Aspects of seasonal variation in breeding success of herring and lesser black-backed gulls (larus argentatus and l. fuscus)

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ASPECTS OF SEASONAL VARIATION IN BREEDING SUCCESS OF HERRING AND LESSER BLACK-BACKED GULLS (Larus argentatus and L. fuscus).

John Dighton
B.Sc. (London)
September, 1973

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

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CONTENTS

SECTION ONE.

INTRODUCTION

Gulls, amongst other sea-birds, have evolved a colonial nesting habit. Such dependence on this social system for breeding may be exemplified by the fact that stimulation from neighbouring birds in the colony, as well as that from the mate, is required to bring about the change in hormonal balance of the female, inducing ovulation. Hence there is intense competition in the colonies for nesting sites within the centre of the colony where, it is thought, the degree of social stimulation is highest and the breeding success correspondingly greater (Coulson 1968 and 1971 in the kittiwake, Rissa tridactyla L.).

Coulson and White (1958) and Coulson (1968) show that position in the colony is also age dependent, such that the young mature birds are usually confined to the edges of the colony, while the older birds obtain nesting sites in the centre of the colony. Young birds are only able to acquire central nesting sites by taking over those vacated by the death of older individuals.

Variation in breeding success may not only be a spatial phenomenon in the colony, but may also have temporal parameters (Parsons 1971). Parsons shows that herring gulls (Larus argentatus Pont.) nesting during the middle of the breeding season have a significantly greater chance of producing offspring than those nesting at the beginning or end of the season. This he attributes to the high incidence of cannibalism by, as yet, non-breeding adults at the beginning of the season and the reduced viability of the smaller eggs laid at the end of the season. Such decrease in egg size as the breeding season progresses has been shown to occur in the kittiwake (Coulson 1963), the gannet (*Sula bassana* L.) (Nelson 1966) and the shag (*Phalacrocorax aristotelis* L.) (Coulson et al. 1969).

Diminution of egg volume with season has been attributed to the seasonal distribution of age classes of females, such that the older females, laying larger eggs, lay at the beginning of the season and younger females laying smaller eggs at the end of the season (Coulson and White 1958, Mills 1973 in the red-billed gull, *Larus novaehollandiae scopulinus* Forster).

A positive correlation between egg size (volume) and survival has been shown to occur in the herring gull (Parson 1971), the black-headed gull (*Larus ridibundus* L.) and the lesser black-backed gull (*Larus fuscus* L.) (Mollart 1972) with reference to the third egg of a clutch, which is characteristically smaller and having a different shape index than the first two eggs of a clutch (Paludan 1951, Harris 1964, Parsons 1971 in the Laridae, Gemperle and Preston 1955 in the common tern, *Sterna hirundo* L.). Such differential survival with respect to egg size has been demonstrated in the herring, *Clupea harengus* L. (Blaxter and Hempel 1963) correlating the degree of success with the volume of yolk in the egg, and egg weight giving differences in favour of the heaviest eggs for percentage fertility, percentage hatchability and feed conversion efficiency in pullets (Tindell and Morris 1964). Such findings may also be correlated with those of Barth (1952) who showed that the rate of loss of weight of eggs, an indication of the rate of yolk metabolism, was greatest in the third egg of a clutch in the Laridae. A simple extension of this phenomenon would be to propose the hypothesis that smaller eggs laid towards the end of the season could account for the decreased chick survival from such eggs as compared with those from the larger eggs of the mid-season nesters.

It has been shown that repeat clutches are laid in nests from which all eggs have been removed, within twelve hours of the last egg being laid (Weidmann 1956 in black-headed gulls). The repeat clutch is laid ten to twelve days later in both herring and lesser black-backed gulls (Salomonsen 1939 and Paludan 1951). Such repeat clutches show a volume decrease in each egg laid (Parsons 1971) and may be considered to be a result of a shift in the season of nesting, which shows a build up to a maximum of breeding success in the middle of that delayed period and a decline towards the end. Such a shift of the inverted u-shaped hatching curve along the date axis is only apparent when the delay is applied to the group as a whole, thus supporting the argument for the requirement of social stimulation for successful breeding.

The proposed study was to evaluate the breeding success of the herring gull, lesser black-backed gull and the common tern. This was to be done by marking and following the fate of a number of clutches at different times during the season and to determine the various parameters affecting their survival.

Following the theories of Parsons (1971) the study was aimed primarily to determine the variation in breeding success during the nesting season.

The common tern usually nests at Rockcliffe Marsh in fairly discrete colonies, mainly restricted to the 'old/new marsh' boundary in the Sarkfoot Point area and a few pairs scattered in the black-headed gull colony in the middle of the marsh. This year, however, the arrival of the birds was much later than in previous years, and although the numbers reached approximately seventy per cent of the previous year's total, the nests were widely distributed throughout the black-headed gull colony and scattered individuals around Sarkfoot Point. No distinct colonies were formed and the possibility of any efficient search for nests and chicks was negligible. This part of the proposed study was, therefore, abandoned.

SECTION TWO.

DESCRIPTION OF THE STUDY AREA

2.1. The Marsh

Rockcliffe Marsh lies at the head of the Solway Firth about seven miles north-west of Carlisle and two miles from Rockcliffe Village (Nat. Grid Ref. NY325 635). 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 the Lake District Naturalists' Trust during the nesting season.

The 800 hectares (2,000 acres) 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 which intersect the marsh at numerous points. The main vegetation of the marsh being fescue grass, <u>Festuca rubra</u> L. which is grazed in the winter by geese and in the summer by cattle (1,150 head in 1973).

The herring and lesser black-backed gull colony is situated on the Point of the marsh, approximately three kilometres from the Esk boathouse (Greenbed), covering both mature and 'new' marsh to an area of approximately 300 hectares. About 1,700 pairs of lesser black-backed and herring gulls in the ratio of four to one respectively breed here at low density, with nests being between five to thirty metres (mean fifteen metres) apart. This area is rarely grazed by cattle and the vegetation of <u>Festuca rubra</u>, <u>Carex</u> spp., <u>Juncus</u> spp. and scurvy grass, <u>Cochlearia officinalis</u> L. (in the gullies) grows to a height of three hundred millimetres on the mature marsh, whereas the vegetation of common salt-marsh grass, Puccinellia maritima (Huds.), thrift, Armeria maritima (Mill.) and sea milkwort, Glaux maritima L. of the 'new' marsh is generally much shorter.

The study area was mainly confined to the colony on the mature marsh, since nests on the 'new' marsh were flooded early in the season by a wind-blown high tide, and twice more subsequently during the season. The area was conveniently divided into twenty one sections by drainage channels, thus searches for nests and chicks were made by quartering the areas between channels.

2.2. The Gull Population.

The herring and lesser black-backed gull colony is restricted to the point of the marsh. This large area being occupied almost entirely by gulls, with skylark and oystercatcher nests sparsely scattered through it. This lack of diversity of nesting species is probably due to the predatory behaviour of the gulls, since the flora and topography of the area is little different from other areas on the marsh supporting a larger diversity of nesting species.

The distribution of gulls is non-homogeneous, both in species and individual distribution. An average distance of 15 m. between nests gives a false impression of the structure of the colony. The colony appears to be split into a number of sub-colonies, forming concentrations of birds nesting in mutual close proximity. These aggregations are connected by birds nesting more sparsely between them. The social structure of the colony must similarly split, as it is inconceivable that birds on one side of the Point receive any communication from gulls on the other side, hence any social stimulation for breeding must be restricted to these aggregations of birds.

The reason for this non-homogeneous distribution is not clearly evident. It is thought that site preference may have some bearing on the distribution, but the ultimate factor of site selection is unclear, as a variety of sites, with regard to vegetation and topography were found in use.

Similarly there is a non-uniform distribution of species. On the 'old' marsh, the colony area most studied, had a lesser black-backed to herring gull ratio~~n~~ of approximately 6:1, and that of the 'new' marsh 3:1. This may have been due directly to site preference, where the herring gulls preferred to nest in lower vegetation on more exposed sites.

Figure 1

Geographical location of Rockcliffe Marsh, showing the area contained within a 30 mile radius of the marsh (the estimated feeding range of herring gulls, Pearson 1969).

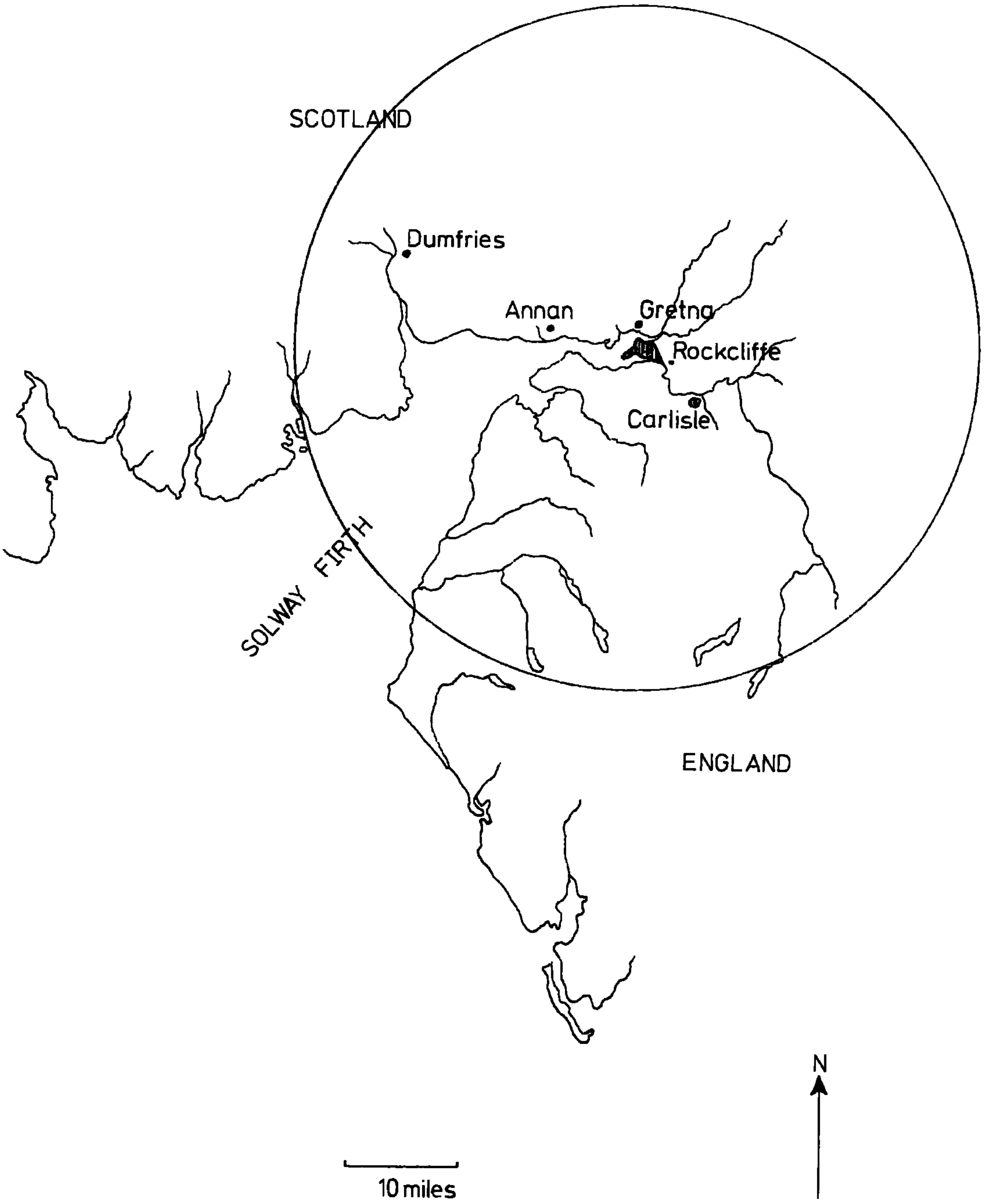
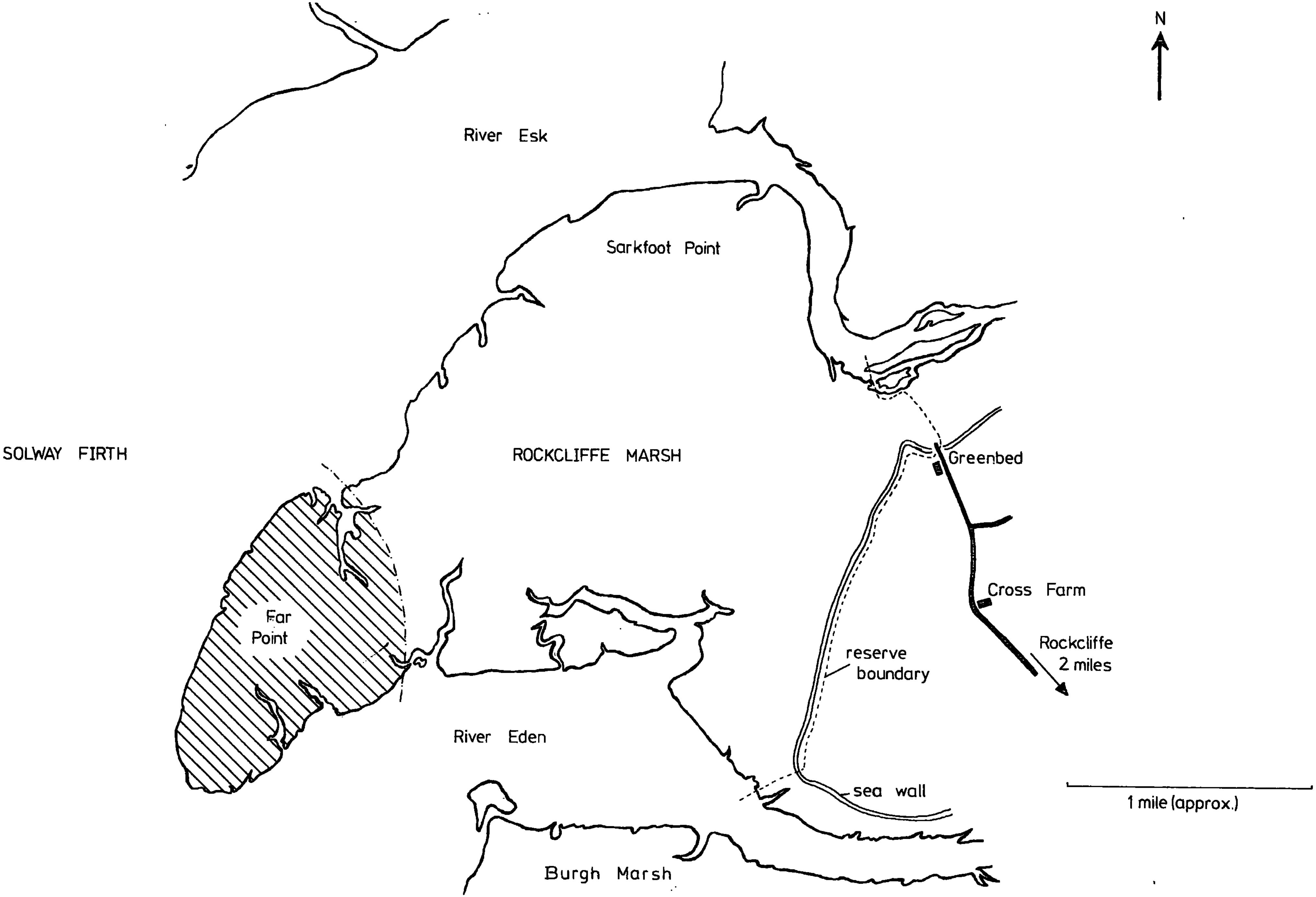

SCOTLAND
Dumfries
Annan
Gretna
Rockcliffe
Carlisle
SOLWAY FIRTH
ENGLAND
N
10 miles

Figure 2

Map of Rockcliffe Marsh, showing the position of the herring and lesser black-backed gull colony.


N
River Esk
Sarkfoot Point
SOLWAY FIRTH
ROCKCLIFFE MARSH
Greenbed
Far Point
Cross Farm
Rockcliffe 2 miles
reserve boundary
River Eden
sea wall
1 mile (approx.)
Burgh Marsh

SECTION THREE.

GENERAL METHODS

3.1. Marking nests and eggs.

Nests were marked with wooden stakes (300 x 25 x 7 mm) sharpened to a point at one end and numbered at the other by black waterproof ink felt-tip pen. The stakes were pushed into the ground about 250 - 300 mm from the nest, such that about 200 mm of the numbered end of the stake appeared above ground. The stakes appeared to cause little disturbance of the nsting birds except in one instance where the nest and clutch of three eggs was moved a distance of 500 mm further away from the stake.

Eggs were marked, using the same waterproof felt-tip pens, according to the sequence of laying. Thus the first or a - egg (nomenclature of Paludan 1951*) bearing the number 1, b - egg the number 2 and c - egg the number 3. Each egg was marked as soon as possible after its being laid and before the next egg was laid.

*Throughout this study the nomenclature of Paludan (1951) will be used. This, in summary, means that the first, second and third eggs to be laid are referred to as the a -, b - and c - eggs respectively, subsequent eggs being d -, e - eggs etc., and the chicks from a -, b - and c - eggs being referred to as A -, B - and C - chicks respectively.

Plate 1

Method of marking nest and eggs.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The maximum length and breadth of each egg was measured using Etalon vernier calipers, measuring to the nearest 0.1 mm. From these measurements the volume and shape index of each egg were calculated using the following formulae:

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

where l is the length of the egg

b is the breadth of the egg

k is a constant for the particular species under consideration. Here the value $k = 0.476$ (Harris 1964) was used.

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

3.2. Marking newly hatched chicks.

The chicks were marked on hatching by the use of a leg ring numbered according to the nest number and sequence of laying of the egg from which it hatched thus the first laid egg of nest 150 produced a chick which would be numbered 150a. The rings were made from 7 mm sections of 10 mm diameter yellow p.v.c. tubing, which were cut open lengthwise and held in place around the left leg by rejoining the loose ends with one end of a staple, reducing the effective diameter such that the ring would not slip over the foot.

The rings were removed after 10 days, wherever possible, or at subsequent retrievals after this period. Should a chick not be retrieved the combined effects of rusting of the staple and tension on the ring produced by growth of the diameter of the leg would cause the natural shedding of the ring.

Plate 2

Method of marking chicks,

The rings were marked with black waterproof ink from a fine pointed felt-tip pen, figures remaining clearly visible for the duration of the study period.

The wing length, tarsus length (between the proximal side of the joint of digit I to the joint with the tibia) and the mid-toe length (between the proximal side of digit I along the underside of digit III to the distal end of the fleshy tissue beneath the claw) were measured at each visit (Fig 3) (Maunder and Threlfall 1972).

3.3. The analysis of food samples regurgitated by chicks.

An attempt to study the nature of the food of the gulls in the colony was carried out by collecting regurgitated food from the crops of recently fed chicks. These vomited remains were collected in polythene bags and preserved in four per cent formaldehyde. Into each bag was placed a slip of paper bearing the chick number and date, such that the species and age of all chicks sampled was known. The polythene bags were then sealed by knotting the top.

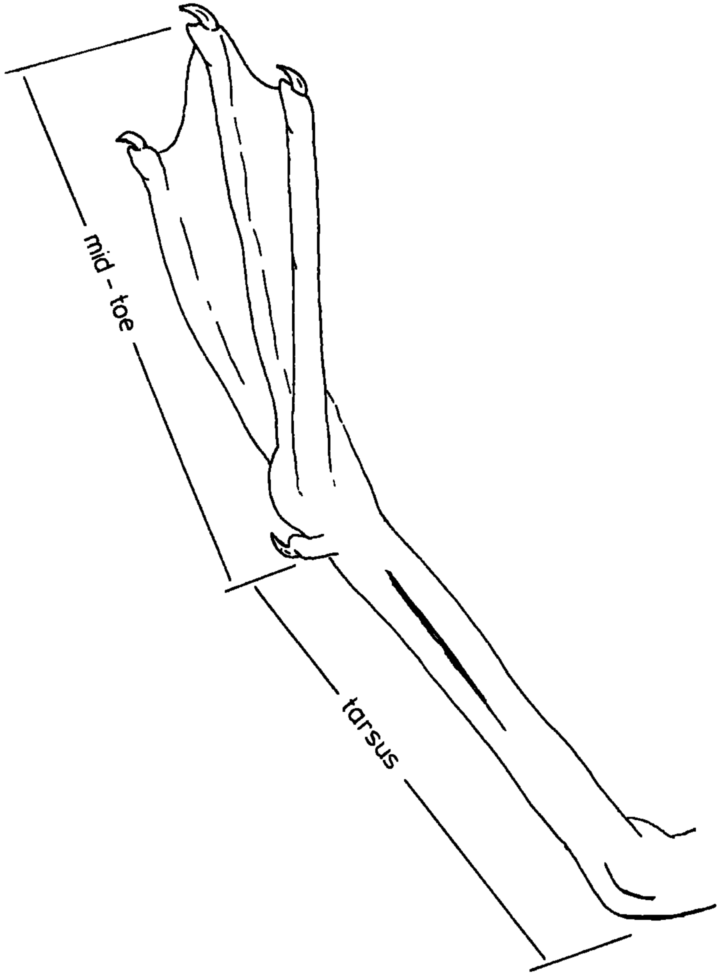
Samples were analysed in the laboratory in a white enamel tray, a dissecting microscope being used to identify small remains. The remains were sorted into the categories shown in section eight.

3.4. Efficiency of search and division of the season.

The study area was naturally divided into twenty one areas by drainage channels. Nests, and subsequently chicks, were searched for by quartering the areas between these drainage channels. Periodic checks on the efficiency of search were made by noting all nests or

Figure 3

Parameters measured on the chick leg.


mid - toe
tarsus

chicks found on a certain day and calculating the percentage of those found out of the total number known to have been marked. The efficiency of finding marked nests varied from 95 per cent to 96 per cent and that for finding marked chicks 57 per cent to 71 per cent.

Measurement of eggs commenced on May 7th and continued until June 18. This season was divided into weekly divisions in each of which it was hoped to collect data from 100 new nests. Table 1 shows the distribution of numbers of nests of known laying sequence in each of the weeks samples.

Table 1. Number of nests, of known laying sequence, marked in each week of the season.

Date	Days from start of season based on the first day of each week.	Number of nests with eggs marked
May 7 - 13	0	100
May 14 - 20	7	102
May 21 - 27	14	84
May 28 - June 3	21	62
June 4 - 10	28	15
June 11 - 17	35	8

Note: Season here refers to the period during which observations were made until no new nests with eggs could be found, the true nesting season began a few days before May 7.

In the last two periods more nests were actually marked, but these were severely affected by flooding before measurements could be completed. Due to the small sample size in these groups data from these two groups are often grouped together at day 31 from the start of the season. Data from the last group was sometimes omitted from the analysis of data since many nests in this period contained relaid clutches due to the effects of flooding of the 'new' marsh population early in the season.

3.4. Statistical Methods.

Statistical methods employed in the analysis of data are described in the appendix.

SECTION FOUR.

THE NEST AND EGGS

4.1. Introduction

Herring and lesser black-backed gulls on the marsh are very much alike in their nesting habits. Both make crude nests on the ground consisting of little more than a shallow scrape, lined with a variable amount of dried grass or similar vegetation. It was noticed that nests were often decorated with predominantly white objects, such as bones, shells, stones and the flowers of scurvy grass. Nest sites were varied with respect to degree of exposure and nature of surrounding vegetation. Some nests were found among tussocks of grass, others among very short vegetation.

The usual clutch of three eggs are laid consecutively with an interval of about 46 hours between the a - and b - eggs and 47 hours between the b - and c - eggs (Barth 1955) (these times were not verified in this study, but in most cases a visit to the colony on alternate days allowed individual eggs to be marked prior to the laying of the next egg).

The nests of 464 pairs were marked, the laying sequence of 351 of which were known. The third egg of the other clutches was estimated by calculating the volume and shape index of the eggs, the third egg of a clutch having a characteristically smaller volume than the a - and b - eggs. (Paludan 1951, Harris 1964, Parsons 1971).

The average length, breadth, volume and shape index of the a -, b - and c - eggs are shown in table 2.

The difference between the average values of these parameters for a - and b - eggs are not statistically significant, but differences between length and breadth between a - and c - eggs, b - and c - eggs

Table 2. Measured and calculated parameters of eggs. (All mean values ± one standard error, standard deviations follow in parenthesis.)

	length (mm)	breadth (mm)	volume (cm^3)	Shape index	n
a - egg	68.05 ± 0.17 (3.10)	47.74 ± 0.10 (1.80)	74.62 ± 0.39 (7.38)	70.27 ± 0.18 (3.48)	350
b - egg	67.80 ± 0.21 (3.18)	47.76 ± 0.12 (1.84)	74.46 ± 0.51 (7.64)	70.62 ± 0.24 (3.57)	221
c - egg	66.66 ± 0.26 (3.33)	46.63 ± 0.13 (1.66)	69.74 ± 0.54 (6.74)	70.09 ± 0.28 (3.55)	155
a + b - egg	67.96 ± 0.13 (3.13)	47.75 ± 0.08 (1.91)	74.55 ± 0.31 (7.48)	70.39 ± 0.40 (9.56)	571

and a + b - and c - eggs are significant ($P<0.05$). Barth (1967) shows that there is significant difference between the volumes of various species of the Laridae. No significant difference was found between the volumes of herring and lesser black-backed gulls in this study area ($t = 0.797$, d.f = 59), hence, both species were considered together.

Coefficients of variance were calculated for the length and breadth of all eggs, using the following formula:-

$$\text{Coefficient of variance (c.v)} = \frac{\text{Standard deviation}}{\text{mean}} \times 100.$$

CV (length) = 4.66

CV (breadth) = 3.67

This shows that the breadth of the egg is the more stable character.

Using the working hypothesis that smaller eggs (in this context the size of the egg throughout the text refers to the volume, unless otherwise stated) have lower hatchability and lower potential of producing viable young (Blaxter and Hempel 1963, Tindell and Morris 1964, and Parsons 1971) a seasonal trend of variation in egg size was looked for.

4.2. Variation in egg volume with respect to season.

A significant seasonal decrease in egg volume is shown in figs 4 and 5. Significant differences were not found between successive weeks, but between laying dates fourteen or more days apart the difference was significant ($P < 0.05$).

Table 3. Decrease in egg volume through the season.

	Decrease in volume (cm^3)	Percentage decrease
a + b - eggs	6.81	8.7 %
c - eggs	5.46	7.0 %
		($P < 0.05$)

Figure 4

Graph showing variation of egg volume with laying date. (Pecked line indicates combined data of 28 and 31 days)

(all values ± 2 standard errors)

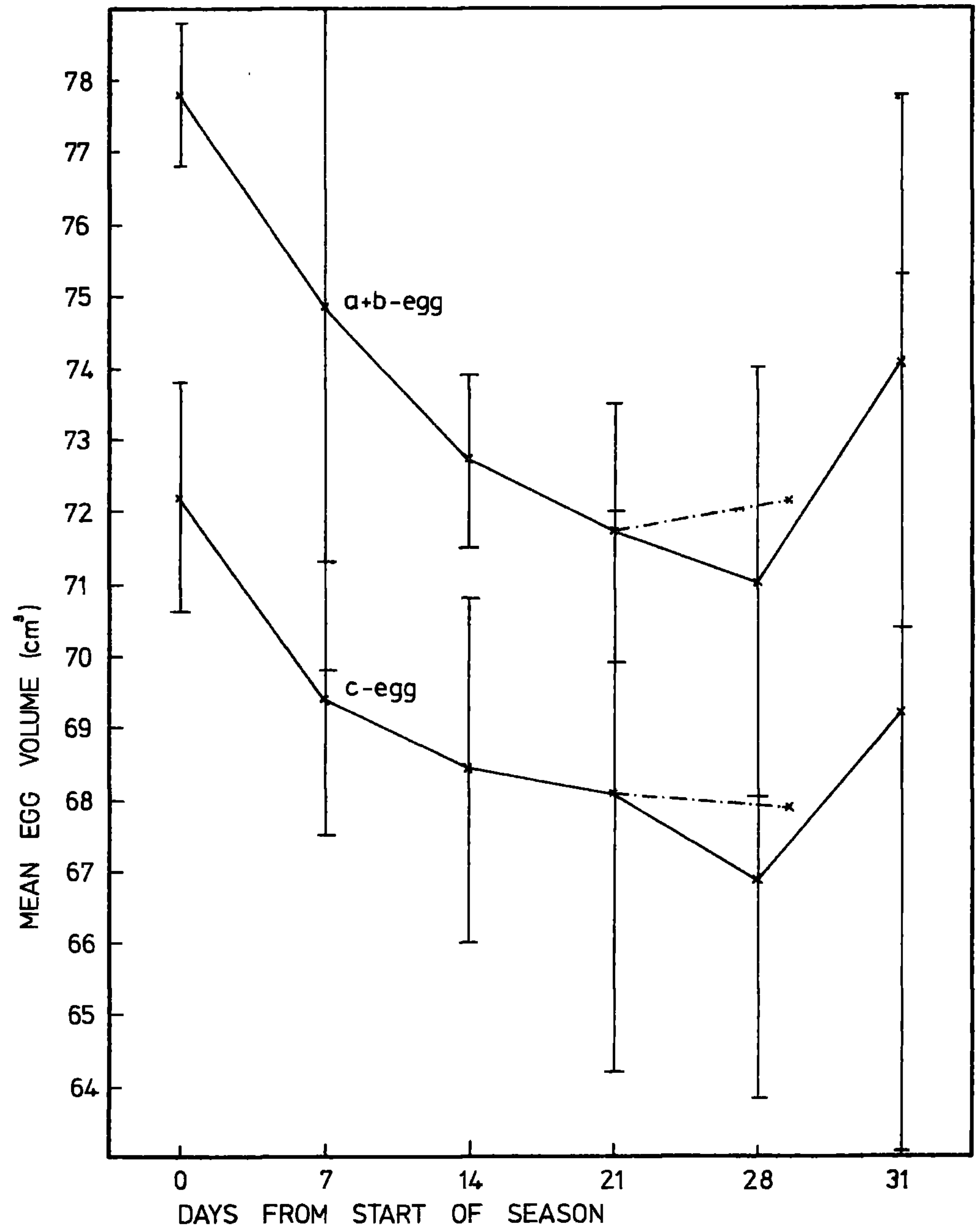

MEAN EGG VOLUME (cm^3)
78
77
76
75
74
73
72
71
70
69
68
67
66
65
64
a+b-egg
c-egg
0
7
14
21
28
31
DAYS FROM START OF SEASON

Figure 5

Regression lines of egg volume with log season.

a - egg $y = -3.77x + 77.65$ $r = -0.903$.

b - egg $y = -5.46x + 78.45$ $r = -0.976$.

a+b - egg $y = -4.57x + 78.05$ $r = -0.990$.

c - egg $y = -3.39x + 72.28$ $r = -0.989$.

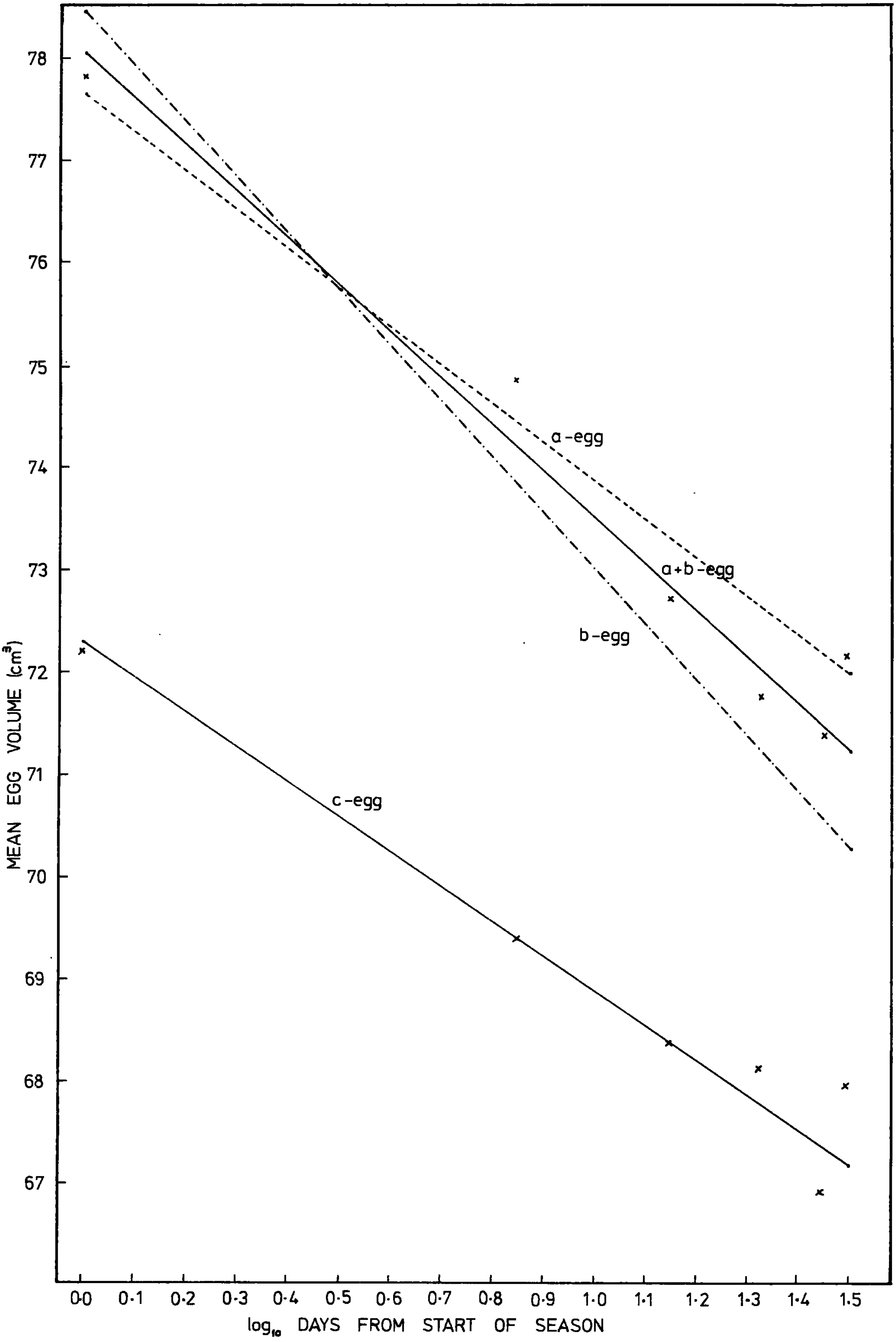

MEAN EGG VOLUME (cm^3)
78
77
76
75
74
73
72
71
70
69
68
67
a-egg
a+b-egg
b-egg
c-egg
0·0
0·1
0·2
0·3
0·4
0·5
0·6
0·7
0·8
0·9
1·0
1·1
1·2
1·3
1·4
1·5
log$_{10}$ DAYS FROM START OF SEASON

Fig. 4 shows the plot of mean egg volume against days from the beginning of the season. The resultant curves tend to approach an asymptote of egg volume which may be considered to be the lower egg volume threshold which must be exceeded in order to allow successful incubation and hatching of the egg.

The seasonal decrease in egg volume of a + b - eggs is greater than that of the c - egg (shown by the regression lines in the plot of egg volume against log days from the start of the season, Fig. 5). The possible existence of a threshold is supported by the data in Fig 5, where the percentage seasonal volume decrease of a + b - eggs is larger than that of the c - egg. Since the initial size of a - and b - eggs are greater than that of the c - egg it is possible for a larger volume decrease to occur in the a - and b - eggs without reaching the critical egg volume.

Smaller variation in the volume of the c - eggs with season has been noted by Barth (1967) and in the kittiwake (Coulson 1963) and herring gull (Andersen 1957).

Reasons for variation in egg volume within a breeding season have been attributed to the age composition of the community at various times throughout the season. It has been shown (Coulson and White 1958 and Mills 1973) that older females tend to breed early in the season and younger females towards the end of the season and correlated with Andersen's data (1957) which shows that the breadth of the egg increases with the age of the female, would account for the observed seasonal decrease in egg volume. Coulson (1963) and Andersen (1957) show that the c - egg becomes more and more different from the a - and b - eggs as the age of the female increases.

Parsons (1971) however, debates this problem with respect to herring gulls and concludes from his evidence that there is greater variation in the volume of the c - egg as the season progresses, i.e. that the effect of decrease in volume with season overrides the effect of the distribution of older birds at the beginning of the season.

Results from this study tend to favour the views of Coulson and Andersen (regression lines of Fig. 5), assuming that such a temporal distribution of older breeding birds occurs, ageing and sexing of birds having not been carried out in this study.

The increase in egg volume at the end of the season and its consequent effects on hatchability and survival of young are discussed more fully in section seven, and are thought to be due to the higher percentage of relaid clutches in this period than in other periods. These relaid clutches would be of older birds whose first clutches were destroyed early in the season by flooding.

No significant variation in clutch size was detected. Mills (1973) however, demonstrates significant differences between the clutch size with season of females of the same age group and also significant variation between the size of the clutch laid by females of different ages when the difference between the ages is two years or more.

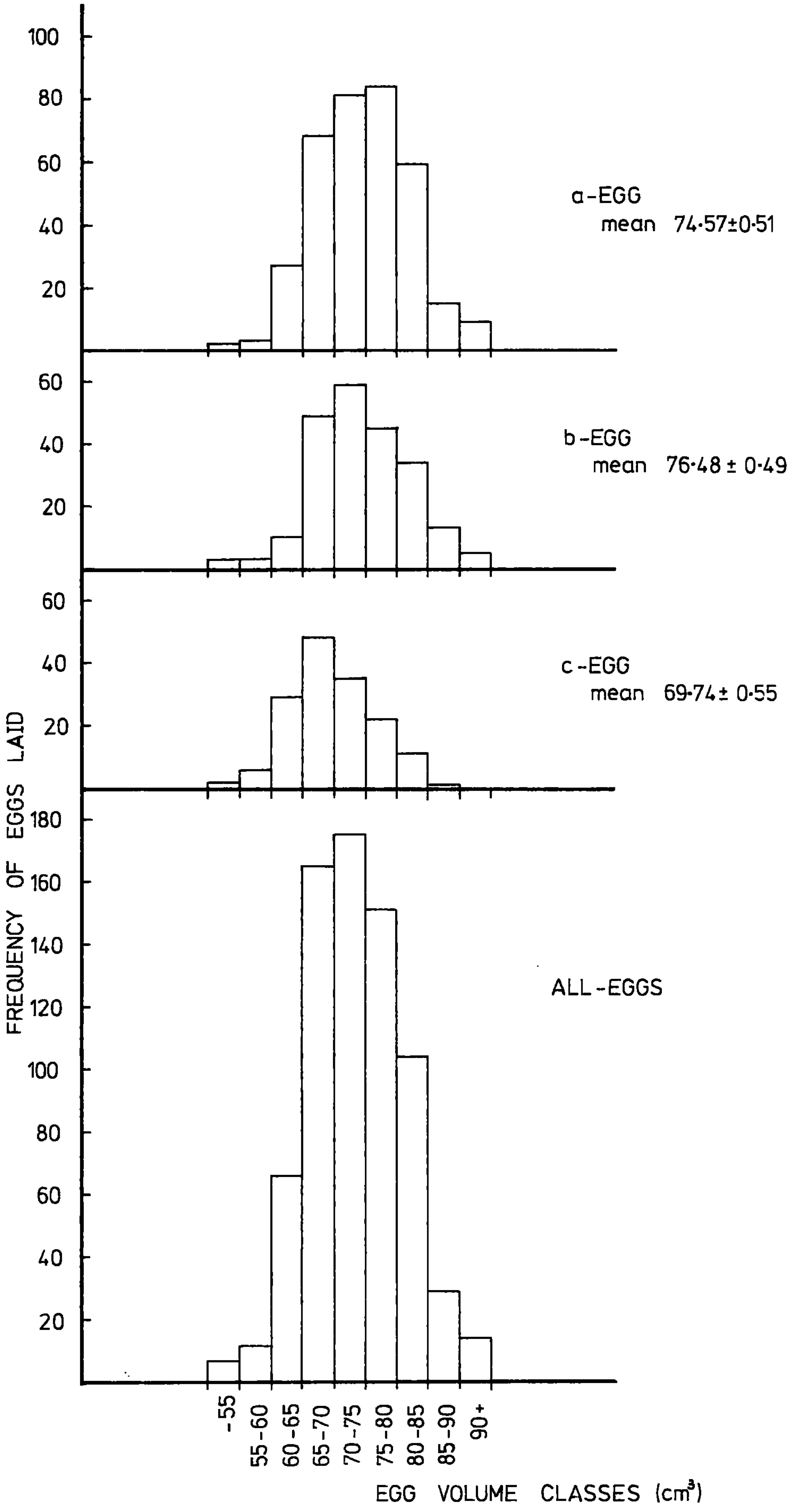
Table 4. Variation in mean clutch size during the season.

Days from start of season	Mean clutch size
0	2.11 ± 0.62
7	2.23 ± 0.63
14	2.09 ± 0.51
21	1.83 ± 0.53
28	2.00 ± 1.32
Overall mean clutch size	2.08 ± 0.57

(All values ± one standard error)

Figure 6

Frequency histogram of number of eggs laid at different volume classes.


100
80
60
40
20
a-EGG
mean 74·57±0·51
60
40
20
b-EGG
mean 76·48 ± 0·49
60
40
20
c-EGG
mean 69·74 ± 0·55
FREQUENCY OF EGGS LAID
180
160
140
120
100
80
60
40
20
ALL-EGGS
-55
55-60
60-65
65-70
70-75
75-80
80-85
85-90
90+
EGG VOLUME CLASSES (cm³)

4.3. Clutch removal and egg predation.

In order to delay the breeding season of pairs of birds to see the effects of extending the overall nesting season on egg size, hatchability and chick survival, a number of clutches were removed as soon as possible after the third egg had been laid.

Salomonsen (1939), Paludan (1951) and Weidmann (1956) show that a complete clutch of three eggs is laid 11 to 12 days after the removal of a full clutch, providing the clutch is removed within 12 hours of the c - egg being laid. Fourteen full clutches were removed in the last three season sections as soon as the c - egg had been laid. The exact time of removal after the last egg had been laid was not known, but it is estimated that this was never more than 24 hours, which may account for the lack of repeat clutches, since no evident relay clutches were found.

Due to the high percentage of egg predation (discussed later) only a limited number of clutches were removed, in order that a sufficient number of clutches would be left to complete the incubation process.

In the colony, being of such low density, it is possible that an underestimate of the size of the territory around the nest was made, such that the finding of a new nest near to the removed clutch was not considered as a repeat clutch, but as an entirely new nest.

The variation in the number of nests predated with respect to the number of nests at risk between successive weeks during the season was significantly different $(P < 0.001)$ (table 7). The highest incidence of predation is early in the season, which correlates with the hypothesis that there are a large number of non-breeding birds at the beginning of the season, as the season progresses more and more birds become involved in nesting and hence the percentage of egg predation becomes less. There are also significant differences between the percentage predation of a -, b - and c - eggs ($P < 0.001$) (table 5), the a - egg suffering greater than expected predation.

Table 5. Variation in percentage egg predation with laying sequence.

	a - egg	b - egg	c - egg	total
Number of eggs predated	144 (93.11)	39 (61.06)	14 (42.83)	197
Number of eggs not predated	193 (243.89)	182 (159.94)	141 (112.17)	516
Number of eggs laid	337	221	155	713
Percentage predation	42.72	17.64	9.03	27.62

$\chi^2 = 76.26$ degrees of freedom = 2 $P < 0.001$

(Expected values in parenthesis)

Egg predation is mainly due to conspecific predation, which was witnessed on several occasions. Other predators on the marsh are few, consisting mainly of a few pairs of carrion crows, which were seen on the gull colony. Stoats, foxes and hedgehogs, although seen on 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, kestrel and barn owls have also been seen around the marsh, but are similarly not considered to have any major effect on the survival of eggs or chicks.

Table 6. Seasonal variation in egg predation.

	Days from start of season					
	0	7	14	21	28	total
Number of nests marked	100	102	78	57	14	351
Number of nests completely predated	33	34	26	28	4	125
Percentage complete predation	33.00	33.33	33.33	49.12	28.57	35.61
Number of nests partly predated	12	12	11	1	1	37
Percentage partial predation	12.00	11.76	14.10	1.75	7.14	10.54

Table 7. Seasonal variation of complete nest predation with respect to the number of nests at risk. (expected values in parenthesis).

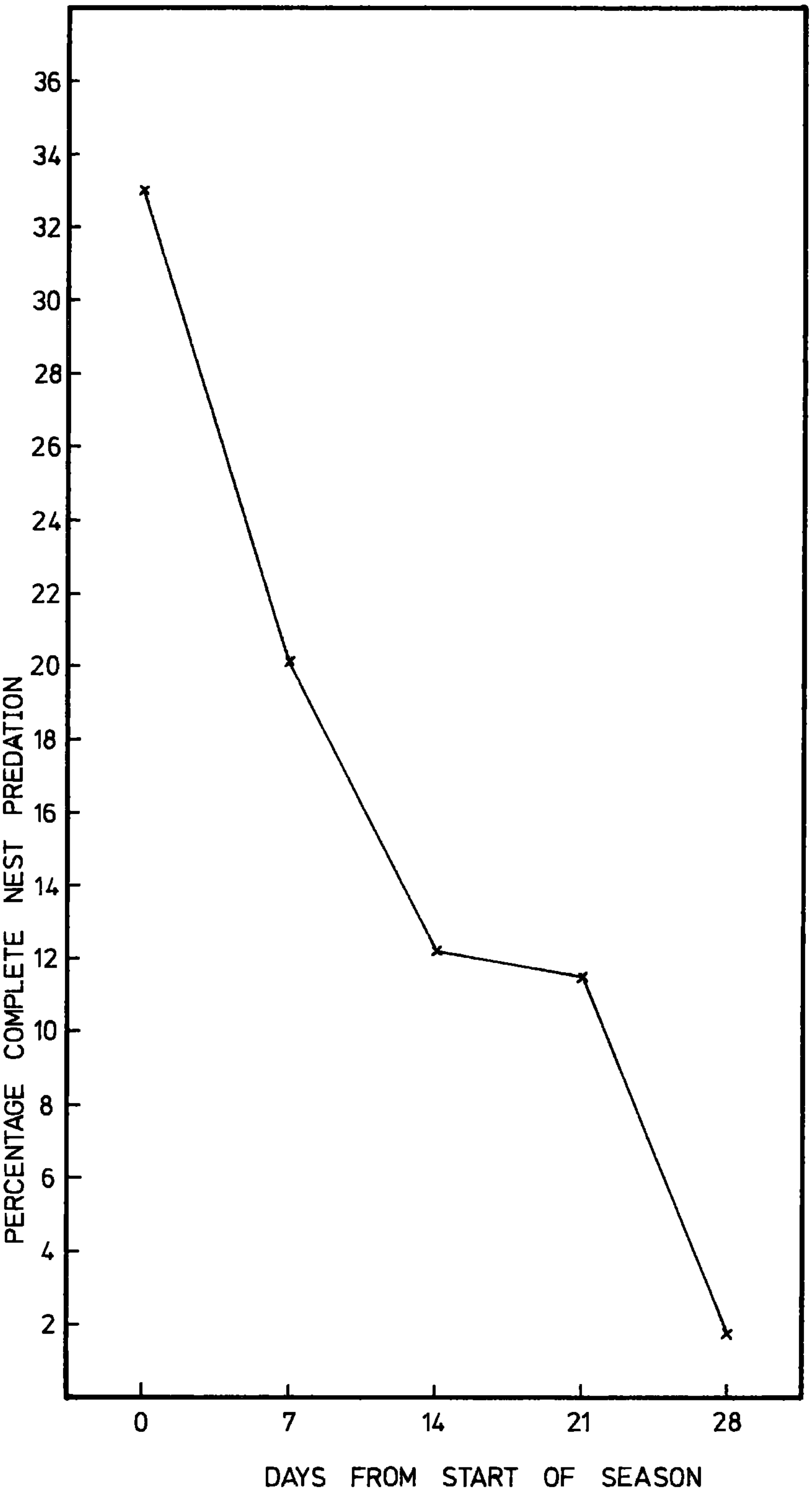
	Days from start of season					
	0	7	14	21	28	total
Number of nests predated	33 (13.08)	34 (22.10)	26 (27.85)	28 (31.90)	4 (30.07)	125
Number of nests not predated	67 (86.92)	135 (146.90)	187 (185.15)	216 (212.10)	226 (199.93)	831
Number of nests at risk	100	169	213	244	230	956
Percentage nest predation	33.00	20.11	12.20	11.49	1.73	13.07

$\chi^2 = 68.97$ degrees of freedom 4 $P < 0.001$.

(note: complete nest predation refers to nests with more than one egg which were completely predated, and those nests from which the a - egg, being the only egg in the nest at the time, was predated and the nest subsequently deserted without further eggs being laid. Partial nest predated refers to nests containing more than one egg, from which a fraction of the total number of eggs was lost due to predation).

Figure 7

Graph of seasonal variation in percentage complete nest predation.


PERCENTAGE COMPLETE NEST PREDATION
36
34
32
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
7
14
21
28
DAYS FROM START OF SEASON

SECTION FIVE.

HATCHING SUCCESS

5.1. Introduction

Variation in hatching success of eggs has been shown, with respect to laying date, (Parsons 1971) who shows that the hatching success declines at the end of the season.

Hatching success has also been shown to be dependent on egg volume (Mollart 1972) where small and large eggs show a lower percentage hatching success than eggs of middle volume range. It may be postulated from this that the c - egg should probably have a lower hatching success than the other eggs of the clutch.

5.2. Hatching success and the nature of the egg.

No significant difference was found between the number of a -, b - or c - eggs hatching (table 8).

Table 8. Variation in hatching success with laying sequence (expected values in parenthesis).

	a - egg	b - egg	c - egg	total
Number of eggs hatching	153 (148.63)	129 (126.80)	90 (96.57)	372
Number of eggs not hatching	24 (28.37)	22 (24.20)	25 (18.43)	71
Total number of eggs incubated	177	151	115	443
Percentage hatchability	86.44	85.43	78.26	83.97

$\chi^2 = 3.83$ degrees of freedom = 2 P NS.

Similarly there is no variation in hatching success with clutch size (table 9).

Table 9. Variation in hatching success with clutch size (expected values in parenthesis).

	Clutch size			
	3	2	1	total
Number of eggs hatching	260 (259.48)	82 (83.98)	30 (28.55)	372
Number of eggs not hatching	49 (49.52)	18 (16.03)	4 (5.45)	71
Number of eggs incubated	309	100	34	443
Percentage hatchability	84.14	82.00	88.23	83.97

χ^2 = 0.75 degrees of freedom = 2 P NS.

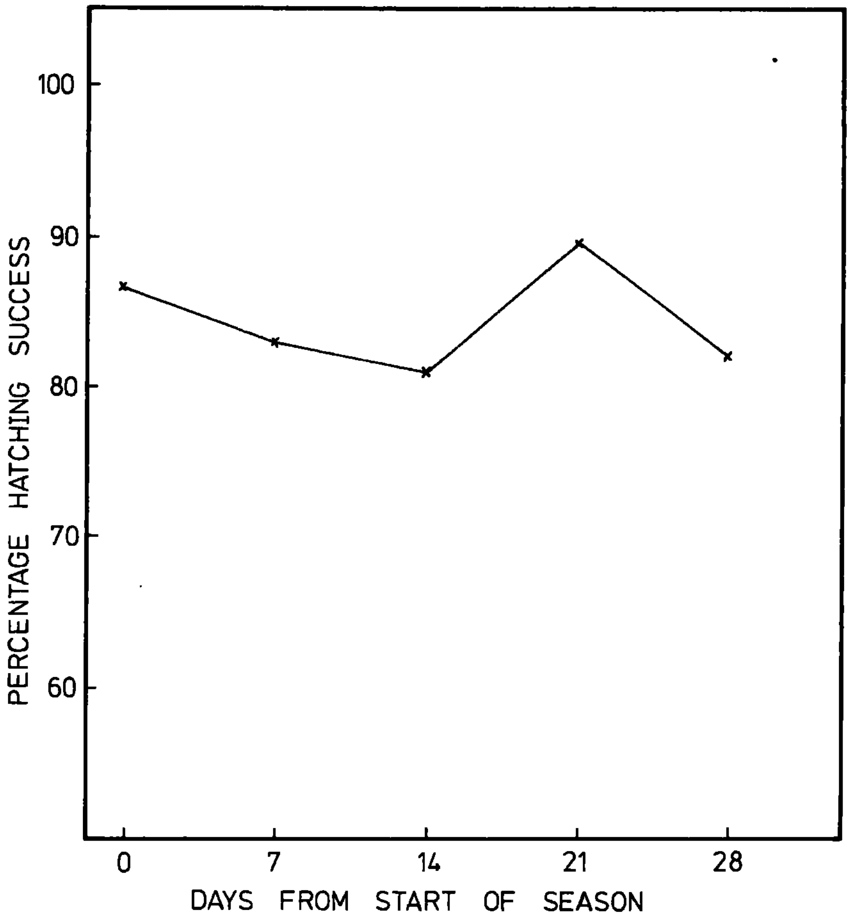
5.3. Hatching success and laying date.

There is found to be no significant difference in hatching success with respect to laying date (table 10).

Fig. 8 shows the plot of hatching success with laying date and, disregarding the seemingly anomalous result at 21 days from the start of the season, there seems to be a slight trend to reduced hatchability with season. Such a trend would be expected if there were reduced hatchability with smaller eggs (see section 5.4.), knowing that there was a significant decrease in egg volume as the season progresses.

Figure 8

Graph of seasonal variation in percentage hatching success.



100
90
80
70
60
PERCENTAGE HATCHING SUCCESS
0
7
14
21
28
DAYS FROM START OF SEASON

5.4. Hatching success and egg volume.

Although there is no significant difference in the variation of hatching success with egg volume, a definite trend of increased hatching success with increased volume may be seen (Fig.9).

The scatter of points in Fig. 9 are positively correlated ($r = +0.774$) and significantly different from zero ($t = 3.24$, $P < 0.02$).

Parsons (1971) shows the same effect and demonstrates significant negative correlation at the high egg volumes. This tendancy is also evident here, showing that there is probably an upper value of egg volume (about 80 cm^3) which gives maximum hatchability. Regression lines for the two fractions of the curve have been calculated:

Volume classes 55 to 75-80 cm^3 $r = +0.901$, $t = 4.156$ $P < 0.02$.
Volume classes 75 -80 to 90 + cm^3 $r = -0.664$, $t = 1.256$ P NS.

From the equation of the regression line B (Fig. 9), the intercept on the x - axis, i.e. at zero percent hatching success, was calculated to be about 34 cm^3. It can be seen, therefore, that this volume must be exceeded in order that successful hatching of any egg may occur. The lower asymptote of egg volume approached with progress of the season is above this level, at about 67 cm^3 i.e. at 76% hatchability.

Fig. 6 shows a frequency histogram of the number of eggs laid at each volume class (regardless of laying sequence). It can be seen that the high frequency classes correspond, closely to the highest percentage hatchability (75% to 90%).

Table 10. Variation in hatchability through the season.
(expected values in parenthesis)

	Laying date (days from start of season)					
	0	7	14	21	28	total
Number of eggs hatching	127 (125.96)	131 (132.68)	61 (62.98)	44 (41.15)	9 (9.24)	372
Number of eggs not hatching	23 (24.04)	27 (25.32)	14 (12.02)	5 (7.85)	2 (1.76)	71
Number of eggs incubated	150	158	75	49	11	443
Percentage hatchability	84.66	82.91	81.33	89.79	81.81	83.97

$\chi^2 = 2.14$ degrees of freedom = 4 P NS.

Table 11. Variation in hatching success with respect to egg volume.

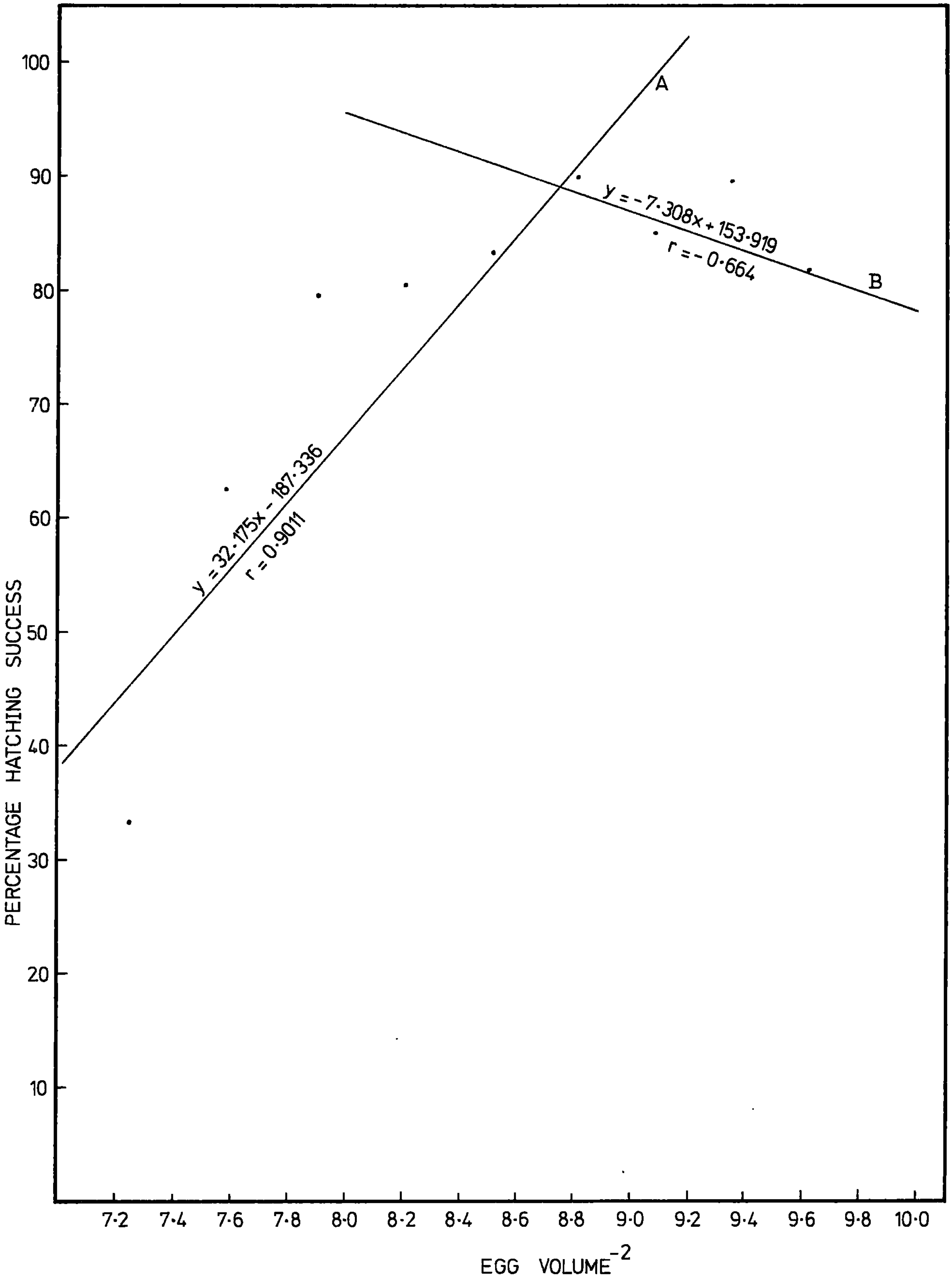
(expected values in parenthesis)

	Volume classes (cm^3)									
	up to 55	55–60	60–65	65–70	70–75	75–80	80–85	85–90	90 +	total
Number of eggs hatching	1 (2.20)	5 (6.67)	31 (32.60)	79 (81.92)	84 (84.43)	89 (82.76)	57 (56.01)	17 (15.88)	9 (9.20)	372
Number of eggs not hatching	2 (0.49)	3 (1.31)	8 (6.40)	19 (16.08)	17 (16.57)	10 (16.25)	10 (10.99)	2 (3.12)	2 (1.80)	73
Number of eggs incubated	3	8	39	98	101	99	67	19	11	445
Percentage hatchability	33.3	62.5	79.5	80.6	83.2	89.9	85.1	89.5	81.8	

$\chi^2 = 12.52$ degrees of freedom = 8 P NS

Figure 9

Regression lines of the two fractions of the curve of percentage hatching success with square root of egg volume.



PERCENTAGE HATCHING SUCCESS
100
90
80
70
60
50
40
30
20
10
EGG VOLUME^{-2}
7·2
7·4
7·6
7·8
8·0
8·2
8·4
8·6
8·8
9·0
9·2
9·4
9·6
9·8
10·0
A
B
y = 32·175x - 187·336
r = 0·9011
y = -7·308x + 153·919
r = -0·664

It can be seen from Fig. 10 that the percentage hatchability of eggs is reduced to a very low level when the egg volume falls below about 57.5 cm^3. This poor hatching success at low volume may be expressed as energy wastage of the adult (Fig. 11).

The calorific values of eggs of different sizes (using calorific values of yolk and albumen only) were calculated by use of the regressions of egg volume on egg weight and weight of components of the egg on total weight of egg given by Parsons (1971) (see appendix). Calorific values of 3.48 k.cal. g^{-1} for yolk and 0.51 k.cal. g^{-1} for albumen (Altman and Dittmer 1968) were used.

It can be seen, therefore, that for a small increase in energy output (in terms of yolk and albumen) of 9 k.cal, in increasing the size of the egg from 52.5 cm^3 to 62.5 cm^3, a 50% increase in hatching success is obtained with the corresponding reduction of energy wastage per egg of 36.95 k.cal.

Hence it may be proposed that evolutionary genetic selection results in the gulls tending to lay eggs in the 62 cm^3 to 83 cm^3 range (Fig. 6) giving maximum utilisation of energy output.

It is realised that this energy budget is not truly representative of the events under consideration. The representation of energy output of the female as calculated by the calorific values of yolk and albumen of the egg, does not account for the many other sources of energy expenditure during egg laying particularly when a comparison of eggs of differing sizes is made, but it is thought that the values given above are an index of the total energy expenditure during ovulation.

Table 12. Estimation of energy wastage per egg due to failure of hatching.

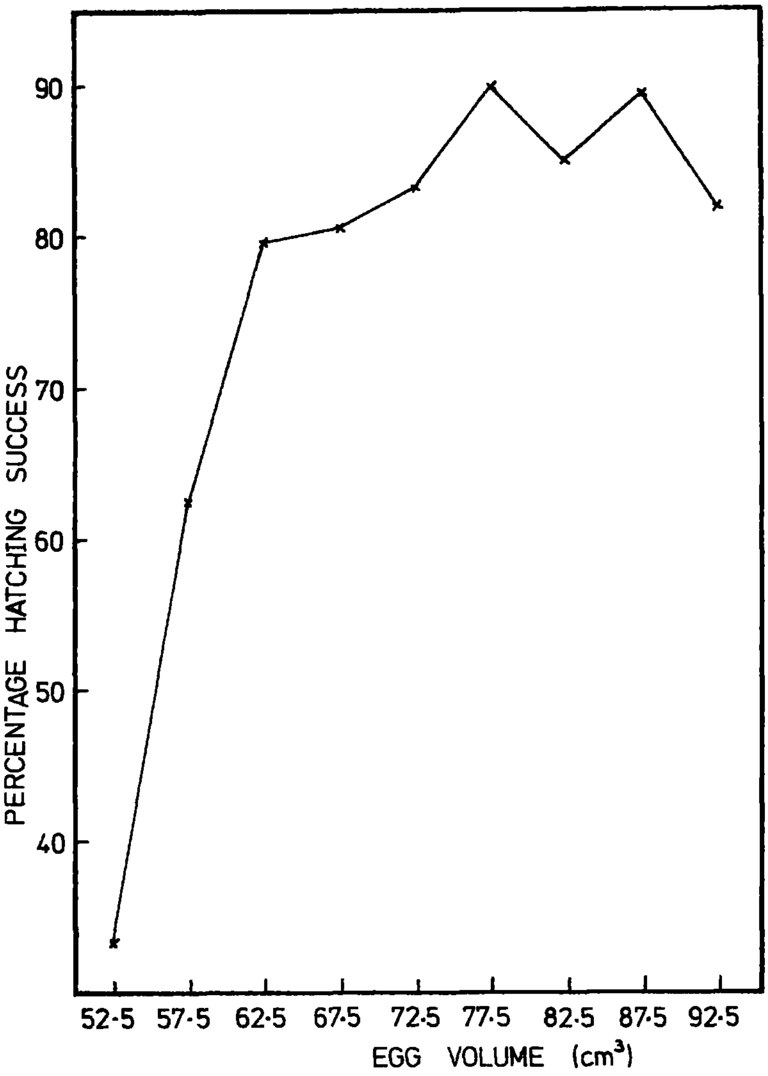
Egg volume (cm^3)	Calorific value of yolk + albumen for an egg of corresponding volume	Percentage failure to hatch	Energy wastage (k cal.)
52.5	84.01	66.7	56.03
57.5	88.56	37.5	33.21
62.5	93.12	20.5	19.09
67.5	98.43	19.4	19.10
72.5	102.38	16.8	17.20
77.5	106.91	10.1	10.80
82.5	111.43	14.9	16.60
87.5	116.08	10.5	12.19
92.5	120.73	18.2	21.97

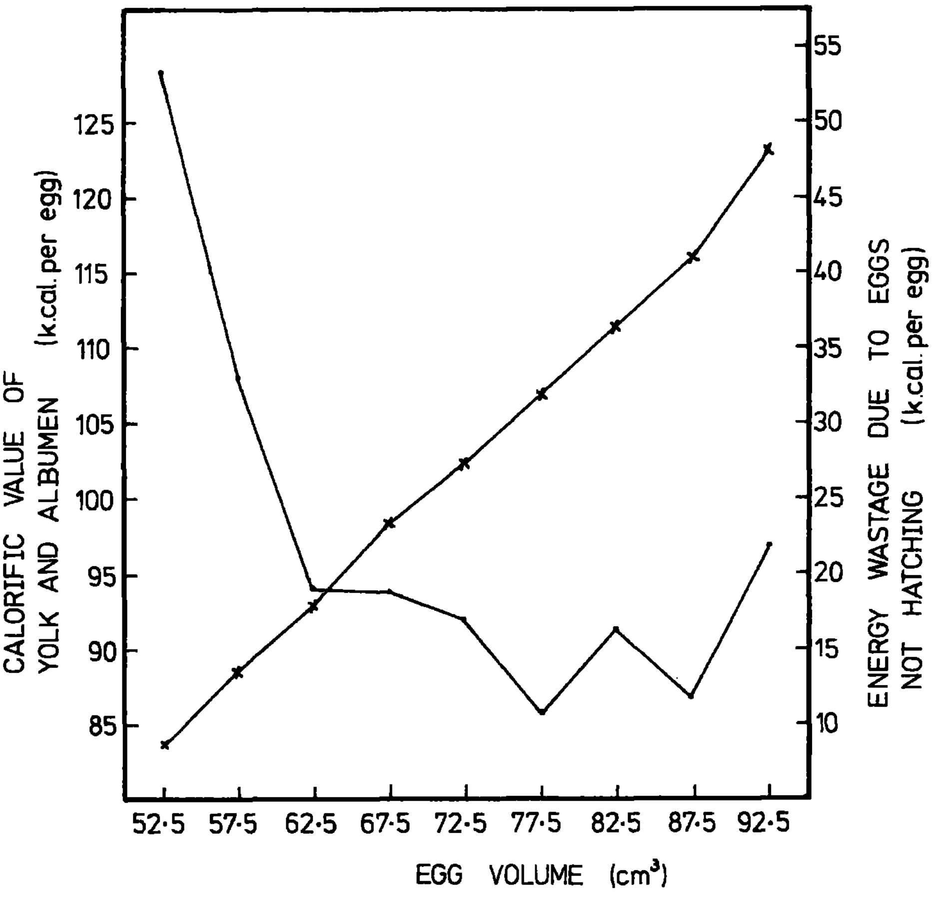
Figure 10

Graph of percentage hatching success with egg volume.

Figure 11

Graph showing calorific value of eggs of various volume (crosses) and the energy wastage at each egg volume class due to the non hatching of eggs (Fig. 10) (dots).


PERCENTAGE HATCHING SUCCESS
90
80
70
60
50
40
52·5
57·5
62·5
67·5
72·5
77·5
82·5
87·5
92·5
EGG VOLUME (cm³)


CALORIFIC VALUE OF YOLK AND ALBUMEN (k.cal. per egg)
125
120
115
110
105
100
95
90
85
ENERGY WASTAGE DUE TO EGGS NOT HATCHING (k.cal. per egg)
55
50
45
40
35
30
25
20
15
10
52·5
57·5
62·5
67·5
72·5
77·5
82·5
87·5
92·5
EGG VOLUME (cm³)

SECTION SIX.

GROWTH OF CHICKS

6.1. Introduction.

The rate of chick growth was estimated by measurements of wing, tarsus and mid-toe increase in length, measurements being made on alternate days. The date of hatching was determined as accurately as possible, but since the colony was visited on alternate days, a chick may be from 0 to 2 days old when first found in the nest, hence age classes used cover a range of two days.

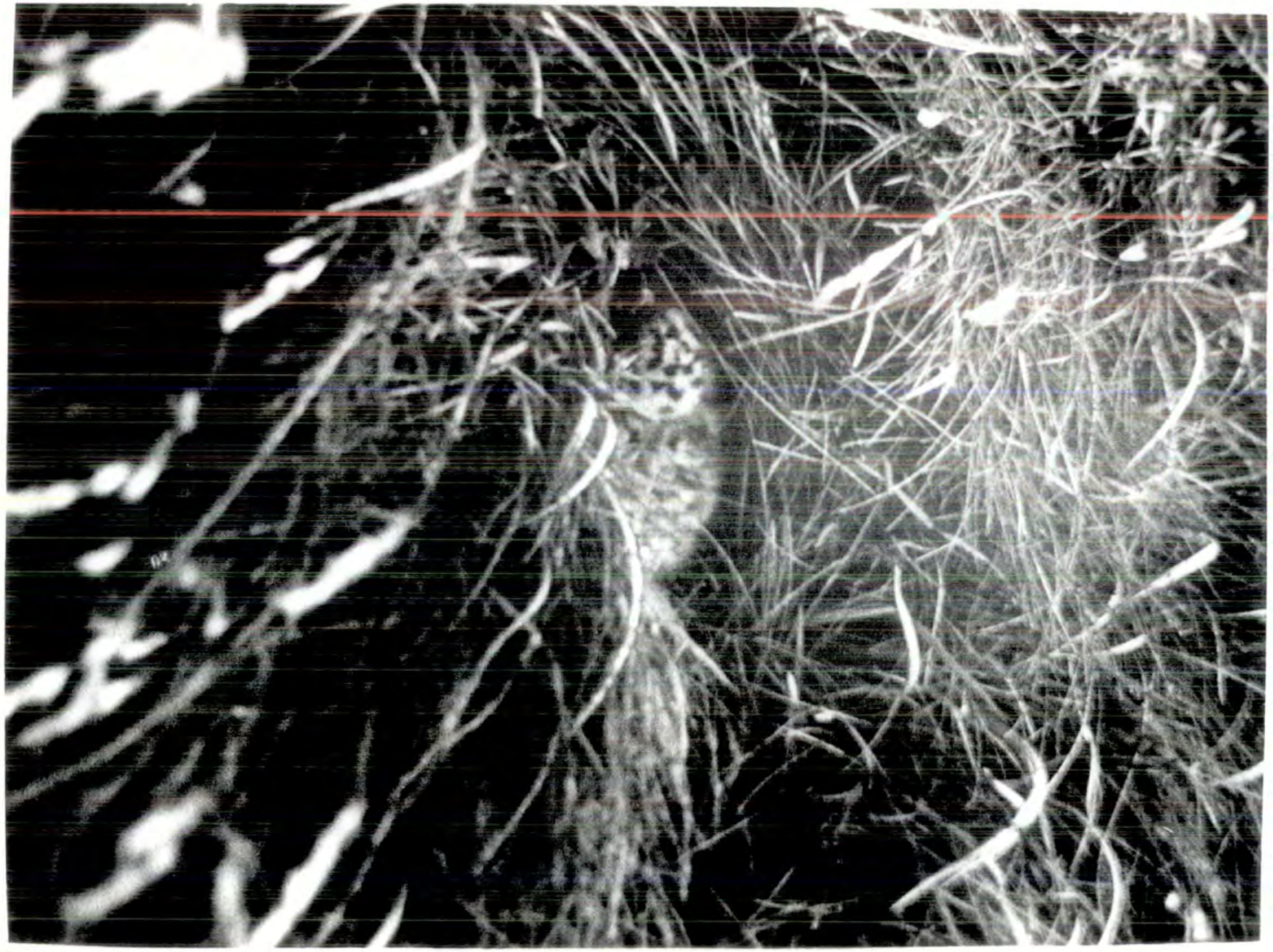
Most authors (Harris 1964 and Kadlec et al. 1969) suggest that it is possible to follow the fate of chicks during the first week of life, the period when chick mortality is at a maximum (Kadlec et al. 1969). Some difficulty was experienced in finding chicks on successive visits to the colony, due to the cryptic behaviour of the chicks and the low density of nesting, giving the chicks a large area around the nest (still within the parent's territory) in which to hide. Chicks often left the nest site at the age of four to eight days and readily concealed themselves in tunnels in the vegetation (Plate 3). Larger chicks concealed themselves in drainage channels, under overhanging banks and vegetation. Such difficulties in searching for chicks accounts for the reduced efficiency of search as compared with that for nests, referred to earlier.

6.2. Variation in growth with respect of laying and hatching sequence.

Since some incubation starts prior to the laying of the third egg, the C - chick is the last of the clutch to hatch. The A - and B - chicks usually hatch on the same day, or within one day of each

Plate 3

A 4-6 day old chick in grass near to the nest.



other (the B - chick often hatching first). The C- chick generally hatches one to two days after its siblings. It is therefore reasonable to propose that the C - chick will be smaller than its siblings at any one age group, having firstly, hatched from a smaller egg and, secondly, having to compete for food against chicks larger than itself.

Table 13 shows the wing length of chicks with increasing age, with regard to laying sequence. No significant differences between the A - and B - chicks were found at any age group. Significant difference in only one age group (4 - 6) was found between A + B and C - chicks ($P < 0.05$, $t = 2.2$).

It can be seen in the A - and B - chicks that there is much greater variation in wing length in the first age group than in the second. This may be partially explained by the difficulty in obtaining this measurement to a high degree of accuracy when the wing length is small. There is also rapid growth of down feathers during this period and chicks of this age group were found with more or less naked wings (recently emerged), to those with large numbers of down feathers on the wing making measurement difficult.

Significant differences between A - and C - chicks, B- and C - chicks and A + B - and C - chicks were found in the first four age groups for tarsus length. The results shown in table 14 are of greater significance than the results of wing and mid-toe length, since the coefficient of variance of tarsus length is less than that of mid-toe or wing length, and thus a less variable character.

Table 13. Mean wing length of chicks at different age classes with respect to the hatching sequence. (All values ± one standard error, standard deviations in parenthesis).

	Age classes (days)				
	0 - 2	2 - 4	4 - 6	6 - 8	8 - 10
A - chick	60.05 ± 1.02 (12.56)	69.91 ± 0.58 (6.44)	81.61 ± 0.84 (7.88)	98.15 ± 1.43 (11.20)	123.96 ± 3.03 (20.53)
B - chick	61.66 ± 0.60 (6.60)	70.69 ± 0.61 (5.91)	82.64 ± 0.99 (8.50)	100.92 ± 1.61 (12.58)	117.94 ± 2.90 (17.13)
C - chick	59.01 ± 0.56 (5.21)	67.56 ± 1.18 (9.71)	78.02 ± 1.19 (8.11)	95.72 ± 2.21 (11.91)	117.45 ± 5.02 (58.93)
A + B - chicks	60.76 ± 0.49 (8.25)	70.25 ± 0.42 (6.21)	82.08 ± 0.64 (8.15)	99.64 ± 1.08 (11.93)	121.23 ± 2.20 (19.64)
t and p, A+B/C	1.66 NS	1.68 NS	2.21 P<0.05	1.19 NS	0.52 NS

Table 13a. Coefficients of variance of chick parameters measured.

Parameter	Coefficient of variance
Tarsus length	8.5
Mid-toe length	11.9
Wing length	20.2

Fig 12 shows a plot of mean wing, tarsus and mid-toe lengths for all chicks against age class. Fig. 13 shows a plot of mean tarsus length of A + B - and C - chicks against age class, from which it may be seen that the rate of growth of the C- chick is as great as that for the A + B chicks although starting at a lower level. Since there is no significant difference between the tarsus length of A + B - chicks and C - chicks in the last two age groups it is thought that the rate of growth of the C - chick is actually greater than that of its siblings (i.e. the two growth curves become closer and closer together as age increases), however there is no statistically significant difference between the increments of length with age (table 15 and Fig. 13).

6.3. Variation in growth rate with respect to laying date.

There is no significant difference between the rates of growth of the wing or mid-toe lengths at various times during the season. Significant difference ($P < 0.05$) were found between some season sections at difference age groups for the tarsus length, but no trends were evident (tables 16, 17 and 18).

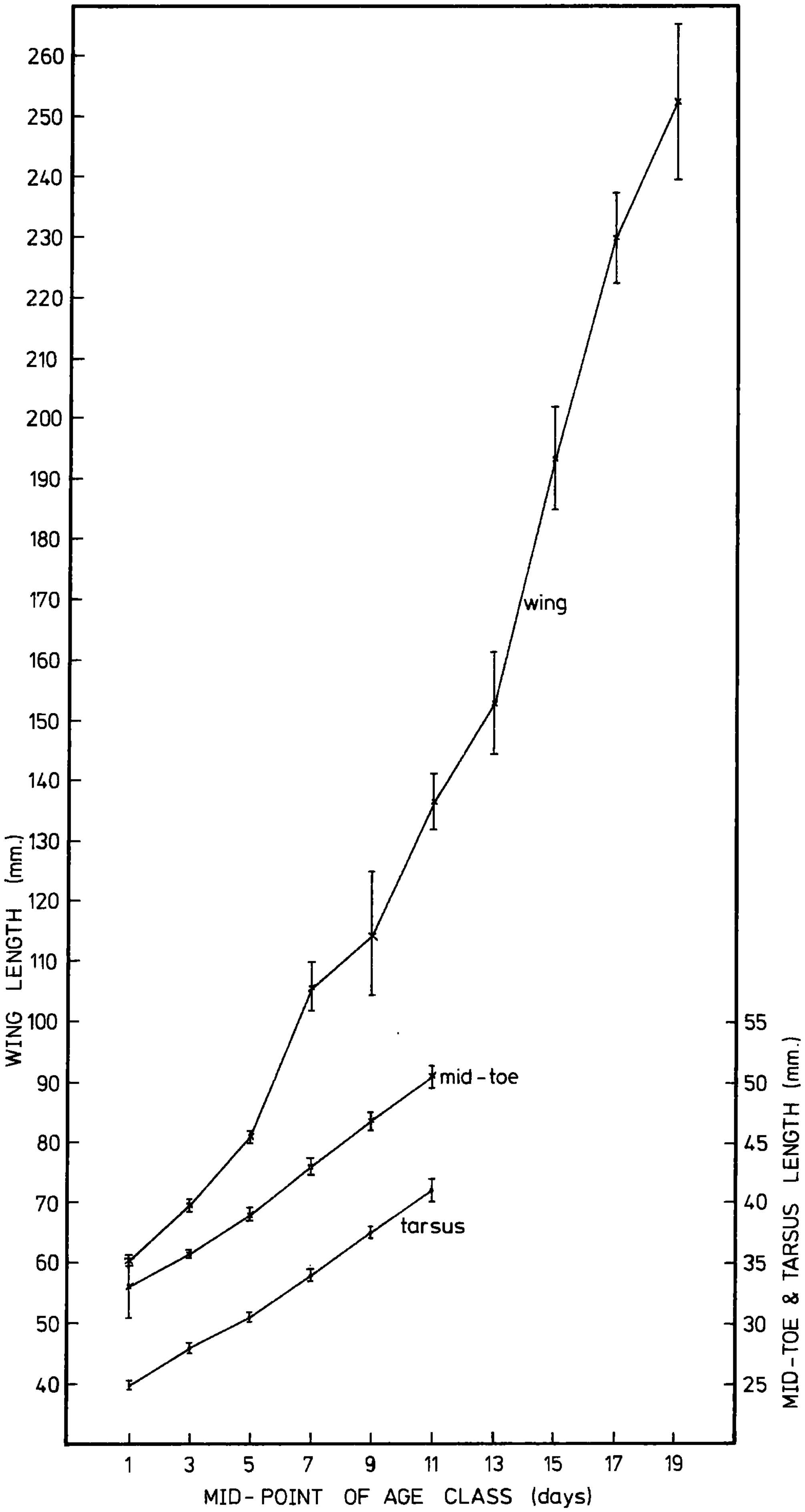
6.4. Variation in growth rate with respect to clutch size.

In both wing length and tarsus length at different age classes there was found to be no significant differences between the growth

Figure 12

Graph of wing, mid-toe and tarsus length with age of chick.

(all values ± 2 standard errors)



260
250
240
230
220
210
200
190
180
170
160
150
140
130
120
110
100
90
80
70
60
50
40
WING LENGTH (mm.)
55
50
45
40
35
30
25
MID-TOE & TARSUS LENGTH (mm.)
wing
mid-toe
tarsus
1
3
5
7
9
11
13
15
17
19
MID-POINT OF AGE CLASS (days)

rates of chicks from clutches of three, two or one chick (table 19).

It would be expected that chicks from smaller clutches would obtain more food per capita from the parents than those of larger clutches, and show a corresponding increase in growth rate. It would appear, however, from the data presented here, that a physiological upper limit of growth rate exists, and food supplied over and above the quantity and/ or quality required to produce this maximal growth rate can cause no further increase in growth rate.

Table 14. Variation in mean tarsus length at different age groups with respect to hatching sequence. (All values ± one standard error, standard deviations in parenthesis).

	Age classes (days)					
	0 - 2	2 - 4	4 - 6	6 - 8	8 - 10	10 - 12
A - chick	25.03 ± 0.16 (1.90)	28.15 ± 0.19 (1.99)	31.02 ± 0.26 (2.46)	33.88 ± 0.37 (2.83)	38.16 ± 0.50 (3.34)	42.46 ± 1.04 (5.28)
B - chick	25.24 ± 0.18 (1.92)	27.95 ± 0.17 (1.64)	30.54 ± 0.25 (2.13)	34.42 ± 0.40 (3.09)	36.94 ± 0.59 (3.44)	41.00 ± 0.71 (3.45)
C - chick	24.48 ± 0.17 (1.54)	26.79 ± 0.21 (1.65)	29.11 ± 0.35 (2.35)	33.36 ± 0.59 (3.09)	36.59 ± 0.82 (3.83)	39.27 ± 0.88 (3.39)
A + B - chick	25.30 ± 0.14 (2.24)	28.06 ± 0.13 (1.84)	30.80 ± 0.18 (2.33)	34.15 ± 0.27 (2.97)	37.63 ± 0.38 (3.42)	41.76 ± 0.64 (4.51)

By the use of paired t - tests no significant differences were found between A - and B - chicks at any age group. Significant differences ($P < 0.05$) between A + B - and C - chicks for the first four age groups were found.

Table 15. Variation in increment of tarsus length between age classes, with repect to hatching sequence. (values ± one standard error, all values are positive).

	Increments between age classes				
	0-2/2-4	2-4/4-6	4-6/6-8	6-8/8-10	8-10/10-12
A + B - chick	2.76 ± 0.19	2.75 ± 0.22	3.25 ± 0.33	3.48 ± 0.47	4.13 ± 0.73
C - chick	2.30 ± 0.26	2.33 ± 0.41	4.25 ± 0.68	3.23 ± 1.00	2.68 ± 1.20
t	1.02	0.67	0.89	0.17	0.75

The difference between the increment 0-2/2-4 and 4-6/6-8 in the C - chick is statistically significant ($t = 2.06$ $P < 0.05$).

Figure 13

Graph showing variation in tarsus length with age of chick between A + B - and C - chicks, increments between age classes are also shown.

(all values ± 2 standard errors)

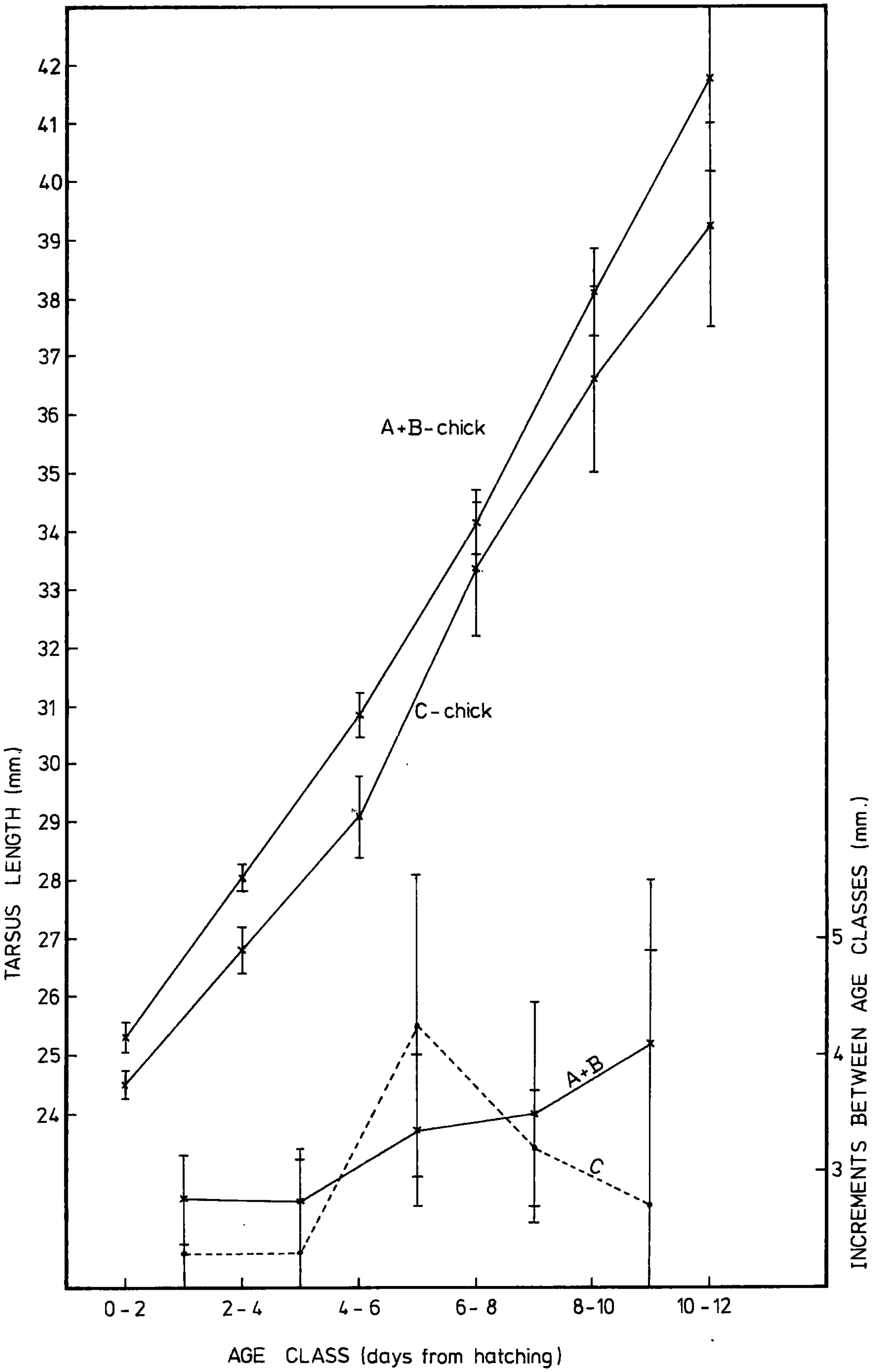

42
41
40
39
38
37
36
35
34
33
32
31
30
29
28
27
26
25
24
TARSUS LENGTH (mm.)
A+B-chick
C-chick
A+B
C
5
4
3
INCREMENTS BETWEEN AGE CLASSES (mm.)
0-2
2-4
4-6
6-8
8-10
10-12
AGE CLASS (days from hatching)

Table 16. Variation in mean wing length at different age groups with respect to season (laying date). (all values ± one standard error, standard deviations in parenthesis).

Days from start of season	Age classes (days)				
	0 - 2	2 -4	4 - 6	6 - 8	8 - 10
0	59.08 ± 0.56 (6.18)	69.54 ± 0.58 (5.58)	83.00 ± 0.77 (6.60)	102.65 ± 1.62 (10.77)	121.82 ± 2.21 (11.72)
7	61.59 ± 0.57 (6.65)	70.79 ±0.70 (6.82)	81.47 ± 1.21 (9.95)	100.77 ± 1.66 (12.25)	135.37 ± 5.00 (28.25)
14	59.54 ± 0.62 (4.78)	68.16 ± 1.46 (10.64)	77.75 ± 1.21 (7.14)	97.05 ± 2.07 (12.43)	117.85 ± 4.14 (21.92)
21	60.69 ± 0.89 (5.88)	68.73 ± 0.99 (6.15)	80.16 ± 1.71 (8.38)	94.33 ± 2.97 (10.28)	116.45 ± 4.52 (14.98)
All	63.87 ± 0.75 (13.80)	69.59 ± 0.44 (7.32)	81.14 ± 0.58 (8.32)	99.90 ± 0.71 (8.55)	114.38 ± 5.45 (54.26)

Table 17. Variation in mid-toe length at different age groups with respect to season (laying date). (all values ± one standard error, standard deviations in parenthesis).

	Age classes (days)					
Days from start of season	0 - 2	2 - 4	4 - 6	6 - 8	8 - 10	10 - 12
0	32.78 ± 0.25 (2.82)	35.61 ± 0.27 (2.56)	39.45 ± 0.35 (2.99)	43.07 ± 0.44 (2.91)	46.89 ± 0.58 (3.07)	50.58 ± 0.93 (4.75)
7	32.70 ± 0.23 (2.66)	35.60 ± 0.25 (2.46)	38.51 ± 0.37 (3.01)	42.93 ± 0.50 (3.75)	46.82 ± 0.82 (4.73)	50.63 ± 0.70 (3.64)
14	32.64 ± 0.25 (1.98)	35.72 ± 0.25 (2.15)	39.28 ± 0.47 (3.00)	42.82 ± 0.62 (3.63)	46.83 ± 0.74 (4.00)	50.62 ± 1.09 (3.93)
21	32.98 ± 0.30 (1.96)	35.63 ±0.37 (2.28)	39.48 ± 0.50 (2.52)	42.00 ± 0.76 (2.83)	46.00 ± 1.03 (4.00)	47.00 ± 3.00 (4.24)
28	34.00 ± 0.93 (2.62)	37.83 ± 1.66 (4.07)	38.75 ± 1.80 (3.60)	43.75 ± 1.89 (3.77)		
All	32.78 ± 0.69 (1.33)	35.67 ± 0.15 (2.46)	39.11 ± 0.21 (2.96)	42.88 ± 0.27 (3.39)	46.73 ± 0.39 (3.98)	50.50 ± 0.50 (4.12)

Table 18. Variation in mean tarsus length at different age groups with respect to season (laying date).

(all values ± one standard error, standard deviations in parenthesis)

	Age classes (days)					
Days from start of season	0 - 2	2 - 4	4 - 6	6 - 8	8 - 10	10 - 12
0	25.23 ± 0.22 (2.48)	28.36 ± 0.24 (2.31)	31.41 ± 0.29 (2.48)	35.11 ± 0.40 (2.66)	38.18 ± 0.54 (2.88)	41.65 ± 0.84 (4.26)
7	25.48 ± 0.17 (1.99)	27.98 ± 0.18 (1.78)	30.29 ±0.33 (2.64)	33.73 ± 0.40 (3.06)	38.06 ± 0.73 (4.19)	40.74 ± 0.87 (4.54)
14	24.56 ± 0.28 (2.19)	27.37 ± 0.24 (1.78)	29.66 ± 0.34 (2.17)	33.32 ± 0.54 (3.06)	36.90 ± 0.62 (3.32)	39.85 ± 1.01 (3.65)
21	24.44 ± 0.31 (1.98)	26.71 ± 0.29 (1.70)	30.04 ± 0.49 (2.40)	32.00 ± 0.58 (2.08)	35.93 ± 0.85 (3.20)	36.00 ± 1.00 (1.41)
28	25.63 ± 0.53 (1.51)	28.17 ± 1.22 (2.99)	30.00 ± 1.47 (2.94)	34.00 ± 1.78 (3.56)		
All	25.13 ± 0.12 (2.22)	27.84 ± 0.12 (2.05)	30.53 ± 0.18 (2.55)	33.91 ± 0.25 (2.99)	37.48 ± 0.35 (3.55)	40.78 ± 0.52 (4.28)

Table 19. Variation in mean wing and tarsus length at different age classes with respect to clutch size. (All values ± one standard error, standard deviations in parenthesis)

	Age classes				
	0 - 2	2 - 4	4 - 6	6 - 8	8 - 10
			Wing length		
3.	60.56 ± 0.40 (5.68)	70.90 ± 0.60 (7.63)	81.22 ± 0.78 (8.74)	98.95 ± 1.22 (12.02)	118.98 ± 1.87 (14.34)
2.	60.56 ± 0.55 (6.32)	69.51 ± 0.66 (6.56)	81.52 ± 0.97 (8.62)	97.75 ± 1.54 (11.64)	121.60 ± 3.90 (25.55)
1.	58.97 ± 0.74 (5.71)	69.43 ± 0.85 (5.74)	80.62 ± 1.59 (8.09)	101.60 ± 2.08 (9.30)	119.61 ± 3.49 (14.80)
			Tarsus length		
3.	24.93 ± 0.13 (1.71)	27.49 ± 0.16 (1.93)	30.35 ± 0.24 (2.47)	34.01 ± 0.36 (3.18)	37.37 ± 0.50 (3.36)
2.	25.09 ± 0.19 (1.98)	27.96 ± 0.20 (1.81)	30.57 ± 0.28 (2.34)	33.41 ± 0.45 (3.03)	37.53 ± 0.63 (3.90)
1.	24.80 ± 0.28 (1.95)	28.00 ± 0.28 (1.72)	30.57 ± 0.50 (2.39)	34.60 ± 0.49 (1.88)	37.21 ± 0.93 (3.49)

By the use of paired t - tests no significant differences were found between the wing lengths at different clutch sizes at each age group.

SECTION SEVEN.

CHICK MORTALITY

7.1. Introduction

Chick mortality has been shown to occur mainly within the first week of life (Kadlec et al. 1969). Parsons (1971) attributes the mortality mainly to cannibalism and attacks by conspecifics on chicks as the chicks wander into neighbouring territories. On the gull colony studied here little cannibalism and attack of this sort was actually observed, probably due to the low density of nesting.

One cause of chick mortality was found to be due to attack by the shepherd's dogs (some egg predation is also thought to have occurred in a like manner), the dogs being on the marsh usually three times a day and not always under the strictest control.

7.2. Variation in chick mortality with season.

Variation in chick mortality with season may be seen to be significant (table 20), the survival of chicks being greater at the beginning of the season than later in the season (regression line of Fig. 14). This correlates well with the hypothesis that older adults tend to breed at the beginning of the season with a higher degree of success than the younger birds, which breed later in the season.

At the end of the season there is a reversion to a high percentage of chick survival. This increase in success has been alluded to in section four and the increase in chick survival may be directly related to the increased size of eggs laid in this period. This period represents an end of season recovery of breeding success. The factors accounting for this success are not clear but it is con-

Table 20. Variation in chick survival with respect to laying date. (expected values in parenthesis).

	Days from start of season					
	0	7	14	21	28	total
Number of chicks dying	50 (57.40)	62 (62.14)	39 (34.15)	32 (25.62)	2 (5.69)	185
Number of chicks surviving	71 (63.60)	69 (68.86)	33 (37.58)	22 (28.38)	10 (6.31)	205
Total	121	131	72	54	12	390
Percentage survival	55.9	52.7	45.8	40.7	83.3	52.6

$\chi^2 = 10.69$ degrees of freedom 4 $P < 0.05$.

Figure 14

Graph showing seasonal variation in percentage chick survival.

Ignoring the value at 28 on the grounds of interference by relaid clutches, the regression line of the first four points shows a significant decrease in chick survival with laying date, $y = -0.75x + 56.65$

$r = -0.991 \quad P < 0.01$.

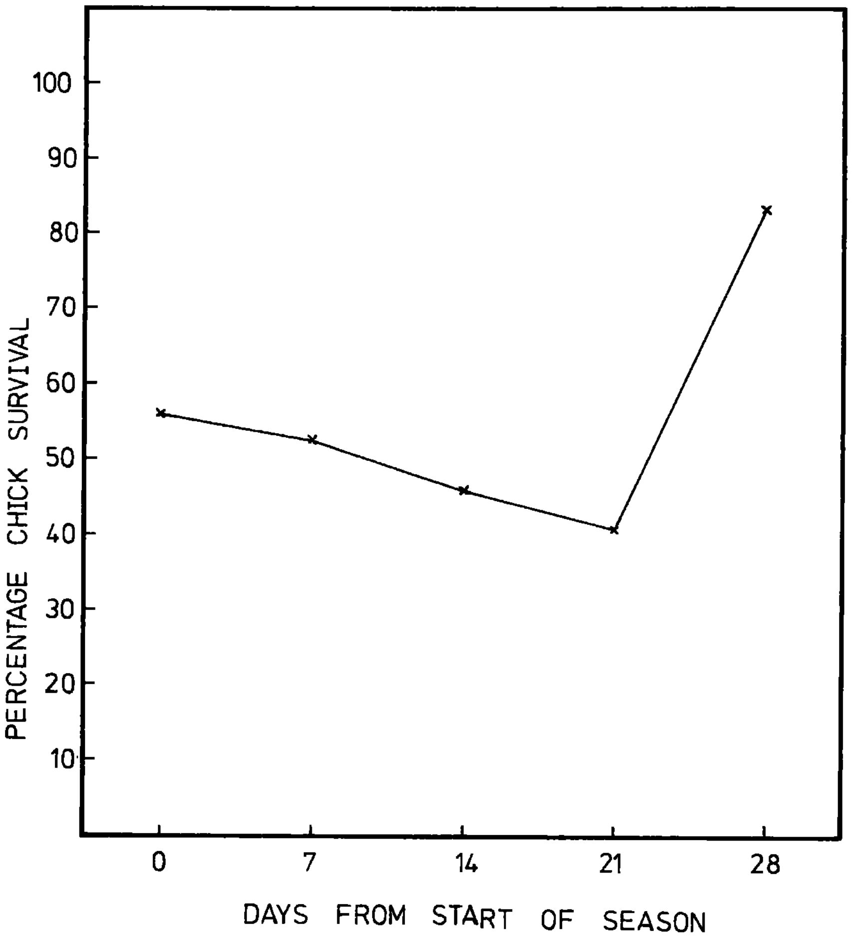

PERCENTAGE CHICK SURVIVAL
100
90
80
70
60
50
40
30
20
10
0
7
14
21
28
DAYS FROM START OF SEASON

Table 21. Variation in chick mortality with respect to age of the chick. (expected values in parenthesis).

	Age classes (days)						
	Dead in shell	0 - 2	2 - 4	4 - 6	6 - 8	8 - 10	total
A - chick							
Number dead	2 (8.89)	3 (8.78)	11 (8.62)	14 (8.02)	15 (7.25)	3 (6.44)	48
Number alive	161 (154.11)	158 (152.22)	147 (149.38)	133 (138.98)	118 (125.75)	115 (111.56)	832
Number at risk	163	161	158	147	133	118	880
Percentage mortality	1.2	1.9	7.00	9.5	11.3	2.5	5.5
	χ^2 = 25.81 degrees of freedom 5 $P < 0.001$						
B - chick							
Number dead	4 (7.32)	5 (7.11)	7 (6.85)	11 (6.48)	11 (5.91)	1 (5.33)	39
Number alive	136 (132.68)	131 (128.88)	124 (124.15)	113 (117.52)	102 (107.09)	101 (96.67)	707
Number at risk	140	136	131	124	113	102	746
Percentage mortality	2.9	3.7	5.3	8.9	9.7	1.0	5.2
	χ^2 = 13.9 degrees of freedom 5 $P < 0.02$						

Continued

Table 21. Continued

		Age classes (days)					
	Dead in shell	0 - 2	2 - 4	4 - 6	6 - 8	8 - 10	total
C - chick							
Number dead	9 (10.74)	5 (9.87)	10 (9.39)	18 (8.44)	9 (6.71)	0 (5.85)	51
Number alive	103 (101.26)	98 (93.13)	88 (88.61)	70 (79.56)	61 (63.29)	61 (55.15)	481
Number at risk	112	103	98	88	70	61	532
Percentage mortality	8.0	4.9	10.2	20.5	12.9	0.0	9.6

χ^2 = 22.3 degrees of freedom 5 $P < 0.001$

All chicks							
Number dead	15 (26.54)	13 (25.58)	28 (24.75)	43 (22.96)	35 (20.21)	4 (17.97)	138
Number alive	400 (388.46)	387 (374.42)	359 (362.25)	316 (336.04)	281 (295.79)	277 (263.03)	2,020
Number at risk	415	400	387	359	316	281	2,158
Percentage mortality	3.6	3.3	7.2	12.0	11.1	1.4	6.4

χ^2 = 54.28 degrees of freedom 5 $P < 0.001$

sidered here that the main reason for its existence is due to the high proportion of relaid clutches of the older adults of the early part of the season which had been subjected to predation and flooding at the time of their laying.

This is not, however, the only reason for the increased survival, as a large proportion of the eggs at 28 days from the start of the season are of smaller volume than earlier in the season. These eggs must, therefore, have greater potential for producing viable offspring, thus a change in physiology towards the end of the season is evident.

7.3. Variation in chick mortality with the age of the chick.

Table 21 shows that there are significant differences in the mortality of chicks in different age classes, mortality becoming highest between the ages of 2 - 8 days, coinciding with the time at which chicks tended to wander away from the nest.

Chicks become harder to find as they wander away from the nest, hence it is probable that difficulty in finding chicks in the age group 4 - 8 days results in the erroneous recording of chick mortality when the apparent mortality resulted from failure to find an extant chick.

The mean age of maximum mortality in A -, B- and C - chicks is not statistically different, but a trend towards a higher mortality rate at a younger age in the C - chick can be seen.

Table 22. Mean age at which maximum mortality occurs.

(means ± one standard error)

	A - chick		B - chick		C - chick
Mean age of maximum mortality (days)	5.02 ± 0.91		4.48 ± 0.98		4.04 ± 0.98
t		← 0.29 →		← 0.22 →	
			← 0.52 →		
p		NS		NS	
			NS		

7.4. Variation in chick mortality with laying sequence.

Table 23 shows the variation in mortality of chicks (regardless of age) with regard to laying sequence. The significant difference shown here shows that the C - chick suffers a higher mortality than its siblings.

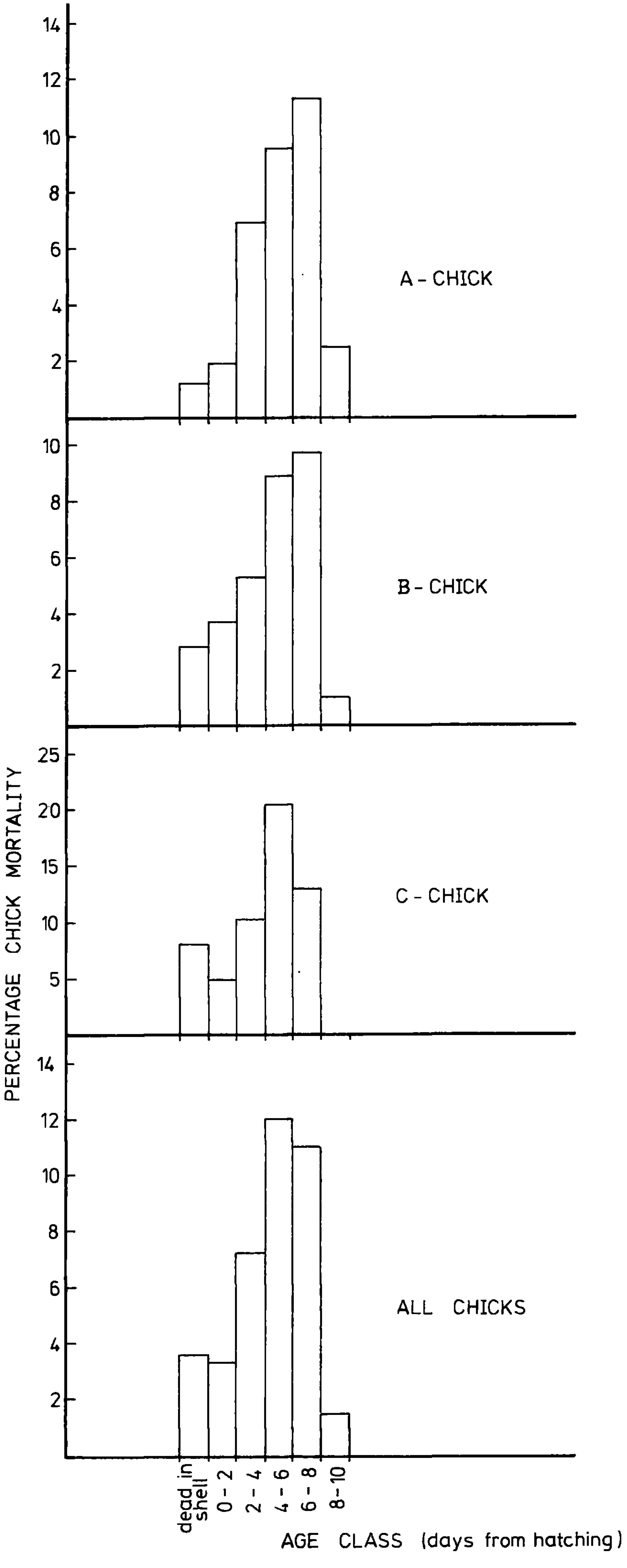
Table 23. Variation in chick mortality with respect to laying sequence. (expected values in parenthesis)

	A - chick	B - chick	C - chick	Total
Number of chicks died within the first week of life	48 (54.20)	39 (46.55)	51 (37.24)	138
Number of chicks survived	115 (108.80)	101 (93.45)	61 (74.76)	277
Total	163	140	112	412
Percentage mortality	29.4	22.1	45.5	33.6

$\chi^2 = 10.514$ degrees of freedom 2 $P < 0.001$

Figure 15

Histograms of percentage chick mortality at various age classes of chicks. Regression lines of egg volume on egg weight and weight of components on egg weight, used in the calculation of the calorific value of albumen and yolk content of eggs of various volume classes (from Parsons 1971).


14
12
10
8
6
4
2
A - CHICK
10
8
6
4
2
B - CHICK
25
20
15
10
5
C - CHICK
PERCENTAGE CHICK MORTALITY
14
12
10
8
6
4
2
ALL CHICKS
dead in shell
0 - 2
2 - 4
4 - 6
6 - 8
8 - 10
AGE CLASS (days from hatching)

The third chick of a clutch is generally last in the peck order and thus liable to receive less food than its siblings. Hence it would be supposed that it is more susceptible to starvation and consequent death. It has already been shown, however, (section six) that the C - chick exhibits the same or even greater rate of growth than the A - and B - chicks, and thus food shortage as such must not be the only factor influencing the higher mortality in the C - chick.

A - and B - chicks hatch more or less synchronously with the C - chick hatching generally some time later (often one to two days). Chicks are brooded by the adults during the adverse weather conditions, and it is proposed here that since the A - and B - chicks hatch first, they are larger and demanding relatively more food than the C - chick at the time of C - chick emergence. Since the parent must then spend a greater amount of time away from the nest site in search of food, at this time, the full clutch cannot be brooded as efficiently as the first two chicks. The young C - chick is more susceptible to wetting and chilling than its elder siblings which have developed more waterproof down. Such chilling of the C - chick is thought to be one of the primary reasons for causing differential mortality with respect to hatching sequence.

7.5 Chick production in the colony as a whole.

Table 24 summarises the variation in chick production per pair of nesting birds in the colony with respect to the date of commencement of egg laying.

Table 24. Chick production per pair with respect to laying date.

	Laying date (days from start of season)					
	0	7	14	21	28	total
Number of nests allowed to develop	100	101	70	54	12	337
Number of eggs allowed to develop	211	228	176	113	30	758
Number of eggs predated	56	57	45	36	5	199
Number of eggs incubated	155	171	131	77	25	559
Number of chicks surviving eight days	71	69	25	15	7	187
Actual number of offspring per pair	0.71	0.68	0.36	0.33	0.58	2.66
Potential number of offspring per pair (I)	1.55	1.69	1.87	1.43	2.08	8.62
Percentage success	45.80	40.25	19.25	23.07	27.88	30.85
Potential number of offspring per pair (II)	2.11	2.26	2.51	2.09	2.50	11.47
Percentage success	33.64	30.08	14.34	15.78	23.20	22.22
Difference in percentage success	12.16	10.17	4.90	7.29	4.68	8.63

Potential offspring per pair (I) refers to physiological potential number of offspring produced per pair, i.e. the number of offspring produced per pair from incubated eggs. Potential offspring per pair (II) refers to the overall potential number of offspring per pair, i.e. overall breeding success. The difference between these values is due to the effect of egg predation.

It may be seen that the gradual decrease in number of offspring as the season progresses is due to a gradual decrease in the ability of incubated eggs to develop to viable chicks. This is a reduction in the physiological aptitude to produce viable offspring. Again the recovery in the last season section is shown to be due to an increase in physiological chick production and not merely an effect due to reduced egg predation at the latter end of the season.

The mean number of offspring produced per pair over the whole season is 0.563 ± 0.078 (means ± one standard error). With an estimated population of 1,700 pairs of gulls nesting at Rockcliffe Marsh the total number of chicks produced is about 957, a 56 per cent increase in the population (ignoring adult mortality).

SECTION EIGHT.

FOOD RESOURCES OF THE COLONY

8.1. Introduction.

Lack (1954) proposes that clutch size in birds is adapted to correspond to the largest number of young for which the parents can, on average, provide enough food. He attributes seasonal variation in clutch size (where two broods are reared in a given year) to the abundance of food in that year.

The importance of availability of sufficient quantity and quality of food to the survival of young prompted investigation of food resources of the colony.

8.2. Composition of the food of chicks.

Collinge (1925) shows that the food composition of adult herring and lesser black-backed gulls is similar, 50 - 80% of the food being composed of fish and molluscs, and 20 -25% of insects, with herring gulls consuming, on average, a larger proportion of vegetation than the lesser black-backed gulls. The high proportion of fish in the diet of gulls is supported by data from Pearson (1968).

Collinge gives the analysis of stomach contents for twenty five herring gull chicks as consisting of 75% insects, 9% earthworms and the rest of fish, molluscs and miscellaneous animal matter (no data is given for lesser black backed gull chicks). Analysis of food vomited by chicks at Rockcliffe Marsh is given in table 26.

Table 25. Percentage composition of the food of herring and lesser black-backed gull chicks by analysis of vomited food remains. (Percentage refers to the number of chicks of the total which exhibited the food as the only or major constituent in the crop at the time of sampling.)

	Food type	Percentage
Lesser black-backed gull	Earthworms	62
(n = 39)	Fish	18
	Offal and insects	20
Herring gull	Earthworms	67
(n = 6)	Fish	33
	Offal and insects	0

(In only 8 (18%) of the samples did the sample contain more than one type of food in the above categories).

Offal consisted mainly of bread and various mammal remains, e.g. ribs and vertebrae (these may have been bones of moles, of which, a number of entire specimens were found around nests, a mole catcher being employed by the estate at this time and his kill often adorned nearby fences, a ready supply for the gulls). Insect remains included beetle larvae, adult tipulids and adult beetles. An entire skylark chick was regurgitated by one lesser black-backed gull chick.

8.3. Direction of flight of gulls in search of food.

Counts were made of the proportions of herring and lesser black-backed gulls flying seaward (westward) and landward(eastward) from the colony. Four hour observation periods were made at a similar time of day, under similar weather conditions, on two occasions. The ratio of herring gulls to lesser black-backed gulls flying landwards was 1 : 7 and that for flying seawards 1 : 3 (sample sizes of 226 and 174 birds respectively), which shows that herring gulls fly, prefertially, seawards. Such a finding correlates with those of various authors who propose that the herring gull is a more marine gull than the lesser black-backed gull.

Pearson (1968) calculated the feeding range of herring gulls at about 30 miles (with respect to the speed of flight and the time spent away from the nests during the search for food). Reference to Fig. 1 shows that the area enclosed by a circle of 30 miles radius around the colony consists largely of land, even west of the marsh. Hence it may be stated that although birds fly in a westward direction they cannot be considered as birds feeding at sea, as it is probable that they too are feeding on pastures, accounting for the high proportion of earthworms in the diet.

Similarly it cannot be said that all birds counted were actually flying in that specific direction to feed, as many individuals flying seaward were found to be loafing on sandbanks in the Solway Firth.

It was interesting to note that most gulls flying inland tended to follow the course of the river Eden back towards Carlisle.

SECTION NINE.

DISCUSSION

Seasonal variation in breeding success has been cited by various authorities for a variety of species of birds (Lack 1954, Coulson 1968 in kittiwakes, Parsons 1971 in herring gulls). Similarly various explanations have been put forward to account for such variation. In the kittiwake the major factors contributing to differential seasonal breeding success are the age of the female and spatial relationships to other birds in the colony, the latter also being a function of age and time of return to the nesting site. Parsons attributes much of the lack of success of chicks to the presence of cannibalistic gulls in the colony and the aggression of adults against chicks from neighbouring nests, which stray into the adult's terriroty.

Some degree of extrapolation of these results may be applied to the colony considered here, but reservations must be made on the use of data directly related to the social system of colonies, since the Rockcliffe Marsh colony is of low density and thus a different social system must exist than that, for example, of Parson's dense herring gull colony. Variation in the breeding success of the colony may, however, be attributed to some factors shown to affect other colonies.

Variations in age structure of the population at different times during the season were not measured, but data from other species (kittiwake, Coulson 1963; gannet, Nelson 1966; shag, Coulson et al. 1969) and the same and similar species (herring gull, Parsons 1971; red-billed gull, Mills 1973) at different sites, showing that a progressive decrease in egg volume with season is a direct function of the age composition of the population, allows the conclusion to be made that this colony conforms, with older birds breeding early in the season and younger birds breeding later in the season.

With such low density of nesting it was not possible to demonstrate that site selection for positions in the centres of social systems, giving higher breeding success, occurred, as has been suggested in the kittiwake (Coulson and White 1958, Coulson 1968), grey seal and shag (Coulson 1971). The colony here could not be considered as a single social unit due to the large area it covered and the non-homogeneous distribution of birds within this area. Variation in hatching success during the season correlates closely with the variation in egg volume (as demonstrated by Paludan 1951, Harris 1964 and Parsons 1971 with respect to the third egg). A minimum egg volume required to produce a viable chick has been estimated by extrapolation to be in the region of 50 cm^3. Eggs of the species considered here are rarely found of such small size since the hatching success of eggs below about 60 cm^3 becomes less than 50%. A tendency to a decrease in hatching success also occurs in eggs over about 80 cm^3 in volume. Evolutionary genetic selection against laying extremely small or large eggs, resulting in the normal frequency distribution of eggs laid about the range of 60 cm^3 to 90 cm^3 has been shown to be possibly due to selection against inefficient energy utilisation. It is shown here that it is energetically more efficient to use a little more energy to produce an egg of this size range as opposed to a smaller egg, with a substantial reduction in the energy wastage due to the non hatching of eggs of low volume.

There is no variation in growth rate of chicks at different times during the season, but a seasonal trend of decreased survival with season is shown.

An interesting phenomenon of recovery from progressively decreasing chick production with season may be seen at the end of the season where there is a sudden increase in the production of viable offspring. Such an increase may be partially explained by the increased incidence of relaid clutches of older birds which suffered egg predation and flooding during the early part of the season. These relaid clutches therefore have larger eggs than those of birds normally nesting at that time and, therefore, greater hatching success and chick survival. This does not entirely explain the phenomenon, and it is evident that there is some physiological change at the end of the season allowing for higher chick production from these eggs of small volume than that of small eggs preceding this period. An influx of good quality young breeding birds into the colony at this time may also be part of the reason, but with no data relating to age composition of the adults in the colony no conclusive evidence of its occurrence may be shown. Weather conditions were also moderably stable during this part of the season and no excessively damp or cold spells would account for variability in chick survival during weekly periods. Weather conditions during the whole season tended to alter from day to day rather than on a period basis.

As in Parson's colony the incidence of egg predation declined as the season progressed, this may be attributed to the higher proportion of non breeding birds at the beginning of the season than later in the season. Despite this high predation in the early part of the season, the production of chicks per pair in the beginning of the season is still higher than that expected, and later in the season chick production per pair is lower than that expected.

The food resources for a gull colony are important in determining the number of offspring reared per pair (Lack 1954). With the recent increase in the number of exposed refuse tips in the country, particularly around large towns, it is thought that there is an adequate supply of food for such gull colonies and a reason for their increase in size. It is shown in this study that the major food resource of the colony is earthworms. Such findings are contrary to those of Collinge (1925) and Pearson (1968) who show that the major proportion of the diet of herring and lesser black-backed gulls is fish. The high proportion of earthworms in the diet of the Rockcliffe Marsh colony may be directly related to the somewhat land-locked location as compared with that of the Farne Islands (Pearson 1968).

Variations in size and shape of eggs and differential survival of chicks with respect to laying sequence in a clutch have been subjected to detailed study (Paludan 1957, Harris 1964, Parsons 1971, Mollart 1972 in the Laridae and Gemperle and Preston 1955 in the common tern), showing that the c - egg is smaller and of different shape index than the first two eggs of a clutch and that the resultant chick suffers a high mortality than its conspecifics. Similar conclusions have been drawn from the data presented here.

SUMMARY

1. The variation in breeding success of herring and lesser black-backed gulls in a low density mixed species colony at Rockcliffe Marsh, Cumberland, was studied.

2. A significant 8% decrease in egg volume with respect to laying date is demonstrated, the c - egg volume decreasing significantly less rapidly than the a - and b - eggs (8.7% decrease in a plus b eggs and 7.0% in the c - egg). This decrease is attributed to the age composition of the colony at different times during the season.

3. Birds were found not to relay clutches when the full clutch was removed as soon as possible after the laying of the third egg, an unusual occurrence for these species.

4. Predation was primarily directed at the a - egg, the incidence of overall nest predation declining from 33% to 2% as the season progressed.

5. There was no variation in hatching success with respect to the laying sequence, clutch size or season, but hatching success is positively correlated with egg volume up to about 80 cm^3 of egg volume and then showing a tendency for the percentage of larger eggs hatching to decline.

6. The frequency distribution of eggs about the volume range of 60 cm^3 to 90 cm^3 is postulated to be due to genetic selection against energy wastage of non-hatching eggs outside this range.

7. In the estimation of chick growth, tarsus length was found to be a more stable parameter than wing or mid-toe length.

8. No variation in growth rates of chicks with respect to laying sequence was found, although the c - chick is significantly smaller than its siblings (at the same age) during the first week of life.

9. No variation in chick growth was found with variation in season or clutch size, postulating that there is adequate food for each member of the clutch to allow the maximum physiological rate of growth.

10. Chick mortality is shown to occur significantly in excess of that expected between the age of four to eight days from hatching (11 - 12%) than at other age groups (2 - 7%), being correlated with time at which chicks tended to leave the nest site.

11. There is no significant difference in the mean age of maximum mortality of chicks with respect to laying sequence, but the c - chick suffered significantly greater mortality than its siblings (percentage mortality of a, b and c - chicks being 29%, 22% and 46% respectively).

12. The number of viable offspring produced per pair declined as the season progressed, except for a sudden recovery in chick production from small volumed eggs at the end of the season.

13. The food resources of the colony consisted mainly of earthworms (62%) with low percentage composition of fish and offal (20% and 18% respectively).

APPENDIX I. List of species and their latin names used in the text.

Carrion Crow	*Corvus c. corone* Linnaeus.
Barn Owl	*Tyto a. alba* Scopoli.
Gannet	*Sula bassana* (L.).
Gull Black-headed	*Larus r. ridibundus* L.
Herring	*L. argentatus* Pontoppidian.
Lesser black-backed	*L. fuscus* L.
Red-billed	*L. novaehollandiae scopulinus* Forster.
Kestrel	*Falco t. tinnunculus* L.
Kittiwake	*Rissa tridactyla* (L.)
Oystercatcher	*Haematopus ostralegus occidentalis* Neumann
Shag	*Phalacrocorax aristotelis* (L.)
Skylark	*Alauda a. arvensis* L.
Sparrow Hawk	*Accipiter n. nisus* (L.).
Tern Common	*Sterna hirundo* L.

Fox	*Vulpes vulpes* (L)
Hedgehog	*Erinaceus europaeus* L.
Mole	*Talpa europaeus* L.
Stoat	*Mustela erminea* L.
Seal Grey	*Halichocrus grypus* (Fabricius).

Herring	*Clupea harengus* L.

Creeping fescue	*Festuca rubra* L.
Rushes	*Juncus* spp.
Scurvy grass	*Cochlearia officinalis* L.
Sea milkwort	*Glaux maritima* L.
Sea poa	*Puccinellia maritima* (Huds.)
Sedges	*Carex* spp.
Thrift (Sea Pink)	*Armeria maritima* (Mill.).

APPENDIX II

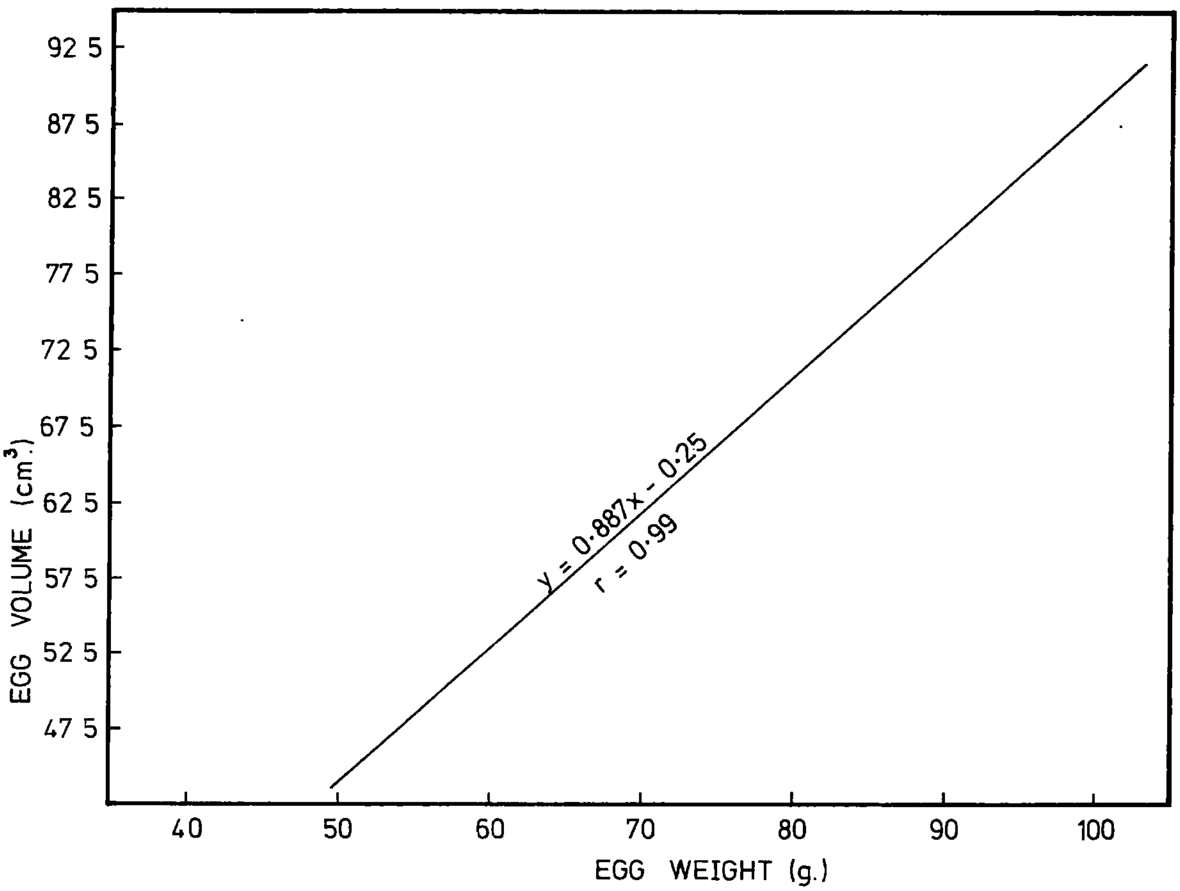
Determination of the calorific values of yolk and albumen per egg at various egg volumes, using regressions of egg volume on egg weight and weight of egg components on egg weight from Parsons (1971). Calorific values of 3.48 k.cal. g^{-1} for yolk and 0.51 k.cal. g^{-1} for albumen were used (Altman and Dittmer 1968).

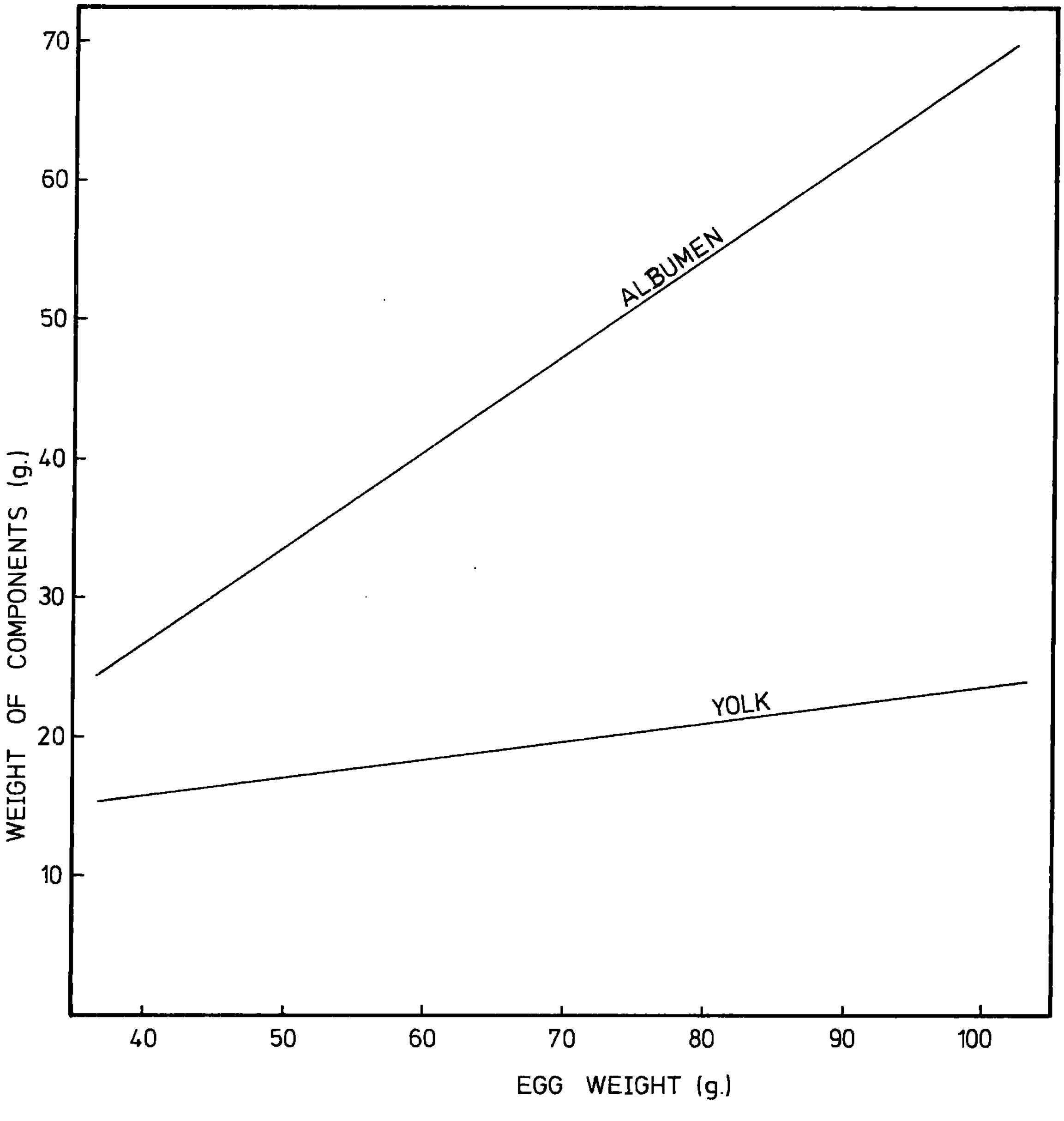
Table 26. Calorific values of yolk and albumen contents of eggs of differing volume.

Egg volume (cm^3)	Egg weight (g)	Yolk weight (g)	Calorific value of this weight of yolk. (k.cal).	Albumen weight (g)	Calorific value of this weight of albumen (k.cal).	Total calorific value (k.cal).
52.5	59.50	18.25	63.51	40.20	20.50	84.01
57.5	65.25	19.00	66.12	44.00	22.40	88.56
62.5	70.75	19.75	68.73	47.75	24.35	93.12
67.5	76.50	20.70	72.04	51.75	26.39	98.43
72.5	82.00	21.25	73.95	55.75	28.43	102.38
77.5	87.50	22.00	76.56	59.50	30.35	106.91
82.5	93.25	22.75	79.17	63.25	32.26	111.43
87.5	98.80	23.50	81.78	67.25	34.30	116.08
92.5	104.50	24.25	84.39	71.25	36.34	120.73

Figures 16 and 17

Regression lines used in the calculation of the calorific value of eggs (from Parsons 1971).


92 5
87 5
82 5
77 5
72 5
67 5
62 5
57 5
52 5
47 5
EGG VOLUME $(cm^3.)$
y = 0·887x - 0·25
r = 0·99
40
50
60
70
80
90
100
EGG WEIGHT (g.)


70
60
50
40
30
20
10
WEIGHT OF COMPONENTS (g.)
ALBUMEN
YOLK
40
50
60
70
80
90
100
EGG WEIGHT (g.)

APPENDIX III

Statistical methods employed in the analysis of data.

Statistical methods used follow those of Bailey (1959).

Standard deviations and standard errors were calculated for means using conventional formulae.

Significance tests of differences between pairs of values were made by use of Student's t - test, using the following formulae:-

$$t = \frac{\bar{x}_1 - \bar{x}_2}{(s/\sqrt{n}\,)_1 + (s/\sqrt{n}\,)_2}$$

Where $t > 1.96$ is significant at the 5% level of significance.

Tests for homogeneity of results were carried out by the use of χ^2 - tests in the form of an n X 2 contingency table (such tables, including expected values, are drawn up in the text). Probabilities of significant deviations from a homogeneous distribution for given ^{2} values are found by consulting statistical tables, the number of degrees of freedom used being (r - 1) (c - 1) (where r is the number of rows and c the number of columns of the contingency table).

Correlations and linear regressions were calculated by the use of an Olivetti computer, giving the correlation coefficient (r) and the equation of the line in the form:

$$y = a + bx$$

The degree of significance of goodness of fit of the line to the given array was calculated using the formula:

$$t = \frac{r\sqrt{n - 2}}{\sqrt{1 - r^2}}$$

The probability of this value of t, with n - 2 degrees of freedom was estimated from statistical tables.

The degree of significance of the difference in slope of two regression lines (Fig. 5) was calculated by use of the following formula:

$$t = \frac{b_1 - b_2}{\sqrt{\frac{Syx_1^2}{n} + \frac{Syx_2^2}{n}}}$$

Where Syx_1^2 is the variance of $\bar{x}$, and Syx_2^2 is the variance of $\bar{x}_2$.

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