Aspects of the breeding biology of common terns (Sterna Hirundo) on Rockcliffe Marsh, Cumbria.

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Aspects of the breeding biology of Common Terns (*Sterna hirundo*) on Rockcliffe Marsh, Cumbria.

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CHAPTER 1

Introduction

The breeding population of Common Terns, Sterna hirundo, on Rockcliffe Marsh has been declining in numbers in recent years. This could be for several reasons; there could be emigration to an expanding colony elsewhere, there might be exceptionally high adult mortality caused by environmental pollutants, natural toxins or increased predation by man in the wintering area. Alternatively, the number of fledged young produced during the breeding season could be insufficient to replace the annual loss of mature birds.

Concurrent with this trend there has been a more dramatic drop in the number of breeding Black-headed Gulls, Larus ridibundus, on the marsh. It is considered by many (e.g. Salmonsen 1943, Lind 1963, Cullen 1960a, Nicholson 1978) that, because of their superior defence of eggs and young, Black-headed Gulls provide a measure of protection from predators of other species which nest among them. Given the steady expansion of the Lesser Black-backed and Herring Gull colony (Larus fuscus and Larus argentatus respectively) on the marsh, at a rate of 47% in eight years (Grieg, 1981), these being considered to be the major predators of the Terns, it is tempting to conclude that it is as a direct result of these two factors that the breeding success of the Terns has been insufficient to maintain the population.

The aim of this study was to investigate the breeding success of the low density colonies of Terns and to calculate if it was sufficient to maintain the population. Also, an attempt was to have been made to study the relationship between the Terns and the Black-headed Gulls in order to assess whether the latter do indeed defend the mixed colony and, if so, whether this produces a greater breeding success in the Terns than that realised in colonies on the marsh where Black-headed Gulls are absent. The breeding success of the Black-headed Gulls was also to be studied in an attempt to explain their population decline.

These aims had to be modified because the decline in Black-headed Gull numbers had resulted in only thirty-six nests being built, this level of presence among the Terns being considered insufficient to have much effect on the defence of the nests in the low density mixed colony. Those that were present had such poor breeding success that few chicks were found more than three days after hatching, this level of mortality reducing further any colony defence on their part.

It was the intention that breeding success should be studied by re-finding as many as possible of the individually marked chicks which were still alive prior to fledging, using the Lincoln Index to estimate the total number of chicks that survived to that age. In the event, because of the low nesting density and the amount of vegetation and other cover available, the chicks were very difficult to find after the first few days of life, once they had left the nest. Thus only minimum and maximum estimates of breeding success of the Common Terns were obtained, and a best estimate based on search efficiency.

CHAPTER 2

Study area

2.1 The Marsh

Rockcliffe Marsh (G.R. NY 325640) is situated at the head of the Solway Firth (Fig. 1) about 10 km. north-west of Carlisle, at the confluence of the rivers Esk and Eden which flank its north and south edges respectively (fig. 2). The marsh is owned by Castletown Estates and is managed as a nature reserve by Cumbria Trust for Nature Conservation during the breeding season. It is classified as a grade 1 S.S.S.I by the Nature Conservancy Council (Ratcliffe, 1977).

The reserve is a dry saltmarsh covering about 1130 ha and is roughly triangular, being about 4.3 km from east to west and 3.4 km from north to south. It consists of firm turf interspersed with muddy drainage creeks which fill at high tide. The whole marsh is likely to be covered by the equinoctial spring tides, the extent of flooding being determined by the presence and strength of a south-westerly wind and the amount of water in the Esk and Eden. The marsh is grazed in summer by cattle (920 head in 1982) and in winter by geese.

The 800 ha of mature saltmarsh grades, at its edges, into less mature, "new" marsh, and eventually to sand in the river channels. The vegetation of the mature marsh is a fescue grassland dominated by *Festuca rubra* L. and, towards the seawall, the taller *Lolium perenne* L. and *Bromus mollis* L.. The "new"marsh vegetation is generally much shorter (15 cm) and consists of such species as Thrift, *Armeria maritima* (Mill.) Willd., common saltmarsh grass, *Puccinellia maritima* (Huds.) Parl. and Sea milkwort *Glaux maritima* L..

2.2 The history of the Tern and Black-headed Gull colonies

The number of breeding pairs of Terns has been between 200 and 250 since the reserve records began in 1970, with the exception of 1973 and 1981 when there were about 100, and 1979 and 1980 when there were about

Fig. 1 : Geographical location of Rockcliffe Marsh

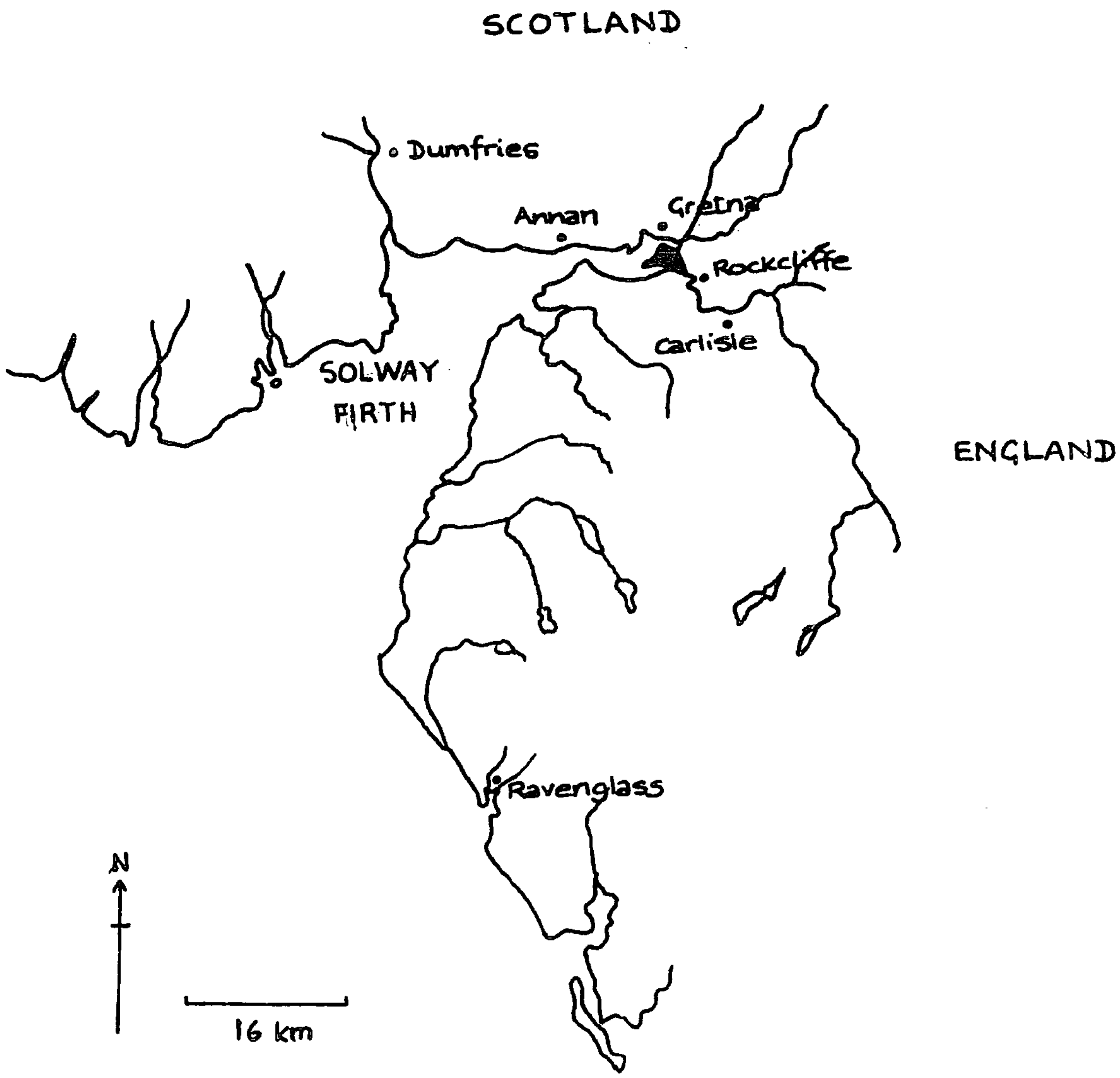
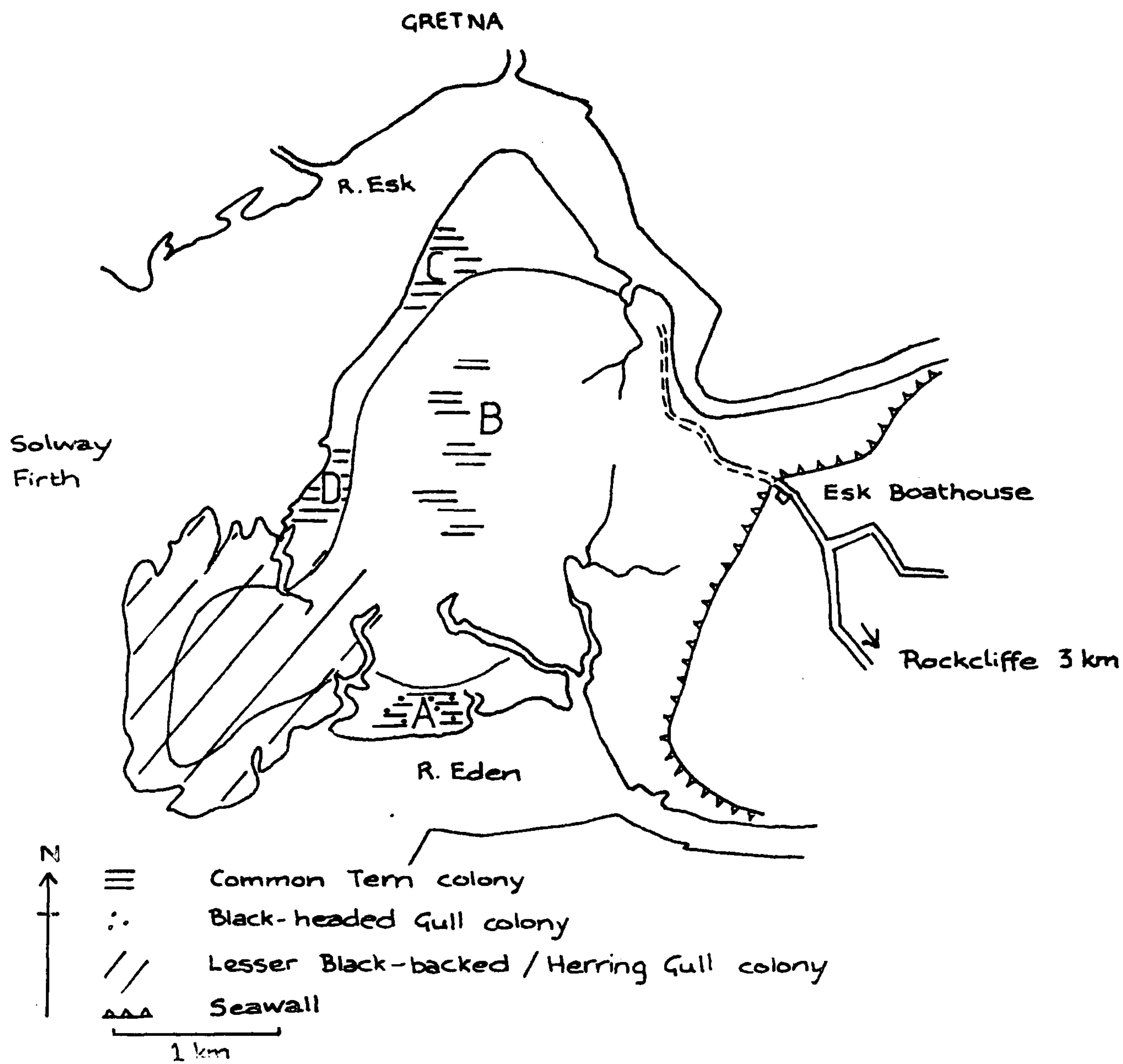


Fig. 2 : Rockcliffe Marsh and the location of the Tern colonies studied .



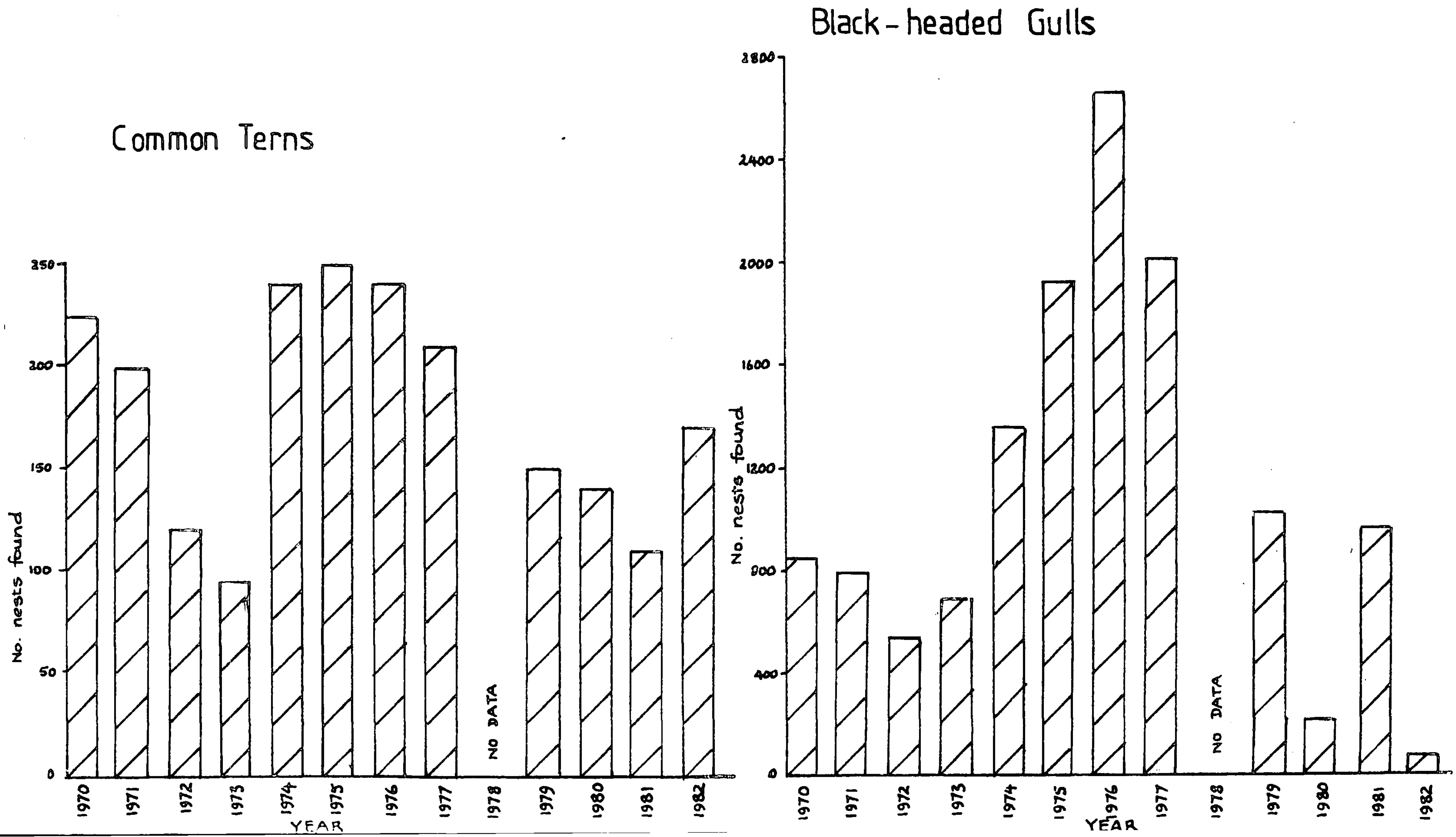
150. All of these figures must be treated with some caution since they are the result of nest counts, and the search efficiency of the different wardens will undoubtedly vary. If the general trend of these figures is to be believed, there appears to have been a decline in numbers of 58% from 1975 to 1981 (fig. 3).

The reduction in the size of the breeding population of the Black-headed Gulls over recent years has been more dramatic. Numbers rose from around 800 in 1970 to peak at 2657 in 1976, since when they have fallen, particularly since 1979, to number only around 36 pairs this year (1982), a drop of 98.7%, despite the presence on the marsh of about 300 non-breeding birds in large flocks throughout the season. A decline of similar magnitude has been reported at Ravenglass on the Cumbrian coast. (G.R. SD 0796) (Rowley, pers. comm.). This could represent a natural cycle of events with the reversal of the past trend of immigration from inland sites, or it could be due to some factor which renders the coastal sites unfavourable. The fact that the eggs of Black-headed Gulls were pricked in 1974 might have played some part in the initial decline since the effect of this would be felt in 1979, four years later, when that year's young were recruited to the breeding population. This seems unlikely, however, since there would probably have been recruitment from elsewhere to counteract this. In view of the increase in numbers reported at inland sites (e.g. Sunbiggin Tarn, Cumbria (Bailey, pers. comm.)), it is unlikely that the decline observed on the marsh was due to mortality during the non-breeding part of the year.

2.3 The Tern colonies studied

The Terns were situated this year on the "new marsh" in two discrete colonies beside the Esk and one by the Eden, and in a less dense colony in the middle of the mature marsh (fig. 2). Altogether 168 nests were found and marked, a total breeding population throughout the marsh of 250 pairs being estimated from aerial counts. The study of many of the nests was later abandoned, either involuntarily if it could not be re-located or through necessity in order that the remaining nests, which formed denser

Fig. 3 : The number of Common Tern and Black-headed Gull nests found on Rockcliffe Marsh, 1970-82.



colonies, and therefore represented a more efficient use of the available time, could be studied more thoroughly.

The ratio of Common to Arctic Terns (<u>Sterna paradisaea</u>) was put as high as 6:1 in 1977 (Rankin, pers. comm.), but this year only one or two Arctic Terns were seen, and none of those studied were Arctic Terns.

Although Black-headed Gulls were present in relatively large numbers - about 300 - only 48 nests were found, these being mainly alongside creeks among the Edenside Terns (colony A), with a few scattered pairs on the mature marsh.

The Tern colonies studied throughout were the Edenside "new marsh" colony (colony A) numbering 49 nests and the Eskside "new marsh" colony (colony C) of 33 pairs. Because of the amount of vegetation cover on the mature marsh, only a small number, about 14 pairs, of Terns of the middle marsh (colony B) were studied. A second Eskside "new marsh" colony (colony D) of 17 pairs was included in the laying studies, but all of the nests were flooded prior to hatching. The Black-headed Gulls which were studied were those among which the Edenside Terns were nesting, numbering 33 pairs, but the chicks were not found beyond a few days after hatching, presumably because they had died, since frequent exhaustive searches failed to find them.

CHAPTER 3

Methods

3.1 Marking nests and eggs

Nests were marked with a wooden stake placed about 1m away from it and numbered with black waterproof ink. There was no evidence that the stakes caused any disturbance to the nesting birds nor increased predation, although the latter cannot be known for certain since all nests in the study area were marked.

Eggs were marked with black waterproof ink according to the sequence of lay where known, and according to egg size where not, the first egg bearing number 1, the second number 2 and the third number 3, or the largest X1, the second largest X2 and the smallest X3.

3.2 Egg measurements

The maximum length and breadth of the eggs was measured using Vernier calipers, measuring to the nearest 0.005 cm. The volume of each egg was calculated using the following formula:-

$$\text{Volume (cc)} = k.l.b^2$$

where l = maximum length of eggs (cm)

b = maximum breadth of egg (cm)

k = constant for particular species. Here the value used was k = 0.48 (Horobin 1971)

3.3 Calculating hatching success

Hatching success was expressed as a proportion of the eggs laid which hatched and as the proportion of the clutch that hatched.

3.4 Estimating nearest neighbour distance

The positions of the nests were mapped using distances measured with a 100m tape to the nearest 0.25m and angles measured with a prismatic compass to 0.5°. The positions of the nests were plotted on graph paper to a scale of 1mm = 1m. Inter-nest distances were then measured from those maps to an accuracy of ± 0.25m.

3.5 Assessment of nest cover

The height of the vegetation surrounding the nest was measured to the nearest 0.25cm. However, because it was very homogeneous throughout the study area, the amount of cover was defined by the density of the vegetation rather than its height. Here, a subjective assessment was made, "cover" areas being the species-rich mature marsh areas of red fescue, Festuca rubra, clover, Trifolium repens, and birdsfoot trefoil, Lotus corniculatus (colony B), while "no cover" areas were the "new marsh" colonies, comprising 15 cm Parapholis strigosa and 2cm Puccinellia maritima at colony C, 15cm Parapholis strigosa and 3cm Plantago maritima (colony D) and 15cm thrift, Armeria maritima and 2cm Puccinellia maritima (colony A). Thus the colonies were characterized by their vegetation, variation within each colony being insignificant.

3.6 Measurement of distance to cover

The distance from each nest to a creek, depression or clump of dense vegetation, which would provide cover for the chicks once they had left the nest, was measured with a 100m tape to the nearest 5cm.

3.7 Measurement of distance to food supply

The distance from each nest to the edge of the rivers Eden or Esk, whichever was the nearer, was measured from the maps of the nests, on which the river banks had been plotted. The accuracy was estimated to be ± 5 m.

3.8 Measurement of distance to other species

The distance from each nest to that of the nearest Black-headed Gull was measured from the maps of the nests to the nearest 0.25m. The distance from each nest to the edge of the mixed Lesser Black-backed and Herring Gull colony (fig. 2) was estimated from the maps to the nearest 25m, since the edge of the colony had not been accurately plotted.

3.9 Marking newly hatched chicks

Chicks were marked within a day of hatching. Tern chicks were individually identified by combinations of colour rings. Black-headed Gull chicks were ringed with sections of 10mm diameter black plastic tubing covered with white tape and marked with the nest numbers and a, b or c, representing hatching sequence, with a black waterproof felt pen. The diameter of these latter rings was reduced with one end of a steel staple; the rusting of the staple would ensure that it dropped off after one or two weeks, allowing the ring to open to its full diameter.

3.10 Assessment of growth rate

The chicks were weighed whenever they were re-located, except for during adverse weather conditions when it was considered that handling might lead to increased mortality. Weighing was done using a Pesola spring balance, measuring to the nearest 0.25g.

3.11 Estimating fledging success

On the basis that most chick mortality occurs during the first week of life (Langham, 1968), survival to ten days was equated with fledging in this study. It will therefore be an overestimate. It was intended to estimate the number of chicks surviving to this age using a mark-recapture technique. This method is based on the fact that not all chicks will be found in any one search. A series of searches or recaptures gives the total number of chicks found and an estimate of the total number of chicks present based on the Lincoln Index. Comparison of these gives an estimate of the number of chicks which escaped recapture. However, an insufficient number of chicks in colonies A and C could be found on each search for this method to be of any value. In colony D a high tide rendered fledging success estimates unnecessary, and in colony B the nature of the vegetation cover made the following of chicks to fledging impracticable in the time available given the size of the area involved.

The best that could be obtained in the circumstances were estimates of minimum and maximum fledging success in colonies A and C, based on known deaths, the few known survivals to fledging, and estimates using assumed deaths of chicks which, when last seen, were losing weight, which was justified by the observation that in no case of known outcome did a chick that was losing weight survive. Unfortunately this still leaves a significant proportion of the chicks unaccounted for. An additional estimate was made for these two colonies based on the known search efficiency (viz. the proportion of chicks known from later finds to have been alive that were found), giving an estimate of the number of chicks still alive after eight days. This was considered to be the best estimate.

CHAPTER 4

Pattern of laying

4.1 Spatial distribution of nests

Nesting density was not measured in colony B because, owing to the nature of the vegetation, an insufficient proportion of the nests could be found in the time available to give anything approaching a realistic nesting density. The mean nearest neighbour distances to a conspecific of the remaining three colonies were significantly different ($p < 0.01$) (table 1), colony C being the most compact and colony A the least dense. All showed a significantly clumped distribution.

4.2 Temporal laying pattern

4.2.1 The laying period

Laying began on 19 May, but a high tide on 25 May caused all of these nests to be lost, the first surviving clutches being started on 29 May. The laying season, from the start of the first to the last clutch, extended over seven weeks, from 19 May to 7 July, this latter date being inferred from hatching dates and therefore subject to an error of two or three days.

4.2.2 Synchrony of laying

Laying was not synchronous over the whole marsh but was relatively so within each of the individual colonies. Colony D could not be compared with the others since laying dates were not known and eggs were lost prior to hatching so that dates could not be inferred from hatching dates, but the pattern for the other three colonies is given in Table 2 and shows a five week difference between the peak laying week of colonies A and B and that of C.

The figures suggest that laying was more synchronous within a more compact colony, colony C, than in a looser one, colony A, as given by mean nearest neighbour distances (table 3). However, although the laying period was longer in colony A than in C, being 25 days compared with 21

Table 1: Comparison of mean nearest neighbour distances between the three colonies in which this parameter was measured.

	COLONY		
	A	C	D
No. of nests	50	35	22
Mean nearest neighbour distance(m)	14.4	7.2	9.3
Standard deviation	12.2	4.5	5.9
Coefficient of dispersion	10.3	2.8	3.8
Clumped(C)/Random(R)/Dispersed(D)	C	C	C

Significance: A vs C $\chi^2_1 = 6.38$ $p < 0.05$
A vs C vs D $\chi^2_2 = 9.68$ $p < 0.01$

Colony B was omitted because difficulties peculiar to that colony and a shortage of time made it impracticable to complete the search for nests and measure inter-nest distances.

Table 2: Cumulative percentage of clutches started in each laying week.

Laying week:	0	1	2	3	4	5	6
Dates:	Up to 29 May	29 May-4 June	5-11 June	12-18 June	19-25 June	26 June-2 July	3-8 July
Colony							
A	0.0	69.6	89.1	95.7	100.0	-	-
B	0.0	61.5	92.3	100.0	-	-	-
C	0.0	0.0	0.0	0.0	26.1	78.3	100.0

None of the few eggs laid prior to 29 May survived the high tide of 25 May and so were omitted from the analysis.

Table 3: Comparison of the standard deviation of the date of the start of clutches from the mean laying date between the three colonies in which laying date was known.

Colony	A	B	C
Standard deviation of mean laying date	5.3	5.0	4.9

Significance: A vs C N.S.

Table 4: Skewness of laying distribution over time for the three colonies of known laying dates.

Colony	Skewness	
A	1.67	Positive skew (i.e. a tail of late laying)
B	0.64	Small positive skew
C	- 0.35	Small negative skew

days, the difference in the deviation of the date of lay of individual eggs from the mean laying date between the colonies was not statistically significant. Synchrony was therefore not related to nesting density.

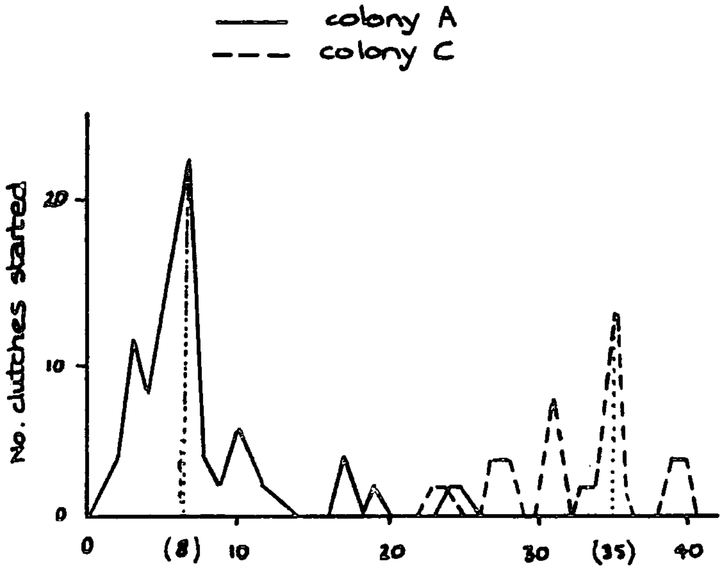
4.2.3 Temporal laying pattern

In colonies A and B the distribution of the start of clutches over time was positively skewed, and in colony C, the later colony, it was negatively skewed (table 4).

A comparison of mean and peak laying dates between colonies A and C are given in table 5 and confirm the skewness results, showing how negative skewness results in the mean laying date preceding the peak and vice versa. Colony B was omitted because the dates of lay of the few clutches followed were too spread out to form any recognisable distribution.

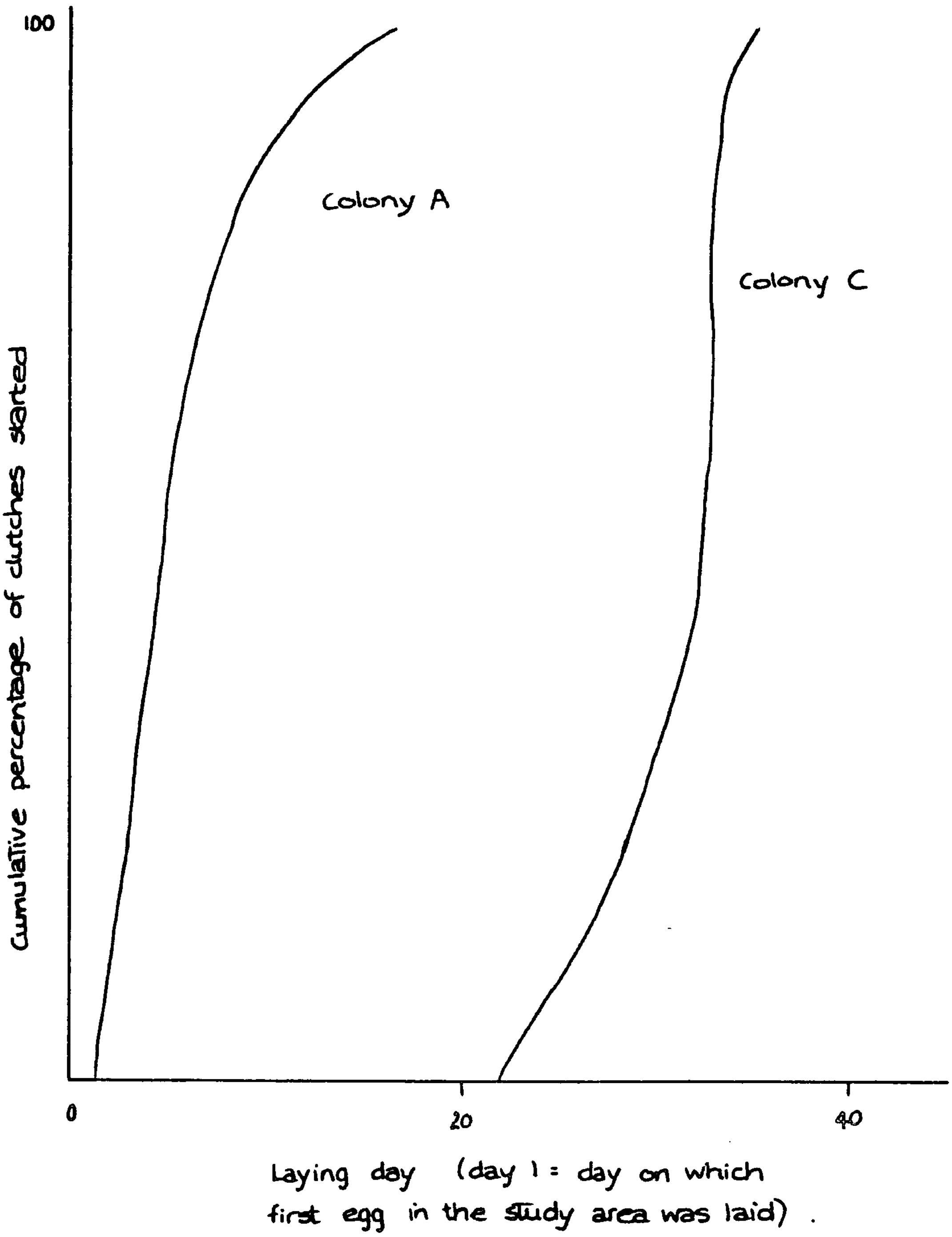
The observed differences in laying pattern between colonies A and C can be expressed graphically (figs. 4 and 5); while laying in colony A increased rapidly to an early peak, laying proceeded slowly in colony C, peaking later in relation to its laying period.

Fig. 4 : The pattern of initiation of clutches over time in colonies A and C .



Laying day (day 1 = day on which first egg laid in the study area) .

Fig. 5 : The cumulative percantage of clutches started in colonies A and C over time. (Days are numbered consecutively from day 1, 29 May, when the first egg was laid).



CHAPTER 5

Clutch size and egg volume

5.1 Clutch size

Although the clutch size of Terns can be from one to four eggs (Nelson, 1980; Harrison, 1975) this upper figure is very rare, and in this study no clutches of more than three were found. The single-egg and some of the two-egg clutches could not be guaranteed not to have had more at a previous date. Clutch size data should therefore be viewed with some caution.

Of the clutches followed, and therefore know to be complete, mean clutch size was 2.40 with a standard deviation of 0.66 (table 6).

5.2 Seasonal variation in clutch size

There was a significant decline in clutch size with season (table 7), from a mean size of 2.7 in laying week 1 to 2.2 in week 6.

5.3 Egg volume

The volume of the 233 eggs measured ranged from 14.9 to 21.0 cc, the mean volume being 18.01 cc (table 8). There was no conscious decision as to which eggs were to be measured, those not measured having hatched or been predated before this was possible.

5.4 Seasonal variation in egg volume

Although Table 9 shows a seasonal decline in mean egg volume, the difference between laying weeks was not significant although laying week and mean egg volume were significantly correlated ($r_s = -0.83$, $p < 0.05$). There was no significant variation in egg volume with clutch size (table 10) so the observed correlation between egg volume and season is unlikely to have been an anomaly due to the relationship between clutch size and season.

5.5 Variation in egg volume with laying sequence

Although table 11 shows the mean egg volume of the first, second and third egg laid of clutches to be in descending order of size, the

Table 5: Mean and peak laying dates for Colonies A and C. ("Peak" here refers to the mode of clutch initiation - Fig. 4)

Colony	A	C
Mean laying date	5 June	30 June
Peak laying date	4 June	2 July

Table 6: Clutch size data for the whole marsh. Only clutches followed and therefore known to be complete are included. Thus the error lies only in predation prior to finding the nest.

(a) All complete clutches.

Clutch size	1	2	3	Total
No. of nests	12	51	62	125
% of nests	9.6	40.8	49.6	100

Mean clutch size = 2.40
Standard deviation = 0.66

(b) Excluding clutches of 1.

Clutch size	2	3	Total
No. of nests	51	62	113
% of nests	45.1	54.9	100

Mean clutch size = 2.55
Standard deviation = 0.50

Table 7: The variation in clutch size with season for the whole marsh.

Laying Week:	1	2	3	4	5	6	Total (1-6)
No.of nests of known laying date and clutch size)	39	13	3	6	12	5	78
% c/1	2.5	8.3	0.0	16.7	16.7	0.0	6.4
% c/2	20.0	41.7	33.3	66.7	75.0	80.0	39.7
% c/3	77.5	50.0	66.7	16.7	8.3	20.0	53.9
Mean clutch size	2.7	2.5	2.7	2.0	1.9	2.2	2.49
Standard deviation	0.5	0.7	0.6	0.6	0.5	0.5	0.60

Significance: Weeks 1, 2, 3 vs weeks 4, 5, 6 $\chi^2_1 = 13.42$ $p<0.001$

Table 8: Mean and range of egg volumes, whole marsh.

No. of eggs	233
Minimum egg volume	14.88
Maximum egg volume	21.00
Mean egg volume	18.01
Standard deviation	1.29

Table 9; The relationship between mean egg volume and season (whole marsh).

Laying week	No. of eggs	Mean egg volume	Standard deviation
1	107	18.2	1.2
2	32	17.8	1.4
3	8	18.0	1.2
4	12	17.9	1.1
5	23	17.8	1.5
6	11	16.6	0.8

Significance: Week 1 vs weeks 2 to 6 N.S.
Week 1 vs week 6 N.S.

Table 10: The variation in egg volume with clutch size.

	c/1	c/2	c/3
No. of eggs	10	83	139
Mean egg volume	17.56	18.00	18.08
Standard deviation	1.87	1.42	1.20

Significance: c/1 vs c/2 vs c/3 - N.S.
c/1 vs c/3 - N.S.

differences are not significant. This may be because of the small sample size, the reason for this being that there were few eggs of known laying sequence because of the large area over which the nests were scattered rendering daily searches of each possible area impracticable. When eggs known to be either the first or second laid were compared with those known to be the third laid, the difference in volume was significant (table 11).

However, there was a significant decline in mean egg volume with hatching sequence throughout the whole sample and also within any one laying period when the effect of decreasing volume with season is reduced (table 12). Albeit with limited data, results here suggest that hatching sequence reflects laying sequence since in no known case was the order of hatch different from the order of lay (n = 2 complete clutches and 13 incompletely known clutches). This is supported on theoretical grounds, since incubation begins with the first egg (Langham, 1968).

Within any one clutch the order of lay could not be obtained from egg volume with complete certainty, "incorrect" order (viz. at least one egg out of place in the sequence of descending size with order of lay) being observed in 26.7% of cases in a small sample (n = 15) of clutches (Table 13). The size of the last egg in relation to the others was more consistant being the smallest in 93.3% and 92.9% of cases of known laying and hatching sequence respectively (Table 14).

The decline in volume with hatching sequence was more consistant in clutches of two than in three-egg clutches (Table 15). This was as expected since it is the last egg which is different from the others, rather than there being any significance in the precise order of lay (Coulson, pers. comm.). In neither case could laying sequence be inferred from egg volume with any confidence. The identification of the last egg by volume would be more reliable, again particularly in clutches of three, but even this would be incorrectly estimated in about one in every ten cases, this error being reduced to one in every fifteen in clutches of three (Table 14).

Table 11: The relationship between egg volume and the sequence of lay (whole marsh).

Sequence of egg in clutch	No. of eggs	Mean volume of eggs	Standard deviation	
1	8	18.5	1.4	Significance:-
2	4	18.1	1.4	1 vs 2 vs 3 N.S.
3	13	17.4	0.8	1 vs 3 N.S.
1 + 2	34	18.46	0.9	Significance:-
3	13	17.4	0.8	1 +2 vs 3 $\chi^2_1 = 4.65$ $p < 0.05$

Single - egg clutches were omitted from this analysis because of the risk of their being incomplete.

Table 12: Change in egg volume with hatch sequence (a) for the whole season (b) in week 1 only and (c) in weeks 2 -6.

	Hatch Sequence	No. of Eggs	Mean Egg Volume	Standard Deviation	
a) Whole Season	1	38	18.6	1.3	Significance:-
	2	38	18.3	1.2	$\chi^2_2 = 18.45$
	3	28	17.5	0.9	$p < 0.001$
b) Week 1 only	1	22	18.7	1.0	Significance:-
	2	22	18.6	1.0	$\chi^2_2 = 11.04$
	3	22	17.7	1.0	$p < 0.01$
c) Weeks 2 - 6	1	16	18.4	1.5	Significance:-
	2	16	18.0	1.4	$\chi^2_2 = 6.19$
	3	6	17.0	0.4	$p < 0.05$

Table 13: Maximum frequency of occurrence of decreasing egg volume with laying sequence in a small sample of clutches.

No. of Nests	Decreasing order of egg volume with laying sequence		Variable order of egg volume with laying sequence	
	No.	%	No.	%
15	11	73.3	4	26.7

The laying order of 79% of the clutches was incompletely known. The proportion of clutches of decreasing egg size with sequence may therefore be an over-estimate since, while what was known of the sequences was in the "correct" order of size, the unknown egg may have been out of order. Hence the results given show maximum occurrence of "correct" order.

CHAPTER 6

Breeding success

6.1 Hatching success

Hatching success varied considerably between the four colonies, ranging from 83% of the eggs laid to 0% (Table 16). The difference between colonies was statistically significant, as was that relating to the proportion of eggs of each clutch which hatched (Table 17). In colony D, some nests had already been predated when found so the number of eggs laid was not known. From an estimation of the laying season of the colony, viz. weeks 2 and 3, from the one egg which had started chipping at the time of the flood which destroyed all those eggs not previously predated, and given the decrease in clutch size with season (Table 7), the clutch size of the nests of unknown clutch size was assumed to be 50% clutches of two and 50% three-egg clutches. This ratio was supported by the few clutches of known size (n = 8). From this the number of eggs predated was calculated for comparison with the other colonies (Tables 16, 18 and 19).

The results presented in Table 16 show hatching success as a proportion of eggs laid to be significantly different in the four colonies, their descending order of success being A, C, B, D. In terms of the success or otherwise of the clutches, colony A also had a significantly greater proportion of clutches in which all of the eggs hatched and the smallest proportion of completely failed clutches (Table 17). Hatching success for the whole marsh studied was 61% of the eggs laid. Table 17 shows that 34% of the 94 clutches studied failed completely, this number being reduced to 27% with the exclusion of losses due to the tide (this affecting 7 of the 22 nests lost in colony D).

6.2 Factors affecting hatch success

The major reason for the failure of eggs to hatch was predation, presumably by avian predators since few traces of ground predators were

Table 14: The position of the smallest egg in the laying and hatching sequence.

	No. of Nests	c/2				c/3				Total			
		Last egg smallest		Last egg not smallest		Last egg smallest		Last egg not smallest		Last egg smallest		Last egg not smallest	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
a) Laying sequence	15	2	100.0	0	0.0	12	92.3	1	7.7	14	93.3	1	6.7
b) Hatching sequence	42	13	86.7	2	13.3	26	96.3	1	3.7	39	92.9	3	7.1
c) Laying and/or hatching sequence	45	14	87.5	2	12.5	27	93.1	2	6.9	41	91.1	4	8.9

Significance: c/2 vs c/3 N.S.

Table 15: The frequency with which egg volume decreases with hatching sequence in 2- and 3-egg clutches.

Clutch Size	c/2	c/3	c/2 + c/3
No. of clutches	15	22	37
"Correct" order	13	9	22
"Incorrect" order	2	13	15
% "correct" order	86.7	40.9	59.5

Table 16: Hatching success as a proportion of eggs laid.

Colony:	A	B	C	D	Total
No. of nests (of known clutch size)	44	12	13	22	91
No. of eggs	120	31	30	55*	236
No. of eggs hatched	103	16	25	0	144
% of eggs hatched	85.8	51.6	83.3	0.0	61.0

Significance: $X^2_3 = 124.91$ $p < 0.001$

* Estimated value from assumed clutch sizes from approximate laying season given the rate of decline in clutch size with season.

found, those that were comprising occasional dog tracks on the river sands. The other possible causes are that the eggs were infertile, deserted, were trampled on by cattle or that they were washed away by the tide. The relative importance of these is given in Table 18. Trampling was of little significance, accounting for only 4.3% of the total number of eggs lost. The proportion of the total number of eggs laid accounted for by these factors is given in Table 19. Although irrelevant to this study, the number of infertile eggs is likely to be an underestimate, since some of those trampled, predated or washed away might have been infertile. The mean egg volume of the four infertile eggs of known volume which were measured was 16.70 cc compared with the mean for all eggs measured of 18.01 cc.

Given that predation was the major factor affecting hatch success, any selection of nest site that minimises the risk may increase hatch success. It seemed likely that nesting density, vegetation cover, proximity to Black-headed Gulls, distance from the nests of lesser Black-backed and Herring Gulls, nest lining material (for egg camouflage) and distance to feeding grounds (viz. the rivers Eden and Esk) might influence success. Although all of these factors appeared to affect success in the expected way, only Black-headed Gull proximity, the nature of the vegetation and nearest neighbour distance produced a significant affect (Tables 20 to 23).

A significantly greater proportion of eggs in colony C hatched from nests with small nearest neighbour distances than from those less closely spaced (Table 20); the difference, although apparent, was not significant in colony A. Colony D was omitted because no eggs hatched. Colony B could not be included because nearest neighbour distances were not measured because the vegetation cover and the extent of the area involved rendered it impracticable to spend the time necessary to find an acceptable proportion of the nests to make nearest neighbour distances meaningful without losing data from the other colonies in which time could be used more efficiently. The close proximity to conspecifics was considered to produce a greater degree of nest defence because any attempt on one nest

Table 17: Hatching success expressed as a proportion of the clutch which hatched.

Colony:	A	B	C	D	Total
No. of clutches	45	13	14	22	94
% clutches in which no eggs hatched	6.7	38.5	14.3	100.0	34.0
% clutches in which some eggs hatched	93.3	61.5	85.7	0.0	66.0
% clutches in which all eggs hatched	73.3	30.8	71.4	0.0	50.0

Significance: All hatched vs the rest $\chi^2_2 = 8.37$ $p < 0.05$
None hatched vs the rest $\chi^2_2 = 8.49$ $p < 0.05$

Table 18: The proportion of eggs which failed to hatch attributable to each cause.

Colony	No.eggs lost	predation/trampling	infertile/deserted	tide
A	17	82.3	17.7	0.0
B	15	100.0	0.0	0.0
C	5	60.0	40.0	0.0
D	55*	58.2*	0.0*	41.8*
Total	92	69.6	5.4	25.0

*Estimated values from assumes clutch sizes (see Table 16 for explanation).

Table 19: The proportion of eggs laid accountable by each form of failure.

Colony	No.eggs laid	predation/ trampling	infertile/ deserted	tide	total loss
A	120	11.7	2.5	0.0	14.2
B	31	48.4	0.0	0.0	48.4
C	30	10.0	6.7	0.0	16.7
D	55*	58.2*	0.0*	41.8*	100.0
Total	236	27.5	2.2	9.9	39.5

*Estimated values from assumed clutch sizes (see Table 16 for explanation).

Table 20: The relationship between hatching success and nearest neighbour distance. (Only nests of known nearest neighbour distance included)

Nearest neighbour distance	Colony A				Colony C			
	no,of nests	no.of eggs	no.of chicks	% hatch	no.of nests	no.of eggs	no.of chicks	% hatch
< 15m	30	83	72	86.8	12	27	25	92.6
> 15m	14	37	31	83.8	1	3	0	0.0

Significance : colony A – N.S. ; colony C – $\chi^2_1 = 10.67$ $p < 0.005$

would represent a danger to many other nests.

Within colony A there was a significant difference in the proportion of eggs that were predated betweennests of different distance from their nearest Black-headed Gull nests (Table 21). There was also a significant difference in success between colony A, which was the mixed colony of 49 Tern nests among 33 Blackheaded Gulls, and colonies C and D which were not near any Black-headed Gull nests (Table 22), but this affect is inseparable from the other differences between the colonies, viz. nest density and laying season.

Although the effect of vegetation was significant (Table 23), it is inseparable from distance to food source, nesting density and seasonal differences since it reflects the distinction between the colonies. There was no detectable variation in vegetation cover within any one colony. Since it was the area of greatest vegetation cover, colony B, that suffered significantly more predation than the areas of shorter vegetation on the "new marsh", which is the opposite of what was expected, this difference may be reflecting distance from feeding grounds or nesting density, both of which are considered to be detrimental to nest defence in colony B. Hatch success was found to vary with season and with clutch size, but these are related since clutch size declined significantly with season. As shown in Table 24 (a), hatch success declined with season, and Table 25 shows success to have been greater in clutches of three than in two- or one-egg clutches. However, within any one clutch size there was no decline in success (Table 24) indicating that it is the decline in clutch size with season and the seasonal decline in hatching success which produces these results.

6.3 Fledging success

Fledging success was assessed for colonies A and C only; colony B was omitted because the amount of vegetation cover and lack of barriers to movement of the chicks made finding them virtually impossible after their first few days of life. Colony D was omitted because no eggs hatched.

Table 21: The relationship between predation and the distance to the nearest Blackheaded Gull nest (Colony A).

	Distance to nearest Blackheaded Gull Nest	
	< 50m	> 50m
No. of eggs	78	45
No. of eggs predated	4	8
% of eggs predated	5.1	17.8

Significance: $\chi^2_1 = 3.85$ $p < 0.05$

Table 22: The relationship between predation and the presence of Blackheaded Gulls.

	Colony A With Blackheaded Gulls	Colonies C & D No Blackheaded Gulls
No. of nests	46	36
No. nests predated (lost at least one egg)	7	17
% nests predated	15.2	47.2

Significance: $\chi^2_1 = 8.51$ $p < 0.005$

Table 23: The relationship between predation and vegetation cover.

	Vegetation type	
	"cover"	"no cover"
No. of nests	13	60
No. of nests predated	6	9
% of nests predated	46.2	15.0

Significance: $\chi^2_1 = 4.6$ $p < 0.05$

Here, "cover" refers to the species - rich, consistently tall(c.15cm) mature marsh vegetation, whilst "no cover" refers to the "new marsh" vegetation of sparce 15cm tall stems of *Armeria maritima* or *Parapholis strigosa* among a ground vegetation of c.2cm height of *Puccinellia maritima* or *Plantago maritima*.

Table 24: The variation in hatching success with season in Colonies A, B and C. (Colony D was omitted because laying date was not known - only clutches of known laying date were included)

a) All clutches of known hatching success.

	Laying week		
	1	2,3,4	5,6
No. of eggs laid	96	43	18
No. of eggs hatched	91	34	15
% eggs hatched	94.8	79.1	83.3

Significance: Week 1 vs weeks 2 - 6 $\chi^2_1 = 6.65$ $p < 0.01$

b) Two-egg clutches

	Laying week		
	1	2,3,4	5,6
No. of eggs laid	14	18	12
No. of eggs hatched	11	15	10
% of eggs hatched	78.6	83.3	83.3

Significance: Week 1 vs weeks 2 - 6 N.S.

c) Three-egg clutches

	Laying week		
	1	2,3,4	5,6
No. of eggs laid	96	24	6
No. of eggs hatched	80	22	6
% of eggs hatched	83.3	91.7	100.0

Significance: Week 1 vs weeks 2 - 6 N.S.

Table 25: The variation in hatching success with clutch size.

	Colony A + B + C		
Clutch size	c/1	c/2	c/3
No, of nests	10	26	43
No. of eggs	10	52	129
No. of eggs hatched	3	36	108
% of eggs hatched	30.0	69.2	83.7

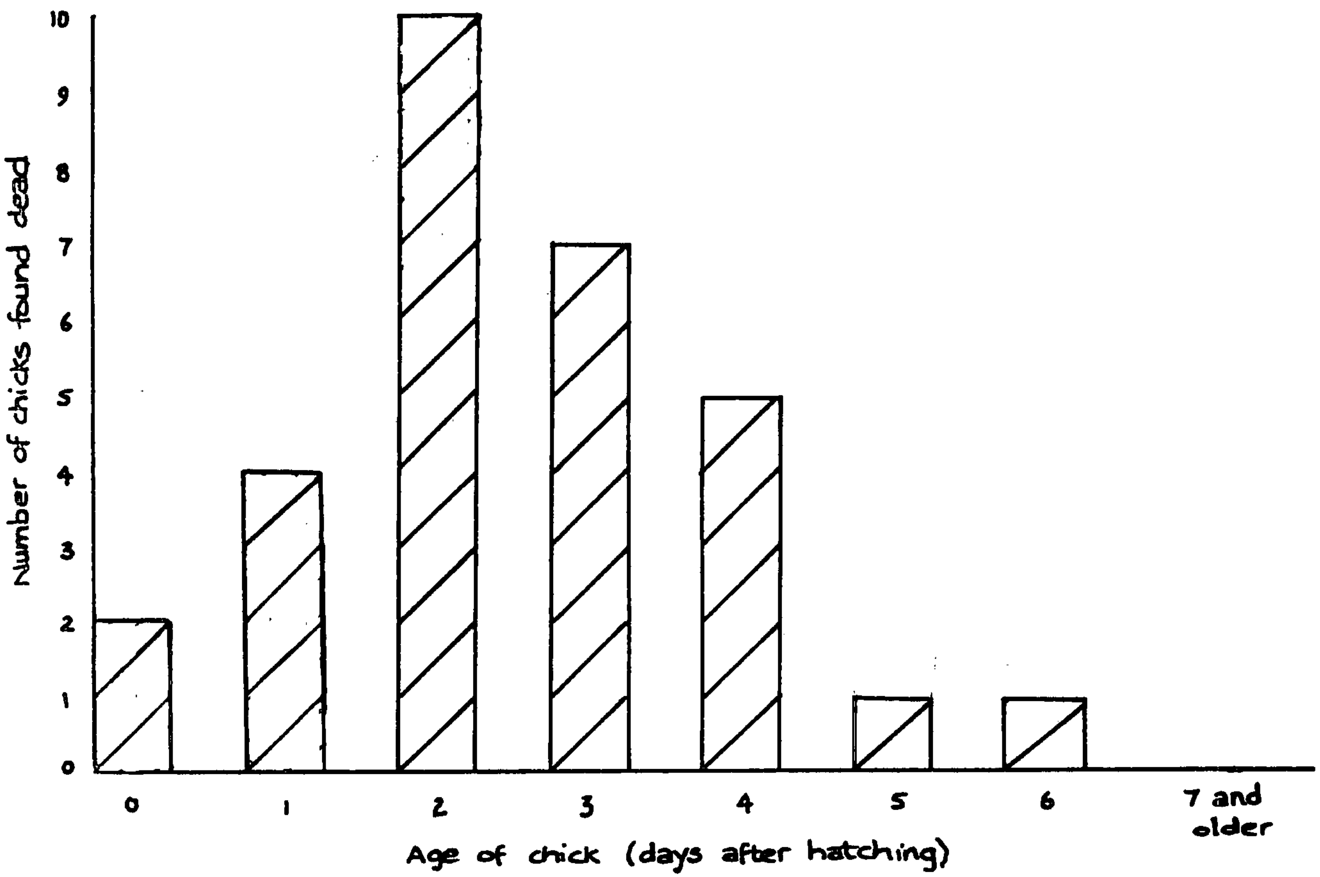
Significance: Colony A + B + C c/2 vs c/3 $\chi^2_1 = 3.94$ $p < 0.05$

Causes of chick mortality operating on the study area were considered to be predation, starvation and choking, this last one being of only very minor importance (two cases only). Many chicks disappeared, their bodies not being found, and these were presumed to have been predated since the area was searched thoroughly on numerous occasions.

Because of the difficulty of finding chicks, for the reasons outlined in Chapter 3, fledging success could not be assessed for individual nests and therefore not related to nest site, season or clutch size as was hoped. For the same reason survival to the age of ten days was equated with survival to fledging, on the basis that most chick mortality occurs in the first week of life (Langham, 1968), a supposition borne out by what is known of the mortality of chicks in this study, none of those found dead having died after the age of six days (n = 41) (fig. 6). Fledging success results are presented in Table 26. In all estimates of fledging success, despite an apparently greater success in colony A than C, the difference was not significant. The known, and therefore minimum, fledging success for colony C is thought to be an underestimate because dogs raided the colony on 25 July, killing many chicks which had not reached the age of ten days. Further searches were therefore futile. This source of mortality was not included in the fledging success figures discussed below since it was not considered to represent a usual source of death, although the resulting fledging success estimates are presented in parentheses in Table 26.

In both colonies only about 7.8% of the chicks were known to have fledged (that is, were found on or after their tenth day of life). In colony A, 29.1% of the chicks were known to have died, the figure being only 20% for colony C, this probably being an underestimate given that there was little time for more deaths to occur because of the interruption of the normal run of events by the dogs. 28% of the chicks of colony C were less than five days old at the time of the attack. Given these known figures, the fate of at least 60% of the chicks from colonies A and C combined was unknown (viz. those not found either dead or at least ten

Fig. 6 : The distribution of known chick mortality with age of chick, colony A*.



* Only in colony A was there sufficient search effort to be able to find a reasonable proportion of dead chicks.

Table 26: Fledging success estimates of Colonies A and C (See notes below)

						(i) Minimum fledging success				(ii) Best estimate of fledging success				(iii) "Assumed maximum" fledging success						(iv) Maximum fledging success					
colony	no. nests of known hatch success	% of the nests in the colony	no. of eggs	no. of chicks	% hatch	no. fledged	% of total chicks	% of eggs laid	mean no. fledged/pair	no. fledged	% of total chicks	% of eggs laid	mean no. fledged/pair	no. fledged	% of total chicks	% of eggs laid	mean no. fledged/pair	no. chicks dead	% of chicks dead	no. fledged	% of total chicks	% of eggs laid	mean no. fledged/pair	no. chicks dead	% of chicks dead
A	44	97.8	120	103	85.8	8	7.8	6.7	0.18	9	8.7	7.5	0.21	60	58.3	50.0	1.36	43	41.8	73	70.9	60.8	1.66	30	29.1
C	13	65.0	30	25	83.3	2	8.0	6.7	0.15	7	28.0	23.3	0.54	20	80.0	66.7	1.54	5	20.0	20	80.0	66.7	1.54	5	20.0
														(14)	(56.0)	(46.7)	(1.08)	(11)	(44.0)	(14)	(56.0)	(46.7)	(1.08)	(11)	(44.0)
A+C	57	73.1	150	128	85.3*	10	7.8	6.7	0.18	16	12.5	10.7	0.28	80 (74)	62.5 (57.8)	53.3 (49.3)	1.40 (1.30)	48 (54)	37.5 (42.2)	93 (87)	72.7 (68.0)	62.0 (58.0)	1.63 (1.53)	35 (41)	27.3 (32.0)

In all cases "fledging" represents survival to the age of 10 days.

(i) Minimum fledging success refers to the number of chicks found alive on or after their 10th day of life.(Day 0 = day of hatch)

(ii) The best estimate is that calculated from search efficiency (viz. the proportion of those known from later searches to be alive which were found on the day of search).

(iii) "Assumed maximum" fledging success is an estimate using the sum of known and assumed mortality. Chicks assumed to be dead are those which were losing weight when last seen, this being justified by the fact that in no cases of known outcome did weight loss result in survival (n = 15). All chicks not known to be dead (by finding the bodies) or assumed to be dead are assumed to have fledged.

(iv) All chicks not found dead were assumed to have fledged. This is therefore an over-estimate.

* Hatching success is greater than that calculated for the whole marsh (Table 16) since here only colonies A & C are included because fledging success estimates were only practicable for these colonies. Fledging success estimates will therefore be over-estimates for the marsh as a whole.

Figures in parentheses refer to fledging and mortality when the mortality due to the raid by dogs in Colony C is included.

Significance: A vs C N.S.

days old). A further 12.6% of the chicks of colony A were assumed to have died because they were losing weight when last seen, given that in no case of known outcome did a loss of weight result in survival (Table 27). The inclusion of these chicks in the "dead" category produced the combined figures for the two colonies of 7.8%, 37.5% and 45.3% as fledged, dead (excluding the effect of the dogs, which were considered to be an abnormal occurrence) and unaccounted for (i.e. lost and not seen again) respectively.

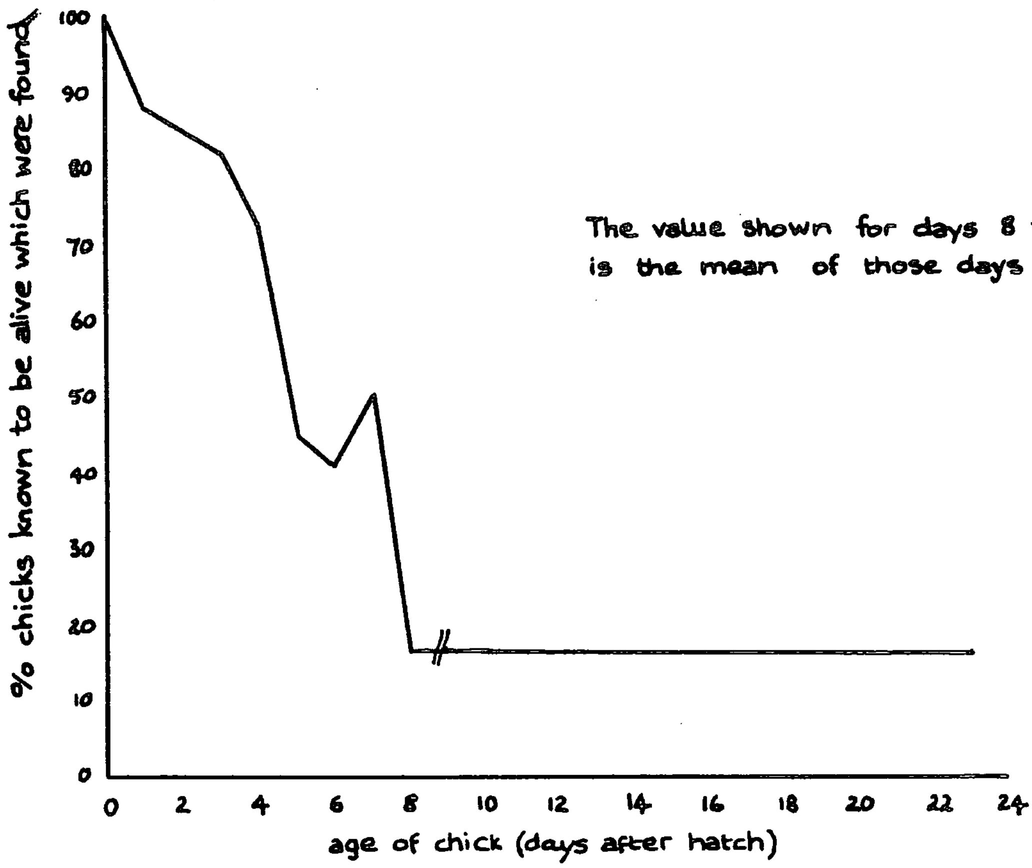
Known and assumed mortality were used to place an upper limit on fledging success. The former represents an absolute maximum fledging success and is sure to be a gross over-estimate since it assumes that all chicks not found dead survived to fledge. It therefore takes no account of death by predation when the chick would almost certainly have been removed, or of any dead chicks not found before they, too, were removed, although this is a less likely source of error. Colony C appears to have had better maximum fledging success than colony A, the figures being 80% and 70.9% respectively, but not significantly so.

By summing assumed and known deaths, a less exaggerated maximum survival to fledging was produced. This gave an upper limit for the proportion of chicks fledged of 58% and 80% for colonies A and C respectively, the latter probably being an over-estimate because of the attack by dogs while 28% of the chicks were less than five days old, but again not significantly different. While still an overestimate, the exaggeration is lessened with this estimate.

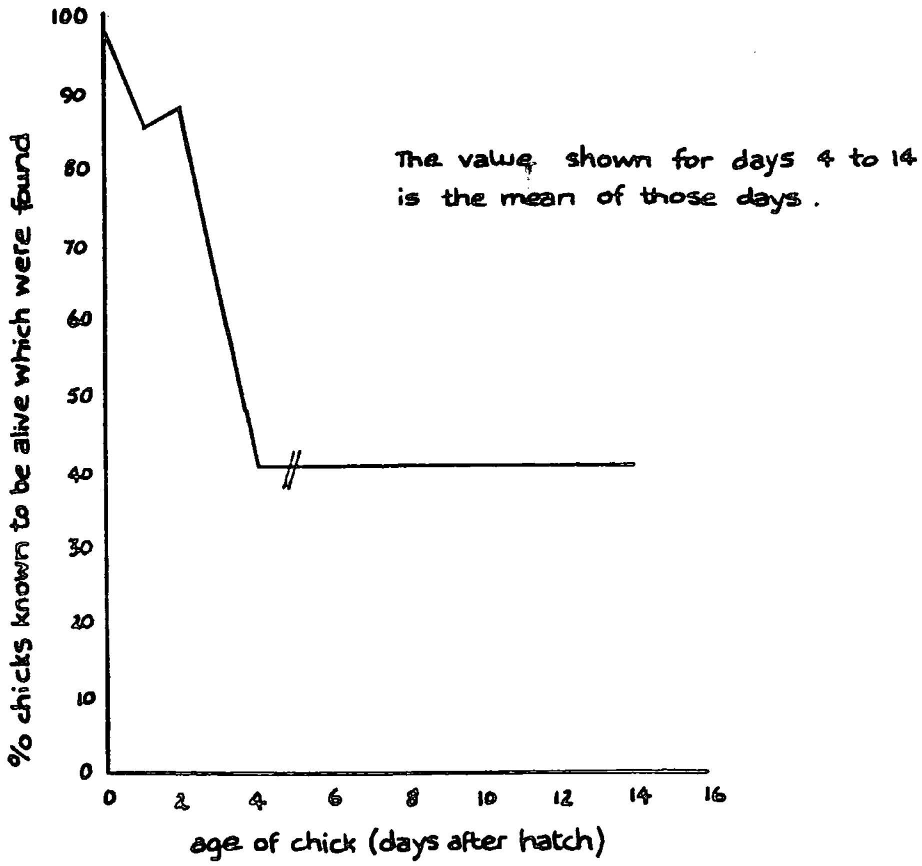
From the proportion of chicks known from later searches to have been alive which were found, i.e. search efficiency, the number estimated to be alive in colony A after eight days was 9, being the maximum number of chicks found from six days' searching at 16.4% search efficiency (fig. 7), which should represent all of those chicks still alive. (The six days in which the greatest number of chicks was found were used to provide this maximum best estimate of fledging success (Table 28)). This represents an estimated fledging success from the 44 pairs of 0.21 chicks fledged per pair, and is very little more than the minimum number fledged, based on

Fig. 7 : The proportion of chicks known from later finds to have been alive which were found at each age.

Colony A



Colony C



the number of chicks found after ten days of age (Table 26). The corresponding value for colony C was 0.54 chicks per pair from an estimated maximum of 7 chicks alive after eight days, given a search efficiency of 40.3% (fig. 7) over three days (Table 28), and 13 pairs. Here survival to eight days was equated with fledging, this being supported by the distribution of known chick mortality with age (fig. 6), none of the chicks found dead having been more than six days old at death. This ignores death by predation in which the chicks would be removed, and so probably represents an over-estimate of fledging success.

From these estimates it appears that breeding success was very poor, at only 0.28 fledged young per pair (averaging the results of the two colonies), being the equivalent of 12.5% of chicks hatched and 10.7% of eggs laid. This poor breeding performance was supported by the low frequency with which birds were observed bringing food to the colony. Although no precise data were obtained, a rate of about one visit every 45 minutes was estimated for the 44 pairs in colony A.

6.4 Growth rate and mortality of chicks

The mean weight of all chicks which were expected to survive (i.e. which were not losing weight and were not found dead later) was plotted for each day after hatching (fig. 8). There were insufficient c-chicks satisfying these criteria to be able to give any indication of mean weight or growth rate after the first day after hatch. From what data were obtainable, the weight of the chicks at hatching was greatest for a-chicks and least for c-chicks (Table 29, fig. 8), but the differences were not significant and the growth rate of a-chicks in the first seven days exceeded that of b-chicks (Table 31).

From fig. 8, b-chicks appear to increase in weight at the same rate as a-chicks but after a delay of about four days. However, all the points in fig. 8 after day 7 are from small samples ($n = 4$) so must be treated with caution. When the weights of all chicks were included, the difference in weight at hatch between a, b and c-chicks was significant ($p < 0.001$, Table 30).

Table 27: The fate of chicks which were known to have lost weight.

No.of chicks which lost weight and found dead	15
No.of chicks which lost weight and known to have fledged	0
No.of chicks which lost weight but fate unknown (i.e.disappeared)	7

Table 28: The number of those chicks known, from later finds, to have been alive which were found on each day after day 8. (Day 0 = day of hatch).

i) Colony A

Day:	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
No.found	0	1	3	1	2	0	1	0	0	0	0	0	1	0	0	1
No.known alive	10	10	9	6	5	3	3	2	2	2	2	2	2	1	1	1

ii) Colony C

Day	8	9	10	11	12	13	14
No. found	1	4	1	0	0	2	1
No.known alive	6	6	3	2	2	3	1

Table 29: The weight on day of hatch of a-, b- and c- chicks, excluding those which later died of starvation or lost weight.

	n	Mean weight(g)	Standard deviation
a- chick	34	14.5	1.6
b- chick	25	13.9	2.3
c- chick	3	12.1	1.7

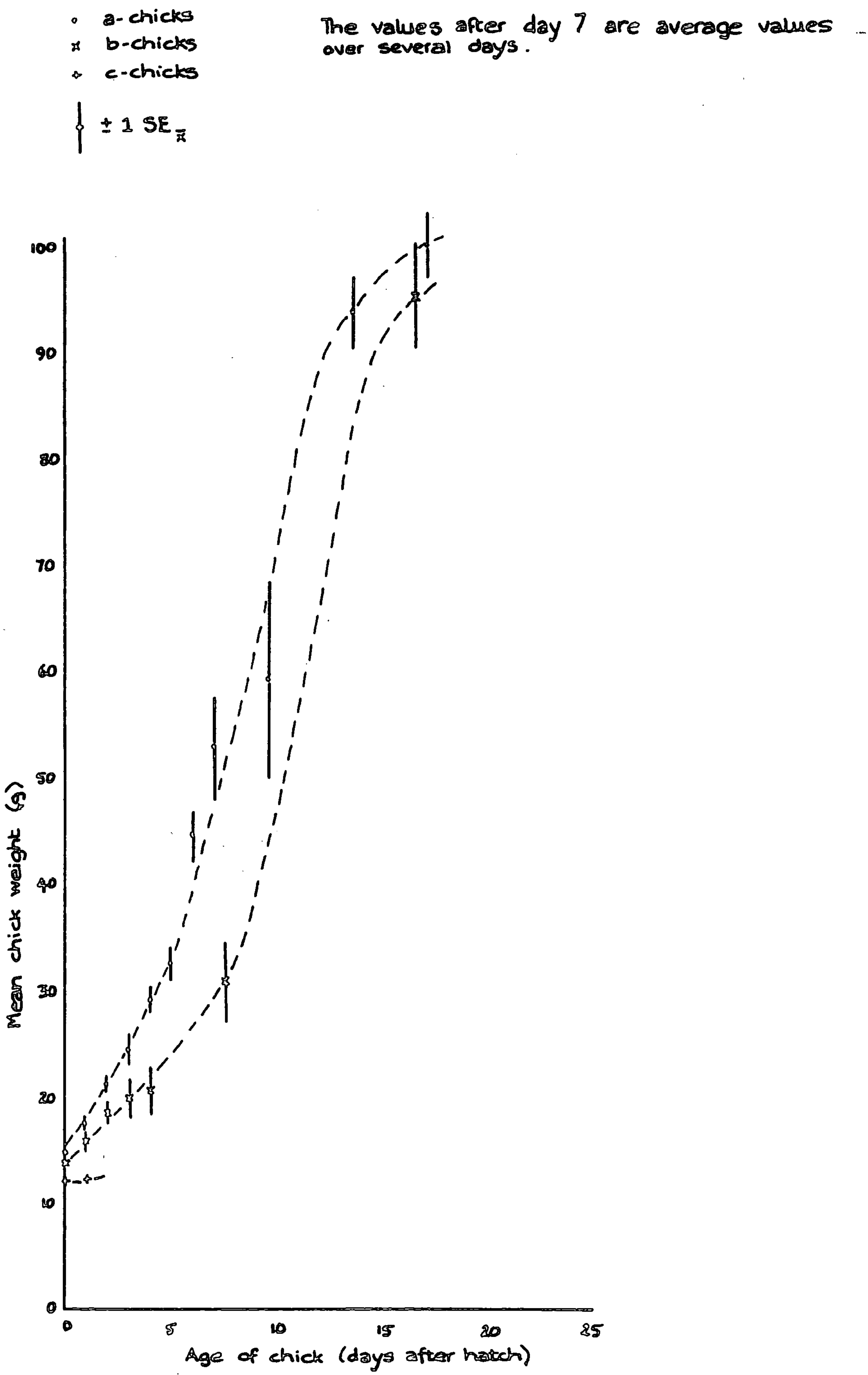
Significance: a vs b vs c N.S.
a vs c N.S.

Table 30: The weight on day of hatch of all a-, b- and c- chicks of known weight.

	n	Mean weight(g)	Standard deviation
a- chick	40	14.6	1.5
b- chick	31	13.9	2.4
c- chick	16	12.2	1.1

Significance: a vs b vs c $\chi^2_2 = 14.4$ $p < 0.001$

Fig. 8 : The increase in weight of a-, b- and c-chicks with age.



Despite the apparent difference in the relative proportion of a, b and c-chicks that were found dead compared with the proportion hatched, c-chicks suffering proportionately greater mortality, the differences were not significant (Table 32). However, fig. 9 shows the proportion of c-chicks known to be alive to fall at the expense of the a and b-chicks.

Fig. 6 shows all known mortality (that is, the dead chicks which were found) to have occurred by the 6th day after hatch, peak known mortality having taken place on the 2nd day after hatching.

The chicks moved away from the nest within three days of hatching, the mean distance from the nest at which they were found on each day after hatch being shown in fig. 10. As they got older and moved further away, fewer chicks were found as a proportion of those known from later finds to have been alive (fig. 7). This explained the reduction in sample size with time in fig. 10.

6.5 Summary of breeding success

Given that the fledging success of the two colonies was not significantly different, what this study has produced is two samples, or a joint estimate, of the upper and lower limits to fledging success of a colony of Terns nesting at low density on the short, "new marsh" vegetation of a dry, cattle-grazed saltmarsh. The fledging success of colony A was found to lie between 7.8% and 70.9% of chicks hatched, this being 0.18 to 1.66 chicks fledged per pair or 6.7% to 60.8% of eggs laid. In colony C the figures are higher, although not significantly so, being 8 to 80% of chicks hatched, 0.15 to 0.54 chicks per pair and 6.7 to 66.7% of eggs laid (Table 26), these figures being derived from known survival (minimum success) and known mortality (maximum success). If all those chicks which were losing weight when last seen were assumed to have died, a less exaggerated maximum breeding success was obtained (Table 26, iii). From the proportion of chicks known to have been alive which were found after the eighth day after hatch the best estimate of the fledging success of the two colonies combined was 12.5% of chicks hatched, 0.28 fledged young per pair and 10.7% of eggs laid.

Table 31: Average daily growth rate in a- and b- chicks of the whole marsh. Only chicks which are not known or thought to have died were included. Thus no c- chick data were available.

Day	a- chicks Mean weight increase(g)	a- chicks Standard deviation	a- chicks n	b- chicks Mean weight increase(g)	b- chicks Standard deviation	b- chicks n
0 - 1	2.83	1.89	9	2.32	1.18	11
1 - 2	3.65	2.00	10	3.14	2.16	11
2 - 3	4.88	3.52	8	2.03	1.61	8
3 - 4	5.75	3.16	5	2.96	1.92	7
4 -55	3.88	2.30	2	5.19	2.21	4
5 - 6	14.38	5.83	2	4.00	3.49	4
6 - 7	11.88	10.08	2	3.63	1.24	2

Mean daily growth rate, days 1 to 4:-

a- chicks: 4.06g (n= 32) Standard deviation = 1.06
b- chicks: 2.62g (n=37) Standard deviation = 0.46

Table 32: Distribution of known dead among a-, b- and c- chicks.

	No. hatched	% hatched	No. dead	% dead
a- chicks	70	45.2	15	39.5
b- chicks	53	34.2	10	26.3
c- chicks	32	20.6	13	34.2
		100.0		100.0

Significance: No. hatched vs No. dead - N.S.

Fig. 9 : The relative proportion of a-, b- and c-chicks known to be alive at each age.

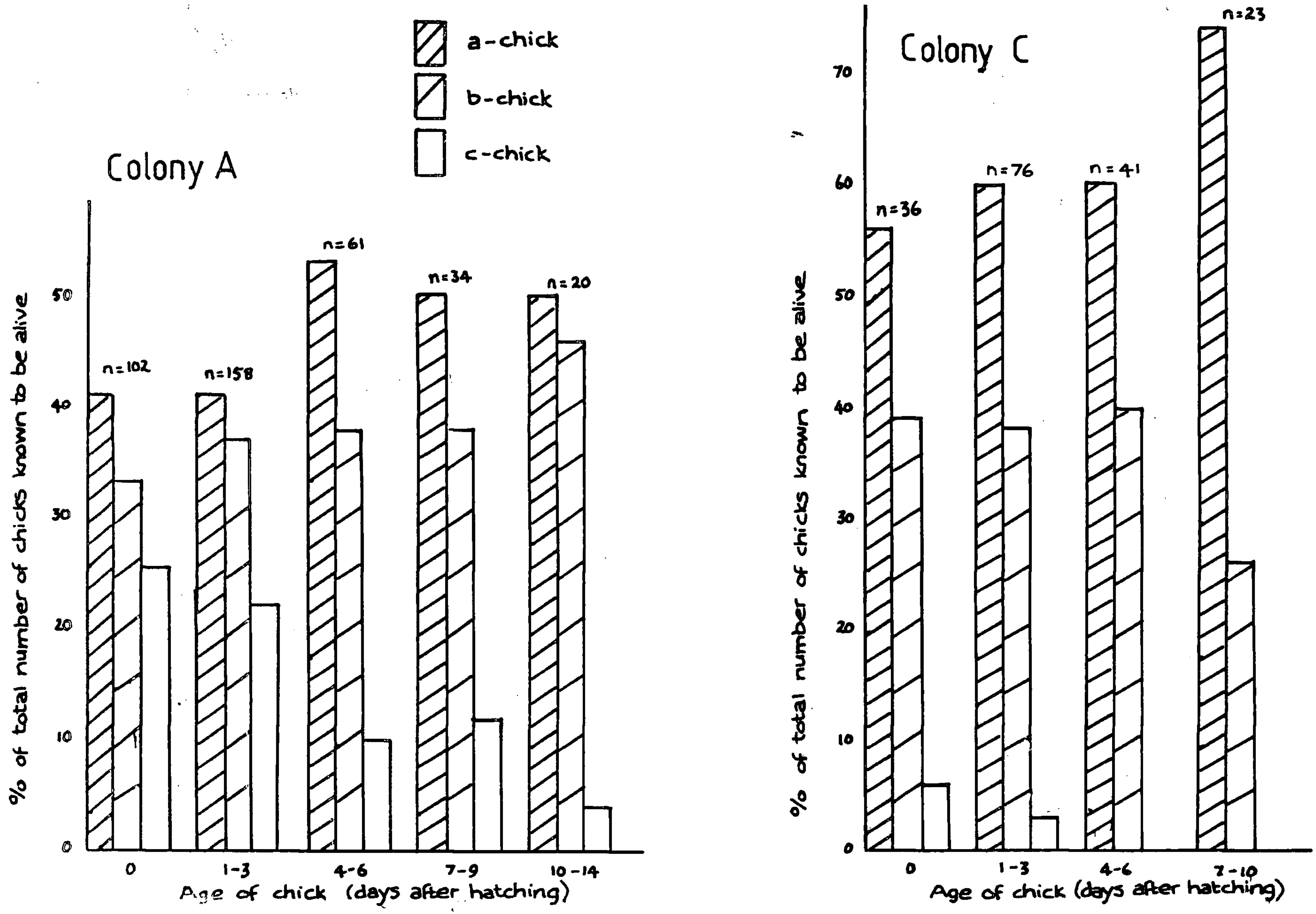
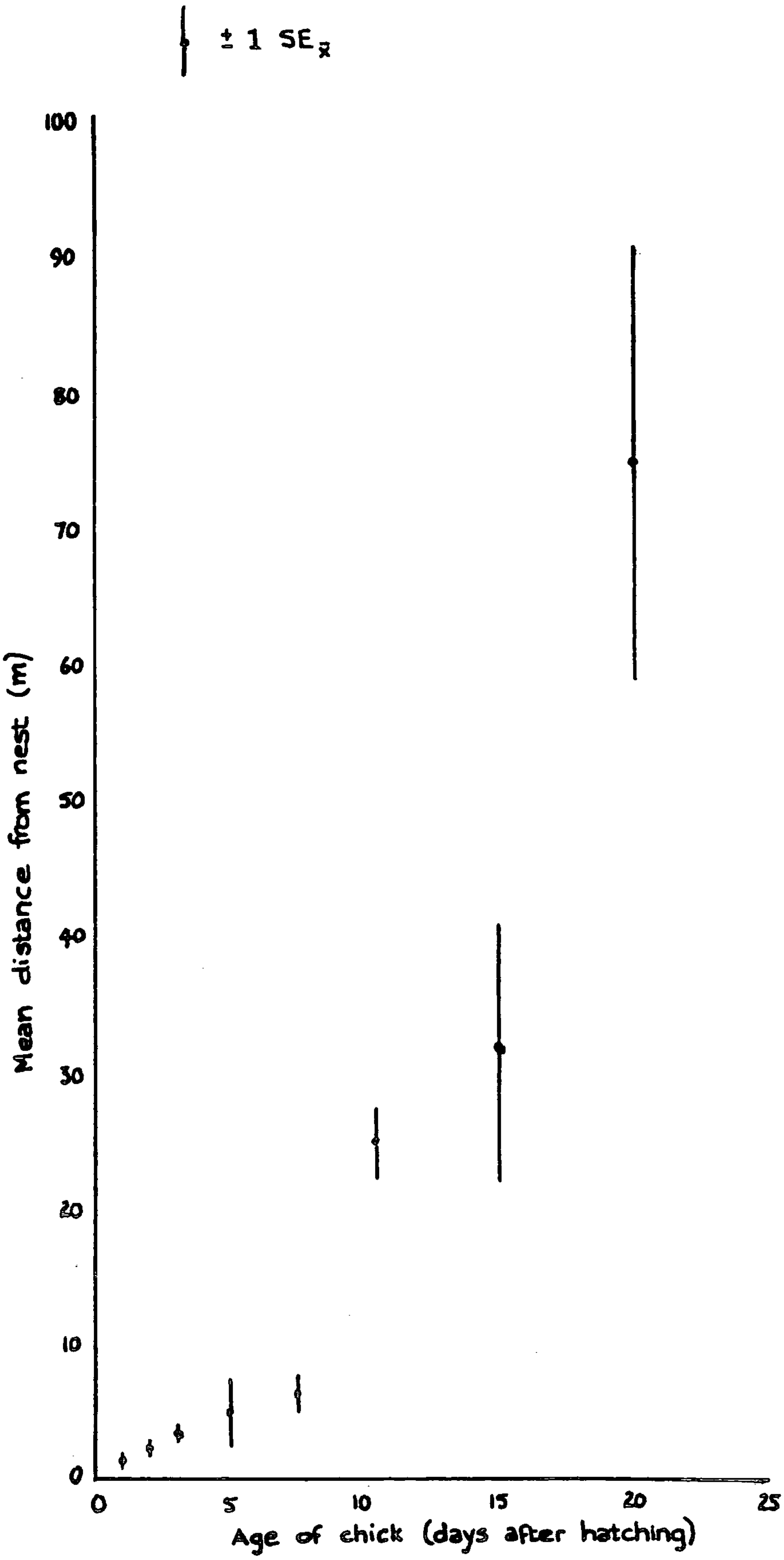


Fig. 10 : The mean distance from the nest at which the chicks of each age were found.

(Day 0 = day of hatch)

Values from days 5 to 25 are mean values for several days.



It should be remembered that the hatching success for the whole marsh of 61% (Table 16) was different from that of colonies A and C, at 85.3%, which was used to produce fledging success estimates (Table 26). This discrepancy is the result of the estimation of fledging success being impracticable in colonies C and D which happened to be the colonies of lower than average hatching success. The fledging success estimates produced will therefore probably be over-estimates for the marsh as a whole.

6.6. The breeding success of the Black-headed Gulls

Table 33 shows the breeding success of the Black-headed Gulls to have been poor. No chicks were found alive after their fifth day after hatch, despite frequent exhaustive searches. It was therefore presumed that they were dead. Hatching success was 42%, and maximum possible fledging success was 37% of eggs laid, being 1.0 chick fledged per pair, but it was thought very likely that only one or two, if any, chicks survived to fledge. Table 34 shows predation to have been the major cause of the failure of eggs to hatch.

Table 33: Breeding success and clutch size of the Black-headed Gulls nesting among the Colony A Terns. ∅

No.of nests	28	
% of total nests on marsh	77.7	
Mean clutch size	2.71	(Standard deviation = 0·54)
No.of eggs	76	
% of eggs hatched	42.1	
No.of chicks	32	
% of chicks known to fledge	0.0	
% of chicks known dead	12.5	
Maximum % of chicks fledged*	87.5	
Maximum % of eggs producing fledged young*	36.8	
Maximum estimate of mean no. fledged per pair*	1.0	

∅ Only nests of known clutch size were included; as only one egg was observed in each of 5 nests among the Colony A Terns, these were omitted as presumably incomplete. This presumption was borne out by the fact that none of these eggs hatched, suggesting desertion. Only those nesting among the Terns of Colony A were included, since only for these were sufficient data available.

* Maximum breeding success was derived from the no. of chicks known to have died; those remaining were assumed to have fledged. This was probably a gross over-estimate of success, therefore.

Table 34: The relative importance of causes of hatching failure in Black-headed Gulls.

				Predation		Infertile		Tide	
No.of nests	No.of eggs	No.of eggs lost	% of eggs lost	% of eggs lost	% of eggs laid	% of eggs lost	% of eggs laid	% of eggs lost	% of eggs laid
28	76	44	57.9	61.3	35.6	4.6	2.6	34.1	19.7

CHAPTER 7

Discussion

Assuming that the figures given by Coulson and Horobin (1976) for the post-fledging survival of Arctic Terns on The Farne Islands approximates to that of the Common Terns of Rockcliffe Marsh, it was calculated that, using the maximum fledging success calculated for colonies A and C (that is, that all chicks not found dead survived to fledge), the number of fledged young reared was sufficient to maintain the population of the colony without immigration (Table 35). This was making the assumption that the breeding success this year (1982) was not abnormal. The number of recruits produced with the less exaggerated success estimate, assuming the death of chicks which were losing weight, was also adequate to replace adult losses, but minimum success as given by these chicks known to have reached ten days of age was insufficient.

Although it is possible that breeding success was sufficient to maintain the population, the estimate of fledging success considered to be the most likely, viz. that based on the proportion of chicks known to be alive which were found, suggested that this number was insufficient to keep the population stable (Table 35). Since even this estimate was probably an over-estimate, it was considered that poor breeding success could indeed be a reason behind the population decline, particularly since the success of colonies A and C was almost certainly greater than that of the marsh as a whole, given what is known of hatching and fledging success of the other colonies (Table 36). In addition, post-fledging mortality of Common Terns was considered to be greater than that of Arctic Terns on which these calculations were based (Coulson, pers. comm.). The number of recruits required was therefore probably an under-estimate, this further supporting an unfavourable discrepancy between the number of recruits needed and the number of fledged young produced. The assumptions made in undertaking these comparisons are outlined in Table 35.

Table 35: Comparison between the breeding success required to maintain the population at its present level and the four estimates of success achieved.

Estimated total breeding population of the marsh	250 pairs
Annual adult survival rate (Coulson & Horobin, 1976)	0.87
No. of recruits needed each year	65 birds

No. of fledged young required per year to maintain population level:-

	Recruitment at 3 years	Recruitment at 4 years
1st year survival rate of half the adult survival rate	0.46/pr.	0.53/pr.
1st year survival rate equal to adult survival rate	0.40/pr.	0.46/pr.
1st year survival rate = 0.81 (Coulson & Horobin, 1976)	0.42/pr.	0.49/pr.

No. of fledged young produced (from Table 23, Colonies A & C):-

Minimum breeding success	0.18/pr.
Best estimate of breeding success	0.28/pr.
"Assumed maximum" breeding success	1.40/pr.
Maximum breeding success	1.63/pr.

Assumptions

1) The breeding success of Colonies A & C (Table 23) is representative of the whole marsh. (In fact it is considered to be an over-estimate).
2) The annual adult survival rate of Arctic Terns on the Farne Islands (Coulson & Horobin, 1976) is applicable to Common Terns on Rockcliffe Marsh.
3) The no. of fledged young required has been calculated assuming
   a) that 1st year post-fledging survival is half that of adult survival, as a minimum survival estimate
   b) that 1st year post-fledging survival is equal to that of adult survival, as a maximum survival estimate.
   c) that 1st year post-fledging survival is 0.81, the figure given by Coulson & Horobin (1976) for Arctic Terns on the Farne Islands.

Table 36: The breeding success of Colonies A, C & D using the best estimate of fledging success. (Colony B was omitted because no fledging success data were available).

Colony	No. of Clutches	No. of Eggs	No. of Chicks Hatched	Best Estimate of Fledge Success	% Hatch	% Chicks Fledged	% eggs producing Fledged Young	No. Fledged per Pair
A+C	57	150	128	16	85.3	12.5	10.7	0.28
D	22	55*	0	0	0.0	0.0	0.0	0.0
A,C,D	79	205	128	16	62.4	12.5	7.8	0.20

*Estimated value based on assumed clutch size, given the laying period and the few clutches of known size.

Colony B:

No. of clutches	12
No. of eggs	31
No. of chicks hatched	16
% hatch	51.6

The results of this study showed poor hatching success for the marsh as a whole. At 61%, hatching success was lower than Langham's (1968) figure of 87.6% for Coquet Island, Northumberland, and Nicholson's (1978) 88.8% for Foulney Island, Cumbria (Table 37), although the 85.3% success in colonies A and C was comparable. Predation was more prevalent at Rockcliffe than on Coquet Island (Langham, 1968), accounting for 69.6% of lost eggs as opposed to 51.4% on Coquet Island.

The comparable fledging success data, viz. maximum fledging success representing all chicks not found dead, are also presented in Table 37. Fledging success in colonies A and C was probably an over-estimate for the marsh as a whole, given the difference in hatching success (Table 37). When colony D is included, in which no eggs hatched, fledging success is obviously very much reduced. This is probably nearer to the actual success of the whole marsh because colony B is omitted, since no reliable fledging success estimates were practicable, and from its relatively low hatching success of 51.6% it seems likely that its inclusion would serve to lower fledging success for the whole marsh.

These comparisons were not considered to be affected by differences in clutch size between the sites concerned since these were similar (Table 37), and the positive skewness in the laying pattern over time noted by Nicholson (1978), supporting the results from this study, would have lessened any differences resulting from the seasonal decline in clutch size.

A reduction in Tern numbers with the spread of Lesser Black-backed or Herring Gulls was quoted by Lloyd, Bibby and Everett (1975) for the Isle of May. Coupled with the evidence of Salmonsen (1943), Lind (1963), Cullen (1960a) and others on the beneficial effect of Black-headed Gulls on Terns, albeit usually the less aggressive Sandwich Terns (Sterna sandvicensis), and given the relative importance of predation as a factor affecting breeding success on the marsh, it would seem reasonable to suggest that the Black-headed Gull decline and the Lesser Black-backed and Herring Gull increase may indeed affect the breeding success of the Terns,

Table 37: A comparison of breeding success between three sites.

Clutch Size		Hatch Success		Fledging Success (% Chicks fledged)		Breeding Success (% eggs producing fledged young)		No.Fledged per Pair		Source
No.	n (No.of clutches)	%	n (No.of eggs)	%	n (No.of. Chicks hatched)	%	n (No.of eggs)	No.	n (No.of pairs)	
2.54	265	87.6	581	59	406	51.7	580	1.48	580	See*(i)
2.31	118	55.0	-	67	238	36.5	422	0.97	422	" *(ii)
2.38	115	-	-	87.8	246	71.3	303	-	-	" *(iii)
2.72	135	88.8	367	-	-	78.1	327	2.2	-	" *(iv)
2.59	57	85.3	150	72.7	128	62.0	150	1.63	57	" *(v)
2.40	125	61.0ø	236	72.7≠	128	45.4≠	205	1.18≠	79	" *(vi)

All fledging success estimates were from known mortality.

øHatching success figure was for the whole marsh (Colonies A,B,C & D)

≠Colony B was omitted from the fledging estimates because no reliable fledging success estimates were practicable, due to the nature of vegetation and topography. Hatching success for Colony B was lower than for the marsh as a whole, at 51.6%. It is therefore probable that breeding success was also poor in Colony B, the above figures thus representing an over-estimate of the breeding success on the whole marsh.

Sources

*(i) Langham (1968) Coquet Is., Northumberland, 1965.

*(ii) " " " " 1966.

*(iii) " " " " 1967.

*(iv) Nicholson (1978) Foulney Is., Cumbria, 1978.

*(v) This study, Colonies A and C, 1982.

*(vi) " " " A, C and D, 1982.

although other factors such as the vagaries of the weather must also play a part. This is supported by the significantly higher hatching success obtained in the presence of Black-headed Gulls compared with colonies lacking them, and within the mixed colony, in the clutches nearer to Black-headed Gull nests (Tables 21 and 22). Although no evidence of superior nest defence on the part of the Black-headed Gulls was observed, this could be because of their paucity and poor breeding success (Table 33) and therefore atypical.

In terms of management of the reserve it might be possible to provide large, level raised nesting areas less prone to flooding on the riverside "new marsh" vegetation, if this degree of interference were considered desirable or even possible in the presence of the cattle and winter floods. The extent of these would have to be such as not to merely provide a focal point for predators, and would involve much effort and no guarantee that the vegetation would not be altered even if the structures survived the winter floods. Although flooding has been more of a problem in previous years, this year it accounted for only 10% of the eggs laid compared with the 25% which were predated, the most likely culprits being the big gulls, so control of the Lesser Black-backed and Herring Gulls to prevent further eastward spread of the colony might also be worthwhile. But these aids alone would not prevent the population decline. The level of grazing of the marsh by cattle in relation to the quality of the growing season, and the continued vigilance of wardens, the reserve managers and the estate to keep human disturbance to a minimum and so avoid a repetition of the displacement of the Terns as at Ainsdale Dunes (Lloyd, Bibby and Everett, 1975) are also of great importance to the management of the marsh.

Thus, as in all natural situations, the multitude of factors which exert some influence on the processes under study render the task of explaining the resulting phenomena far from simple. While the results of this study suggest that the above explanation for the observed population decline is a likely one, since none of the findings negate it, further study on birds of known age and origin, perhaps with more manpower so that the whole area could be studied in sufficient depth, would be required in order to explain with any degree of confidence the reasons behind the observed population trend.

SUMMARY

1. The aim of the study was to assess the breeding success of the low density colony of Common Terns and Black-headed Gulls on Rockcliffe Marsh, Cumbria, and to attempt to explain the factors affecting this, in order to ascertain whether poor breeding success was the reason for the decline in the breeding population over recent years. The relationship between the Terns and the Black-headed Gulls was to be studied in order to determine whether the more dramatic decline in Black-headed Gull numbers had influenced the Tern population. In the event, the Black-headed Gull numbers had fallen to 49 pairs so that only the Terns could be studied in any detail.

2. Laying of the Terns began on 19 May, but flooding caused the first surviving clutches to be started on 29 May. The last egg was laid on 7 July. Laying was relatively synchronous within the four colonies studied but not within the marsh as a whole. In the earliest colonies laying pattern over time showed a positive skew, while the late colony showed a small negative skewness.

3. The mean clutch size was 2.40, declining significantly with season. Mean egg volume was 18.01cc. The decline in egg volume with season produced a significant negative correlation ($r_s = -0.83$). Egg volume declined significantly with hatching sequence ($p < 0.001$), but only the last egg could be identified from egg volume with any degree of confidence (correct in 92.3% of cases).

4. Hatching success (viz. the number of eggs that hatched as a proportion of the total number laid) was 61%. The major cause of loss was predation (27.5% of eggs laid).

5. There was significantly better hatching success from nests of higher density than from those of a larger nearest neighbour distance ($p < 0.005$).

6. The mixed colony of Terns and Black-headed Gulls had a significantly better hatching success than the colonies in which there were no Black-

headed Gulls. This is generally attributed to the superior nest defence of the Black-headed Gulls (Salmonsen 1943, Lind 1963, Cullen 1960a, Nicholson 1978).

7. There was a significant decline in hatching success with season, and clutches of three did significantly better than clutches of two. There was no seasonal decline in success within any one clutch size, indicating that hatching success varied with clutch size rather than with season.

8. Fledging success was not assessed for individual broods and therefore could not be related to nest site or seasonal differences. Because of the low nesting density, the amount of cover for the chicks and the large area which had to be searched, only maximum, minimum and a best estimate of fledging success based on search efficiency were made, and then only in two of the four colonies. Survival to the age of ten days was equated with fledging.

9. The minimum, best estimate and maximum fledging success for the two colonies was 6.7, 10.7 and 62% of eggs laid respectively, being 0.18, 0.28 and 1.63 chicks fledged per pair. These figures were considered to be over-estimates for the marsh as a whole since hatching success of the whole marsh was markedly poorer than that of the two colonies on which the fledging success estimates were based.

10. Assuming that the adult survival rate of the Common Terns here was the same as that of the Arctic Terns on the Farne Islands (Coulson and Horobin, 1976), and assuming that the fledging success estimates for the two colonies were representative of the whole marsh, it was calculated that while the maximum fledging success possible was sufficient to maintain the population, the best estimate of success was not. Given that the success calculated was considered to be an over-estimate for the marsh as a whole, and that it is probable that Common Terns suffer higher adult mortality than Arctic Terns (Coulson, pers. comm.) it is probable that breeding success was insufficient to maintain the population at its present level.

11. The breeding success of the Black-headed Gulls was poor. Only 42% of eggs hatched and no chicks were found alive after the age of five days.

12. The combination of poor breeding success on the part of the Black-headed Gulls, the observed superior hatching success of the Terns that were nearer to the nests of Black-headed Gulls, and the ever-increasing size of the mixed Lesser Black-backed and Herring Gull colony on the marsh (47% increase in eight years, to 2500 in 1981 (Greig, 1981)) given that most egg and chick loss was assigned to avian predators suggests that it is highly likely that it was the Terns' poor breeding success due to the combination of the increase in big gull numbers and the unexplained decline in the breeding Black-headed Gull population which was behind the observed decline in Common Tern numbers. The possibility of increased adult mortality of the Terns exaggerating the effect of poor breeding success cannot be ruled out.

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