (LBB) and Herring Gull (H)

Brood size	1		2		3	
	LBB	H	LBB	H	LBB	H
No. of nests	94	15	182	16	152	9
No. of chicks hatched	94	15	364	32	456	27
No. of chicks fledged	32	4	133	20	153	8
% chicks fledged	34	27	36.5	64.5	34	30

Significance : Herring Gull; $^{c}/_{2}$ vs $^{c}/_{3}$ $\chi^2_1 = 6.34$ $p<0.05$

$^{c}/_{2}$ vs $^{c}/_{1}$ $\chi^2_1 = 5.24$ $p<0.05$

Table 32 : Variation in chick losses in broods of 2 and 3

Repeat clutches : Lesser Black-backed Gull

			Number of chicks lost					
Brood size	2		0	1	2	χ^2	d.f.	p
% chicks predated	63.5%	Obs.	33	67	86	8.36	1	<0.01
Number of nests	186	Exp.	25	86	75			

			Number of chicks lost						
Brood size	3		0	1	2	3	χ^2	d.f.	p
% chicks predated	66%	Obs.	11	39	42	94	54.6	2	< 0.001
Number of nests	186	Exp.	7	43	83	53			

Table 33 : Fledging success and laying date in first and repeat clutches

a) First clutches : all birds

Laying period (week)	3	4	5
Number of nests	41	76	15
Number of chicks hatched	34	108	22
Number of chicks fledged	7	14	4
% chicks fledged	21	13	18

b) Repeat clutches : Lesser Black-backed (LBB) and Herring Gull (H)

Laying period (week)	8		9	
	LBB	H	LBB	H
Number of nests	342	24	34	7
Number of chicks hatched	855	58	69	16
Number of chicks fledged	296	24	24	8
% chicks fledged	35	41	35	50

Seasonal variation in fledging success

Fledging success in first clutches was lower for eggs laid during the peak laying period (week 4) than for early or late layers (Table 33), although the difference is not significant. The number of chicks hatched in Grid 5 was not sufficient to afford any swamping of predators, and it seems likely that the chicks were exploited as a readily available food supply, by the large numbers of neighbouring gulls which had lost their own eggs in the flood.

In the repeat clutches, there was no apparent effect of laying date on hatching success, but this is not unexpected given the high level of synchrony in relaying.

Effect of cover and density on breeding success

In both the Lesser Black-backed and Herring Gull nest in areas with vegetation cover ('cover' nests) had higher fledging success than 'no cover' nests, and in 'cover' Herring Gulls had higher fledging success than Lesser Black-backed Gulls. It is likely that conspecific predation is responsible for most chick losses and so dense vegetation will give greater protection against such visually orientated predators. Brown (1967) also found a higher fledging success for 'cover' nests compared with 'no cover' nests.

Davis and Dunn (1976) were unable to separate the effects of cover and density on breeding success, since intermediate cover was associated both with highest density and highest chick survival. In the present study, although overall nesting density was higher in 'no cover' areas compared with 'cover' areas, a range of densities was found in both, and so it was possible to look at the relationship between density and fledging success in both areas (Table 35). In 'cover' areas, nearest neighbour distance was not correlated with fledging success. However in 'no cover' areas,

Table 34 : Fledging success in 'cover' and 'no cover'; repeat clutches of Lesser Black-backed and Herring Gull

	Lesser Black-backed Gull		Herring Gull	
	Cover	No cover	Cover	No cover
No. nests	282	201	29	39
No. chicks hatched	556	368	34	39
No. chicks fledged	208	113	20	12
% chicks fledged	37	31	59	31

Significance : LBB; Cover vs No Cover $\chi^2_1 = 4.39$ $p<0.05$

H; Cover vs No Cover $\chi^2_1 = 5.80$ $p<0.05$

Cover; LBB vs H $\chi^2_1 = 6.19$ $p<0.05$

Table 35 : Fledging success and nearest neighbour distance in 'cover' and 'no cover'; repeat clutches of Lesser Black-backed Gull

a) 'Cover'

	A	B	C	D
Nearest neighbour distance	(<6m)	(6-9m)	(9-12m)	(>12m)
Number of nests	37	70	73	102
Number of chicks hatched	65	144	146	201
Number of chicks fledged	22	58	58	70
% chicks fledged	34	40	39	35

b) 'No Cover'

	A	B	C	D
Nearest neighbour distance	(<6m)	(6-9m)	(9-12m)	(>12m)
Number of nests	52	88	35	27
Number of chicks hatched	101	158	68	41
Number of 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 $\chi^2_1 = 1.29$ N.S.

fledging success is highest for nests 9-12m apart and significantly lower at smaller nest spacings. Similar analysis for tile area indicates no significant increase in fledging success with increasing tile area (Table 36).

To summarise, in areas where dense cover is available for concealment of chicks, nest spacing has no effect on fledging success. In areas of low cover, overall chick survival is lower, and chicks from closely spaced nests suffer higher mortality than those from more widely spaced nests. The greater visibility of chicks in low cover areas will lead to increased predation and if conspecifics are the main predators, closely spaced nests will suffer higher chick losses than more widely spaced ones.

Table 36 : Fledging success and tile area in 'cover' and 'no cover'; repeat clutches in Lesser Black-backed Gulls

a) 'Cover'

Tile Area	A ($<88m^2$)	B ($88-184m^2$)	C ($>184m^2$)
No. nests	10	40	28
No. chicks hatched	14	83	56
No. chicks fledged	7	28	22
% chicks fledged	50	34	39

b) 'No Cover'

Tile Area	A ($<88m^2$)	B ($88-184m^2$)	C ($>184m^2$)
No. nests	38	69	17
No. chicks hatched	68	126	31
No. chicks fledged	18	47	13
% chicks fledged	26	37	42

6.5 Summary of breeding success

Overall breeding success of first and repeat clutches is shown in Table 37, together with figures from other colonies for comparison. The breeding success of both Herring and Lesser Black-backed Gulls in Grid 5 is very low and mainly due to heavy egg and especially chick losses, the reasons for which have been discussed earlier (Sections 6.3, 6.4).

In the repeat clutches laid by Lesser Black-backed Gulls, the number of chicks fledged/pair is slightly lower than that recorded for Skokholm despite an equivalent mean clutch size and higher hatching success. The lower overall success of repeat clutches at Rockcliffe is a consequence of higher levels of chick predation. In the Herring Gull, lower hatching success and lower clutch size both result in less chicks fledged/pair than that recorded on the Isle of May. The repeat clutches at Rockcliffe also do worse than repeat clutches from the Isle of May, despite a more comparable clutch size, and this is chiefly due to lower hatching success.

The decline in hatching success with decrease in clutch size is very marked in the Herring Gull at Rockcliffe (Table 17). If the number of chicks fledged/pair in clutches of 3 (0.76) is compared with that of clutches of 2 (0.39), it can be seen that the lower overall breeding success is primarily due to the smaller size of repeat clutches combined with increased egg losses in clutches of 2 and 1.

Cover and density also have a marked effect on breeding success. In both gull species, cover nests fledge on average more young than 'no cover' nests (Table 38). In Lesser Black-backed Gulls, higher hatching and fledging success in cover nests is slightly offset by the greater mean clutch size of 'no cover' nests, but there remains a significant difference in overall breeding success. In the Herring Gull, most of the difference in breeding success between 'cover' and 'no cover' nests is explained by the higher fledging success of 'cover' nests.

Table 37 : Summary of breeding success of Lesser Black-backed Gulls and Herring Gulls and comparison with other studies

a) Lesser Black-backed Gull

Study Area	No. nests	No. eggs	Mean Clutch size	% eggs hatched	no. chicks /pair	% chicks fledged	% eggs fledged	No.chicks fledged/pair	Authority
Skokholm (1970)	161	436	2.71	65	1.76	43	27.9	.76	Davis & Dunn(1976)
,, (1972)	111	296	2.67	59	1.57	69	40.7	1.08	,, ,,
Rockcliffe Marsh Grid 5 first clutches	52	134	2.58	51	1.31	20	10.2	.27	This study
Rockcliffe Marsh repeat clutches	546	1455	2.67	71	1.89	34.5	24.5	.65	This study

b) Herring Gull

Study Area	No. nests	No. eggs	Mean Clutch size	% eggs hatched	no. chicks /pair	% chicks fledged	% eggs fledged	No.chicks fledged/pair	Authority
Isle of May (1967)	1101	3062	2.78	64.3	1.79	50.8	32.6	0.91	Parsons (1971)
Isle of May (1968)	903	2463	2.73	69.9	1.91	35.4	24.7	0.67	,, ,,
Isle of May (1967) repeat clutches	500	1199	2.39	61.1	1.47	49.8	30.4	.73	,, ,,
Rockcliffe Marsh Grid 5 first clutches	22	50	2.27	76	1.68	11	8.4	.18	This study
Rockcliffe Marsh repeat clutches	72	159	2.20	48	1.07	43	20.6	.45	This study

Table 38 : Effect of cover on overall breeding success; repeat clutches

		No. nests	No. eggs	Mean Clutch size	% eggs hatched	no.chicks /pair	% chicks fledged	% eggs fledged	no.chicks fledged /pair	Significance of difference in no. eggs fledged Cover bs No Cover
Lesser Black-headed Gull	'Cover'	287	743	2.59	76	1.96	37	28.1	0.73	$\chi^2_1 = 12.67$ $p<0.001$
	'No Cover'	254	697	2.74	67	1.83	31	20.1	0.57	

In Table 39 the effects of 2 measures of density, namely nearest neighbour distance and tile area, on breeding success are shown. Neither nearest neighbour distance nor tile area has any significant correlation with the number of chicks fledged/pair when the nest is in a 'cover' area. However in 'no cover' areas, nests 9-12m from their nearest neighbour have the highest breeding success, fledging on average more chicks/pair even than nests in 'cover'. Breeding success is also lower for nests with the smallest tile areas, and this is due to lower fledging success slightly offset by a greater mean clutch size for nests in this category. The fact that nests with nearest neighbour distances greater than 16m are not represented in the range of (non-truncated) areas used explains why the highest breeding success is associated with the largest tile area.

The intermediate value for optimum nearest neighbour distance of 'no cover' nests is a result of more widely spaced nests having lower hatching success and more closely spaced nests having lower fledging success (Fig. 9). This suggests that in 'no cover' areas external predators are responsible for most egg losses whereas conspecifics are the most important predators of chicks. It is probable that a similar pattern of predation holds for nests in 'cover' areas, but that, here, closely spaced nests are less disadvantaged due to the greater possibilities for concealment of chicks in the vegetation. One might expect hatching success for nests in 'cover' to show a reduced but similar decline to that of 'no cover' nests, at wider nest spacings, but this is not the case (Fig. 10). One possible explanation is that the 'cover' areas, with a pattern of sparsely distributed, semi-concealed nests, are not such profitable areas for egg predators, which therefore concentrate their efforts on the more widely spaced nests in the 'no cover' areas.

Table 39 : Effect of cover and density on breeding success; repeat clutches of Lesser Black-backed Gulls

a) Nearest neighbour distance

	Nearest neighbour Distance	No. nests	No. eggs	Mean Clutch size	% eggs hatched	no. chicks /pair	% chicks fledged	% eggs fledged	No. chicks fledged /pair	Significance of difference in no. eggs fledged in A,B,C and D
'Cover'	A <6m	37	93	2.51	70	1.76	34	23.8	0.59	
	B 6-9m	75	192	2.56	80	2.04	40	32.0	0.82	N.S.
	C 9-12m	73	191	2.62	76	2.00	39	29.6	0.78	
	D >12m	102	267	2.62	75	1.97	35	26.3	0.69	χ^2_1 p
'No Cover'	A <6m	68	190	2.79	70	1.97	28	19.6	0.55	C vs A 5.12 < 0.05
	B 6-9m	112	304	2.71	66	1.79	27	17.8	0.48	C vs B 8.40 < 0.01
	C 9-12m	39	106	2.72	72	1.94	43	30.9	0.84	C vs D 5.05 < 0.05
	D >12m	35	97	2.77	55	1.51	32	17.6	0.49	

b) Tile Area

	Tile Area	No. nests	No. eggs	Mean Clutch size	% eggs hatched	no. chicks /pair	% chicks fledged	% eggs fledged	No. chicks fledged /pair	Significance
'Cover'	A <88m²	10	23	2.30	61	1.40	50	30.5	0.70	
	B 88-184m²	41	103	2.51	82	2.07	34	27.9	0.70	N.S.
	C >184m²	29	78	2.69	76	2.03	39	29.6	0.79	
'No Cover'	A <88m²	51	145	2.84	63	1.80	26	16.4	0.47	A vs B&C $\chi^2_1 = 4.6$
	B 88-184m²	85	227	2.67	68	1.82	37	25.2	0.67	$p < 0.05$
	C >184m²	22	61	2.77	64	1.77	42	26.9	0.75	

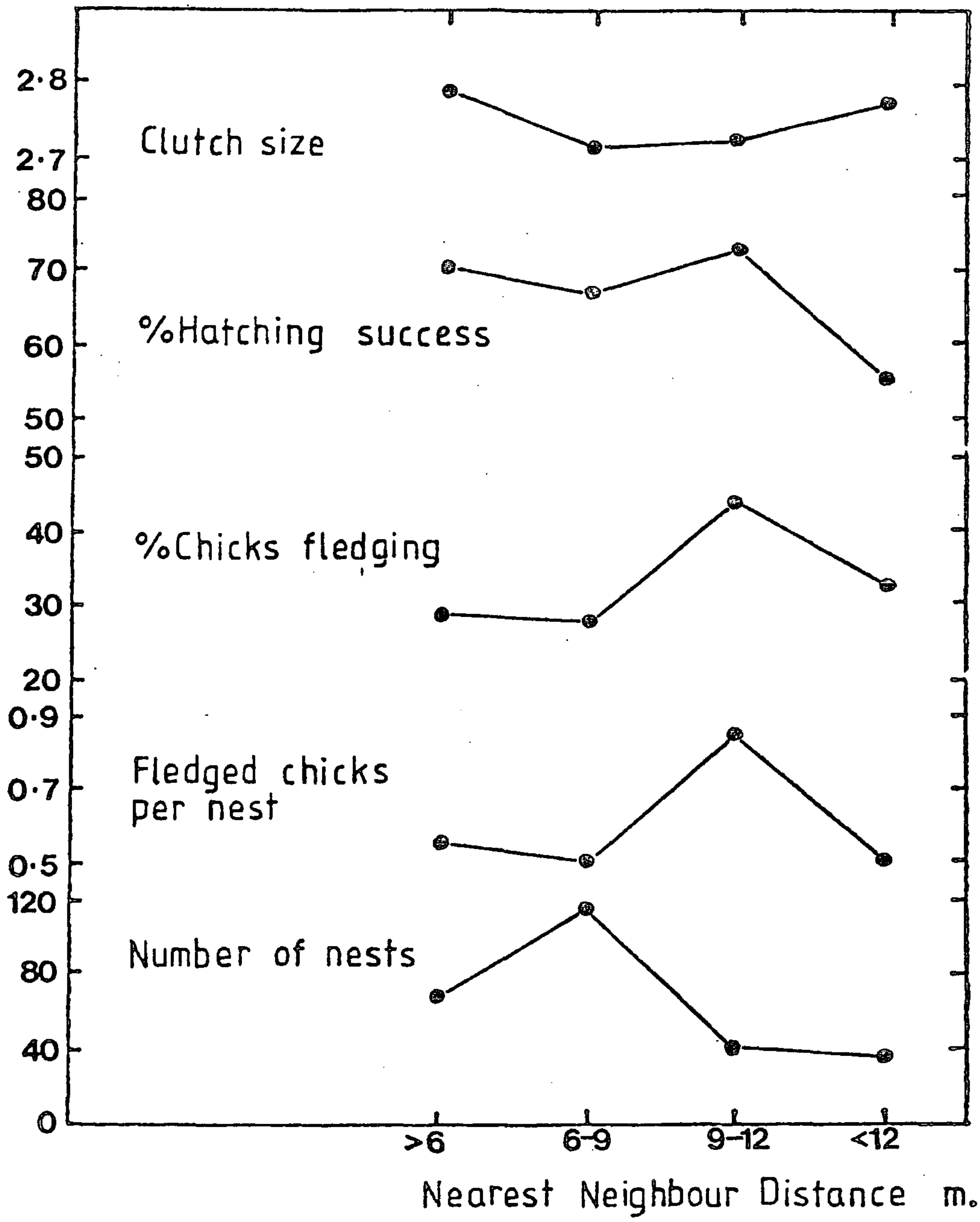


Figure 9 : Graph showing the relationship between nearest neighbour distance and breeding success for repeat clutches laid by Lesser Black-backed Gulls in 'no cover'.

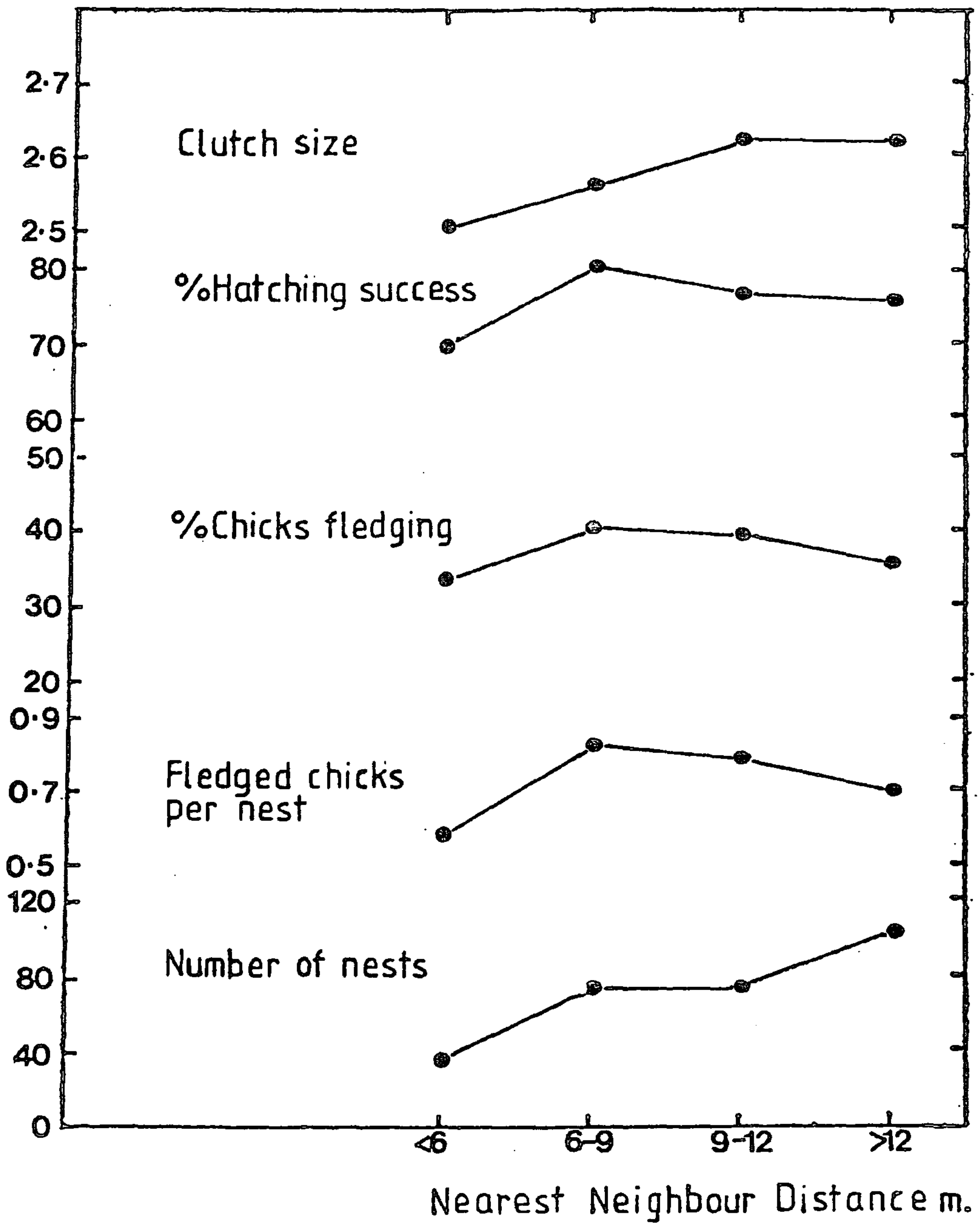


Figure 10 : Graph showing the relationship between nearest neighbour distance and breeding success for repeat clutches laid by Lesser Black-backed Gulls in 'cover'.

Chapter 7

Discussion

The breeding success of Herring and Lesser Black-backed Gulls in this study is lower than that recorded for various other gull colonies, despite the Rockcliffe colony being one of low overall nesting density and there being relatively few predators with access to the colony. The Rockcliffe gull colony has grown from 1700 pairs in 1973 to 2500 pairs at present, an increase of 47% in 8 years. This indicates a slower growth than some of the larger colonies e.g. Walney or Skokholm.

The extremely low breeding success of the group of nests which survived the flood must be considered atypical, given the decreased effectiveness of colonial defence in this small breeding group, and the large numbers of dispossessed birds, constituting potential predators, who were in the area at the time of hatching. However the repeat clutches also fledged few young compared with other colonies. One explanation is that this is a reflection of a seasonal decline in breeding success. The possible role of limiting food supplies in such a decline has already been discussed (Chapter 1). All the evidence from other studies suggests that there is no shortage of food for gulls at present, and the lack of correlation of brood size with fledging success in this study supports this view.

Parsons (1976) found that in Herring Gulls there was no disadvantage in breeding late in the season providing the delay was applied to a large group of nests simultaneously, and he concluded that synchrony, rather than timing, of laying was the most important factor contributing to breeding success. The repeat clutches were highly synchronous, considerably more so than the first clutches and so, on this basis, one might expect an increase in breeding success.

Although the delayed Herring Gulls in Parsons' study showed equivalent hatching and fledging success to that of birds from the peak of normal laying, there was a decrease in the number of fledged young produced per pair, which was due to decreased clutch size. Timing of laying seems to be the primary factor determining clutch size in Herring Gulls and, as the season advances, the mean clutch size decreases due to a fall off in reproductive drive. Combined with this decreased clutch size is a seasonal decline in hatching success, particularly in smaller clutches. This is also likely to be a consequence of a breakdown in normal pair behaviour late in the season, leading to increased infertility and inadequate incubation.

These two factors, seasonal decline in clutch size and in hatching success, especially in smaller clutches, may be sufficient to explain the low breeding success of Herring Gulls at Rockcliffe, since clutch size and hatching success are the main contributing factors leading to the small number of fledged young per pair.

Such an explanation, however, is not applicable to the Lesser Black-backed Gulls in the colony. No seasonal decline in clutch size or hatching success was apparent in the repeat clutches, and evidence from this study suggests that Lesser Black-backed Gulls do not suffer from a seasonal decline in reproductive drive to the same extent, or at least, not as early in the season as do Herring Gulls. The lower breeding success of Lesser Black-backed Gulls at Rockcliffe compared with other colonies is a consequence of lower fledging success.

Although comparisons with other studies are useful means of identifying departures from a general trend or level of production, the next step i.e. elucidating the causal factors involved requires an approach which does not involve such a multiplicity of interacting variables, many of them unknown. One method is to compare that which seems to be the optimum combination of factors for breeding success with that which applies to the majority of birds in the colony; i.e. in this case, to ask the question "are most of the Lesser Black-backed Gulls at Rockcliffe breeding optimally?"

At Rockcliffe, the pairs which produced the greatest number of fledged young were those which nested either in the 'cover' areas or in 'no cover' areas at a nearest neighbour distance of 9-12m. In contrast, as shown by Figure 6, large numbers of breeding pairs were crowded into the 'no cover' areas (47% birds in 33% of the total area) such that 71% of these birds were nesting at suboptimal distances from the nearest neighbour i.e. <9m. Thus, the answer to the above question is clearly, "No."

In order to establish how this nest distribution arose, it is necessary to look at the onset of laying. The pattern of normal laying, which was largely repeated in the relaid clutches, although in a much smaller space of time, showed that the majority of early layers were found at the Point, an area of low vegetation cover. It is likely that these early layers were the older birds and that this is reflected in the higher mean clutch size for nests in this area (2.74 compared with 2.59 in 'cover'). The pattern of growth was then one of spreading out from this original nucleus, presumably by a process of would-be breeders taking up territories as close as possible to other birds. In the Herring Gull, it has been shown (Chabrzyk and Coulson 1976) that recruits are attracted to areas where breeding density is already great even though it is difficult to establish a territory in such areas. This social attraction is an essential part of the colonial breeding habit and has evolved through the selective advantage of colonial defence against predators of other species (Kruuk 1964, Patterson 1965).

However, this social attraction may produce a higher nesting density than that needed for adequate colonial defence. An additional benefit of close spacing may be in increased breeding efficiency, through increased synchrony of laying (Brown 1967). Coulson and White (1960) found density-correlated onset of breeding in the Kittiwake but later studies (Coulson 1968) suggest that differences in age and physical condition may explain most of the differences in onset of breeding. Local synchrony in the onset of laying (Parsons 1976, Burger and Shisler 1980) and a correlation between median laying date and density, denser groups laying earlier (MacRoberts and MacRoberts 1972) have been demonstrated in the Herring Gull. However MacRoberts and MacRoberts (1972) failed to find any correlation between density and the onset and spread of laying in Lesser Black-backed Gulls, and the results of this study support their findings. Colony-wide synchrony though was apparent in this study and was greater for Lesser Black-backed Gulls than for Herring Gulls. Differences in patterns of breeding behaviour between Herring and Lesser Black-backed Gulls are to be expected since the only barrier keeping them as two separate species is reproductive isolation.

Both synchrony and high nesting density may be considered as anti-predator devices which result in decreased losses of eggs and chicks provided that predation pressure is constant and predators are not conspecifics.

At Rockcliffe, closely spaced nests of Lesser Black-backed Gulls have lower fledging success and therefore it is likely that conspecifics are responsible for much of the chick predation. In this situation, the increased synchrony of repeat clutches will result in lower breeding success if these gulls follow the pattern of increased aggression and territory enlargement during the chick stage which has been demonstrated in the Herring Gull (Burger 1980) and in the Glaucous-winged Gull (Hunt and Hunt 1976).

High nesting density and synchrony, leading to high levels of conspecific predation, provides the explanation for low fledging success of Lesser Black-backed Gulls at Rockcliffe. This does not, however, answer the question as to why so many of these gulls are nesting so close together when there is clearly room for expansion.

There are 3 possible explanations:

1) The present level of breeding success may not be sufficiently low to outweigh some unknown advantage in aggregating.
2) Widespread intraspecific predation may be a new phenomena associated with the increasing nesting densities and as such it has not had time to influence the traditional breeding patterns evolved to combat external predators.
3) The higher level of synchrony in the repeat clutches, combined with high nesting density, led to higher levels of conspecific predation than that which would obtain during the normal laying.

The exact nature of the selection pressure acting on gull populations and, most important, the time such pressures might take to influence established behaviour patterns, remains little understood. Further studies which follow the breeding success of a colony, ideally where the life history of a large proportion of the breeding birds is known, and which includes detailed observations on the causes of egg and chick losses, would increase our understanding of the factors affecting breeding success in gulls.

Summary

1. The breeding biology of Lesser Black-backed and Herring Gulls was studied on Rockcliffe Marsh, Cumbria, where they nest in a mixed colony of about 2500 pairs in a ratio of 4 : 1. The colony has grown by 47% in 8 years.

2. Lesser Black-backed Gulls laid, on average, later and more synchronously than Herring Gulls. Colony-wide synchrony was apparent but no evidence for local synchrony or for a correlation between synchrony and nesting density was found.

3. The highest nesting density was found at the Point, an area of low vegetation cover, and this area also had the highest percentage of early laying birds. It was suggested that this situation arose through social attraction, would-be breeders being attracted to areas of already high breeding density. Nesting distributions were clumped at high densities and random at lower densities.

4. The Marsh was flooded on 1 June and all but a small group of nests were destroyed. Over three-quarters (79%) of Lesser Black-backed Gulls relaid on average 11 days later, compared with only 29% of Herring Gulls, relaying on average 12 days later. The repeat clutches were highly synchronous and showed a similar distribution to that of the first clutches.

5. Two measures of density were calculated for the repeat clutches; a) nearest neighbour distance, b) an estimate of territory size calculated from a Dirichlet tesselation on nest distribution. The problems associated with the latter measure are discussed.

6. There was a seasonal decline in the clutch size of both species. This decline was continued in the repeat clutches of Herring Gulls.

It was concluded that timing of laying is the primary factor determining clutch size in Herring Gulls. In contrast, the clutch size of Lesser Black-backed Gulls at the start of the relaying period was equivalent to that found at the beginning of the season. It was concluded that clutch size is primarily determined by age in Lesser Black-backed Gulls and that earlier laying by older birds explains the observed seasonal decline.

7. Infertility, as measured by eggs which failed to hatch, was greater in repeat clutches compared to normal clutches, and greater in Herring Gull repeat clutches compared with those of Lesser Black-backed Gulls. This was attributed to a fall-off in reproductive drive as the season advances, which is particularly marked in the Herring Gull.

8. In first and repeat clutches of both species, most chick mortalities occurred in the first week of life. Few chicks were found dead, whereas many disappeared without trace. It was thought likely that conspecific predation was responsible for most chick losses, since few predators have access to the colony.

9. Breeding success of the small group of nests which survived the flood was very low. This was attributed to high levels of egg and chick predation, due to the decreased effectiveness of colonial defence in this small breeding group, and to heavy predation by the large numbers of dispossessed, neighbouring birds.

10. The repeat clutches of both Herring and Lesser Black-backed Gulls were more successful when in areas of long vegetation ('cover') than in areas of short vegetation ('no cover'). It was suggested that the greater concealment of eggs and chicks in 'cover' areas led to lower levels of predation.

11. No correlation was found between breeding success and either measure of nesting density for Lesser Black-backed Gull nests in 'cover'. In 'no-cover' nests, those at an intermediate density (as measured by nearest neighbour distance) fledged most chicks. More widely-spread nests suffered higher egg predation, whereas at closer nest spacings fledging success was lower. It was concluded that predators of other species e.g. crows were responsible for most egg losses, whereas conspecifics were the main chick predators.

12. Breeding success of repeat clutches of both species at Rockcliffe was low compared with figures from other colonies. In Herring Gulls this was a consequence of a smaller clutch size and lower hatching success, especially in small clutches. It was suggested that these effects reflect a seasonal decline in reproductive drive which results in low egg production, inadequate incubation and inattentiveness. No such decline in reproductive drive was apparent in Lesser Black-backed Gulls. Lower breeding success in this species was a consequence of lower fledging success. This in turn was due to large numbers of birds nesting subcptimally i.e. in 'no cover' areas at close nest spacings. It was suggested that the combination of conspicuous nest site and close nest spacing led to high levels of conspecific predation on chicks.

13. Three explanations were put forward for this apparently suboptimal nest distribution:

    a) There may be some unknown advantage in aggregating which outweighs the apparent disadvantages.

    b) High levels of conspecific predation may be a new phenomenom associated with increasing nest densities, and as such, it has not yet influenced established breeding patterns.

c) The higher level of synchrony in the repeat clutches, combined with high nesting density, may have led to higher levels of conspecific predation than that which would obtain during a normal breeding season.

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