The breeding biology of the Herring gull (larus argentatus)

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How to cite:

Parsons, Jasper (1971) The breeding biology of the Herring gull (larus argentatus). Doctoral thesis, Durham University.

The Breeding Biology of the Herring Gull
(*Larus argentatus*)

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Being a thesis presented in candidature for the degree
of Doctor of Philosophy in the University of Durham 1971

ACKNOWLEDGMENTS

This research was carried out at the University of Durham and was supported by a Science Research Council Studentship. My thanks are extended to Professor D. Barker for allowing me to use the facilities of the Department of Zoology.

I am particularly grateful to Dr. J.C. Coulson for his supervision, encouragement and assistance.

The field research took place on the Isle of May, Scotland, and I wish to thank the Isle of May Bird Observatory Committee and the Nature Conservancy for their help, especially Miss Nancy Gordon, Mr. A. Macdonald, Mr. I. Munro, and Dr. W.J. Eggeling.

Life on the island was made particularly enjoyable by the humour, patience and kindness of the Northern Lighthouse Keepers, of whom I must mention and thank Mr. and Mrs. A. Dundas, and Mr. and Mrs. J. Crawford (not forgetting Glen the Cairn terrier). I am also grateful to Mr. J. Smith and Mr. B. Meldrum of the "Breadwinner" for passage and communication to and from the island.

Much of the field-work could not have been carried out without the help given by Miss Felicity Grammer, Mr. K. Laughlin, and Mr. N. Bell, to whom I am indebted, and I gratefully appreciate the willing assistance given by many visitors to the Low Light.

I also thank my father for reading, and Mrs. Ruth Ashton for typing, the manuscript; Mr. R. Piper for preparing the photographs; and the Ministry of Agriculture, Northern Ireland, for various facilities that assisted the completion of this thesis.

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The Breeding Biology of the Herring Gull
(Larus argentatus)

Abstract

The Herring Gull (Larus argentatus) breeding population on the Isle of May, Scotland, has been increasing at an annual rate of 13.3 per cent since 1907 when the first pair to nest were recorded. The breeding biology was studied from 1966-1969 to ascertain the relationship between nesting success and the timing of the breeding season in a species with an apparently favourable food supply.

It was possible to extend the breeding season by widespread egg removal in various sub-colonies causing re-laying until mid-July. Clutch-size and egg-size in the control areas decreased through the season, and continued to do so in the delayed areas. However, hatching success and pre-fledging mortality were correlated with nesting synchronisation rather than the time of hatching. Predation, and particularly cannibalism, were the primary cause of this relationship since cannibals killed a higher proportion of early and late hatched chicks. This creates a selective advantage for laying in the middle of a well defined breeding season. There was little evidence to suggest that late breeding was a disadvantage providing that this delay applied to the group as a whole.

Various aspects of chick mortality indicate a possible difference in the reproductive drive of the adults rather than

an effect of food shortage. The third chick to hatch in a brood suffers a much higher post-hatching mortality than either of its siblings. An egg transfer experiment showed that both the hatching sequence and the comparative smallness of the c-egg contributed to this differential mortality, as egg size and chick mortality are closely correlated. The period between incubation and parenthood involves behavioural changes that some adults find difficulty in executing, and the mortality differences and the incidence of kronism may be examples of this inability of adults to adjust to a complete brood.

SECTION ONE

INTRODUCTION

Most animals in temperate regions breed at a regular time of the year, and indeed this seasonal activity has long been the subject of authors and poets alike. The occurrence of breeding seasons presupposes both a selective advantage of restricting reproduction to a limited time of the year (ultimate factor), amd also a timing mechanism which ensures that breeding takes place at that time (proximate factor).

Rowan (1926, 1938) pioneered the research showing that variations in day length and other features of the environment affect the time and rate of gonad development. The seasonal supply of food ultimately regulates this time of breeding (Baker 1938), whilst the response to these external stimuli are adaptations so that the young are reared at a time when food is generally abundant (Lack 1954). The proximate factor (e.g. day length) may therefore be quite separate from the ultimate factor of food requirements. For example, it is necessary for some bird species to lay eggs at a time when food is not so plentiful in order that their young hatch during the peak of food availability.

Perrins (1970) has recently summarised the evidence for the advantages of early breeding in birds; namely, that more young are raised, but has also shown that the onset of laying in some species is restricted by the physiological state of the female. In other words, the breeding season may be postponed until the female can find enough food to form eggs. However, it is also possible that some species could breed even earlier than they do, and no evidence was forthcoming to suggest that the young of very early breeders do not survive. Therefore Perrins (1970) concluded that there was "an overwhelming advantage in breeding early".

The termination of laying later in the season must involve other stimuli, for it occurs at a time when there is usually enough food for both adults and young. Various phenomena in the breeding biology of birds have been regarded as adaptations to a worsening food supply for the young. For example, the clutch size of nidicolous species is adapted to the largest number of young which the parents can normally raise (Lack 1954), and the reduction in clutch size noted in the Kittiwake* (Coulson & White 1958a), Great Tit (Kluijver 1951) and Oystercatcher (Harris 1967) as the season progresses merely reflects the poorer chance of raising young later in the season (Perrins 1970).

However, seasonal variation in such factors as clutch size, egg size and breeding success may be complicated by a superimposed variation attributable to the age of the female (Coulson & White 1958b, Snow 1958, Coulson et al 1969), and also to the state of the pair bond relationship (Coulson 1966). Nevertheless, although young birds breed later, lay fewer and smaller eggs, and are less successful parents than older birds, this age effect only accounts for a proportion of the total variation observed. There are exceptions, for although later breeding Shags and Kittiwakes of any age group lay smaller eggs

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*Scientific names are listed in Appendix XII.

than do the early breeders (Coulson et al 1969), the Great Tit lays larger eggs as the season progresses; and Perrins (1970) suggested that the birds "which lay early are presumably laying small eggs because they cannot get enough food to lay larger ones and it is more important to lay early than to lay large eggs".

The ultimate factor of food availability, and to what extent it affects the breeding success of late hatching chicks, is questionable in some species and poorly documented in others. A decline in nesting success with date of laying has been observed in the Lesser Black-backed Gull (Brown 1967), Herring Gull (Paynter 1949, Kadlec et al 1968) and Oystercatcher (Harris 1969), but early hatching Black-headed Gulls were also less successful than those hatching within the peak, as the latter suffered less predation (Patterson 1965). Conversely, Harris (1969) found a marked increase in the survival of Herring Gull chicks as the season progressed. Whether laying dates are important in determining the extent of post-fledging survival is not generally known, although no correlation was observed in the Oystercatcher (Harris 1969). An investigation of this nature requires an extensive ringing and recapture programme and a fore-knowledge of the approximate hatching date of the ringed pulli.

It is difficult to determine whether this seasonal decline in nesting success is directly related to food supply or to alternative factors. Not only do young birds breed later and produce fewer fledglings but later breeding birds of any age group may also show a decrease in nesting success (Coulson et al 1969, Perrins 1970). This may indicate a variation in the physiology and quality of the individuals (Coulson 1968), and the poorer breeding success may merely be a result of a lack of parental care irrespective of the state of food availability. Alternatively, if food is limited, these individuals would compete less favourably than others and their offspring, hatching later in the season, would be the first to suffer.

The numbers of many European sea-bird species have increased over the last half century, none more so than the Herring Gull. Eggeling (1960) described the build up in numbers of breeding pairs of Herring Gulls on the Isle of May, Scotland, where there was only one pair in 1907, but 3,000 pairs in 1953 - 1958. Human waste has provided this species with an improved and relatively constant source of food (Hickling 1967), and this has probably created the comparatively low first year and adult mortality it suffers, particularly in the winter months (Harris 1963). The conflicting views concerning the effect of the season on its nesting success may be indicative of the availability of food. Indeed, the survival of chicks from supplemented broods of the Glaucous-winged Gull (Vermeer 1963), Gannet (Nelson 1964), Gannet and Lesser Black-backed Gull (Harris & Plumb 1965) were regarded by Lack (1966) as the result of an unusually favourable food supply at the colonies concerned.

A study was therefore carried out on the Herring Gulls of the Isle of May, Scotland, to investigate in detail the seasonal aspects of the breeding biology. This was to cover not merely normal breeding, but also an experimentally extended season, so that any effects due to the date of laying would be exaggerated. Furthermore, through a large scale colour-ringing programme it was hoped to compare the post-fledging survival of early and late-hatched chicks. As the Herring Gull is capable of re-laying after a lost clutch the season was extended by the removal of clutches in certain areas of the island. However, egg removal produces its own effects which should be separated from any influence the time of laying may have on the breeding biology. It was therefore necessary to examine the size and component parts of re-laid eggs in case the experimentation created an artificial lowering of nesting success.

The availability of food has wider implications than its ultimate effect on breeding seasons, for it is generally accepted that food limits the numbers of most animals. There is, however, some controversy concerning the processes by which this regulation occurs. Lack (1954, 1966) states that food directly limits numbers and that "starvation outside the breeding season is much the most important density-dependent factor in wild birds". In addition, reproductive rates are regarded as being "as rapid as the environment and the bird's capacities allow", and the balance between birth rates and death rates is attributed to density-dependent mortality. An alternative view has been expressed by Wynne-Edwards (1962) who suggested that food indirectly regulates animal numbers, since behavioural mechanisms keep the populations near the optimum level but below the level where overpopulation and starvation would occur. The major difference between these two theories is that the first relies implicitly on natural selection for its ultimate regulation, whereas the second envisages group selection and a socially induced control in population densities.

It has previously been stated that various aspects of the breeding season may indicate the availability of food. However, there are also forms of behaviour that can be related either to a limited food supply, or to a homeostatic mechanism reducing the potential recruitment of the population to the socially induced level. For example, asynchronous hatching is interpreted by Lack (1954) as an adaptation to an unpredictable food supply, reducing the brood-size to the availability of food without jeopardizing the survival of the older young. Likewise, cannibalism may be regarded as the utilisation of an additional source of food (Ashmole 1963). Alternatively, both asynchronous hatching and cannibalism are "adaptations evolved to curb recruitment" by eliminating a surplus offspring (Wynne-Edwards 1962).

The Herring Gull is known to be cannibalistic (Moreau 1923, Paynter 1949, Paludan 1951, Harris 1964, Brown 1967), but whether the chicks hatch asynchronously or suffer a differential mortality is not clear (Paludan 1951, Harris 1964). It therefore seemed worthwhile investigating whether such pre-fledging mortality occurred on the Isle of May and, if so, the limitations it imposes on recruitment and its relationship with the overall food supply.

To summarise, this research was primarily concerned with the relationship between the breeding biology and the timing of the breeding season in a species whose recent population increase indicated a favourable food supply. Whether the population densities and recruitment of the Herring Gull are under a homeostatic control, or merely governed directly by the availability of food presented an additional and related study. The field data were collected during the years 1967-69 inclusive, and also during the pre-fledging period in 1966.

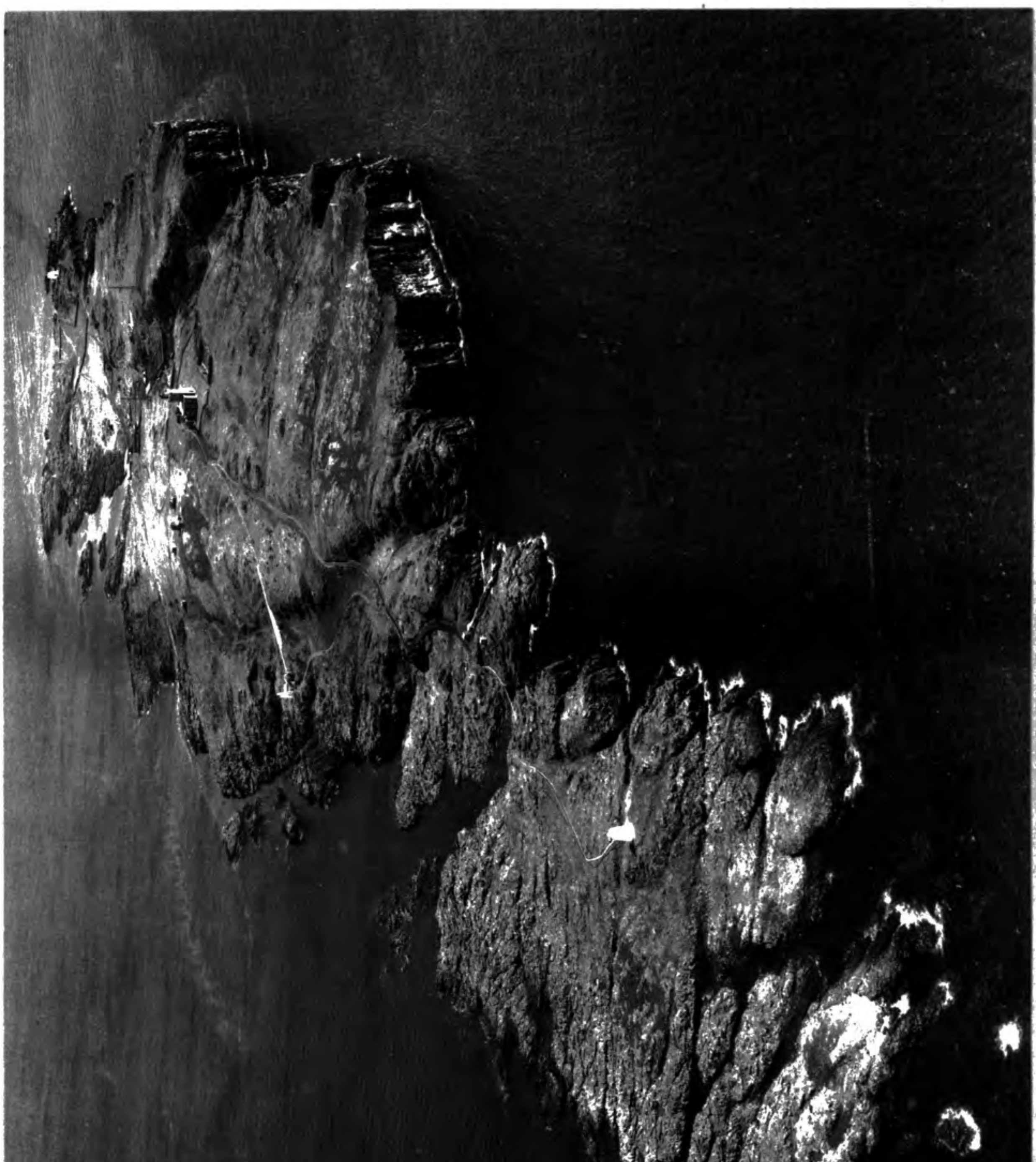


PLATE I. Aerial photograph of the Isle of May.
(kind permission of Aerofilms Ltd.)

SECTION TWO

GENERAL METHODS

2.1 The Study Area

The Isle of May marks the gateway to the Firth of Forth, lying about six miles from the Fife coast to the north, and about ten miles from East Lothian coast to the south (Fig.1) (Nat.Grid.Ref: 655995). With its long axis due north-west south-east, the island is a mile in length and a third of a mile broad, covering an area of 140 acres (Plate 1, Fig.2).

The May is a mass of igneous rock, rising 150 feet out of the sea on the west side, and sloping to sea level on the east. It is part of a single sill of olivine dolerite (greenstone) dating to the Carboniferous age (Walker 1936).

Eggeling (1960) states that the climate of the May is noticeably drier than that of the adjacent coast of the mainland. The average rainfall is less than 22 inches a year, and some of this figure includes spray which can drench the May during gales. Such gales and spray burn the vegetation in the winter causing hardship to the many resident rabbits.

The most abundant of the breeding birds is the Herring Gull. This species has increased progressively and spectacularly from a solitary pair in 1907 to over 14,000 pairs in 1968. Past records show that the Herring Gull colonies were at first confined to the rocky edges of the island. Over the last decade they moved into the more

Figure 1.

South-east coast of Scotland showing the Isle of May

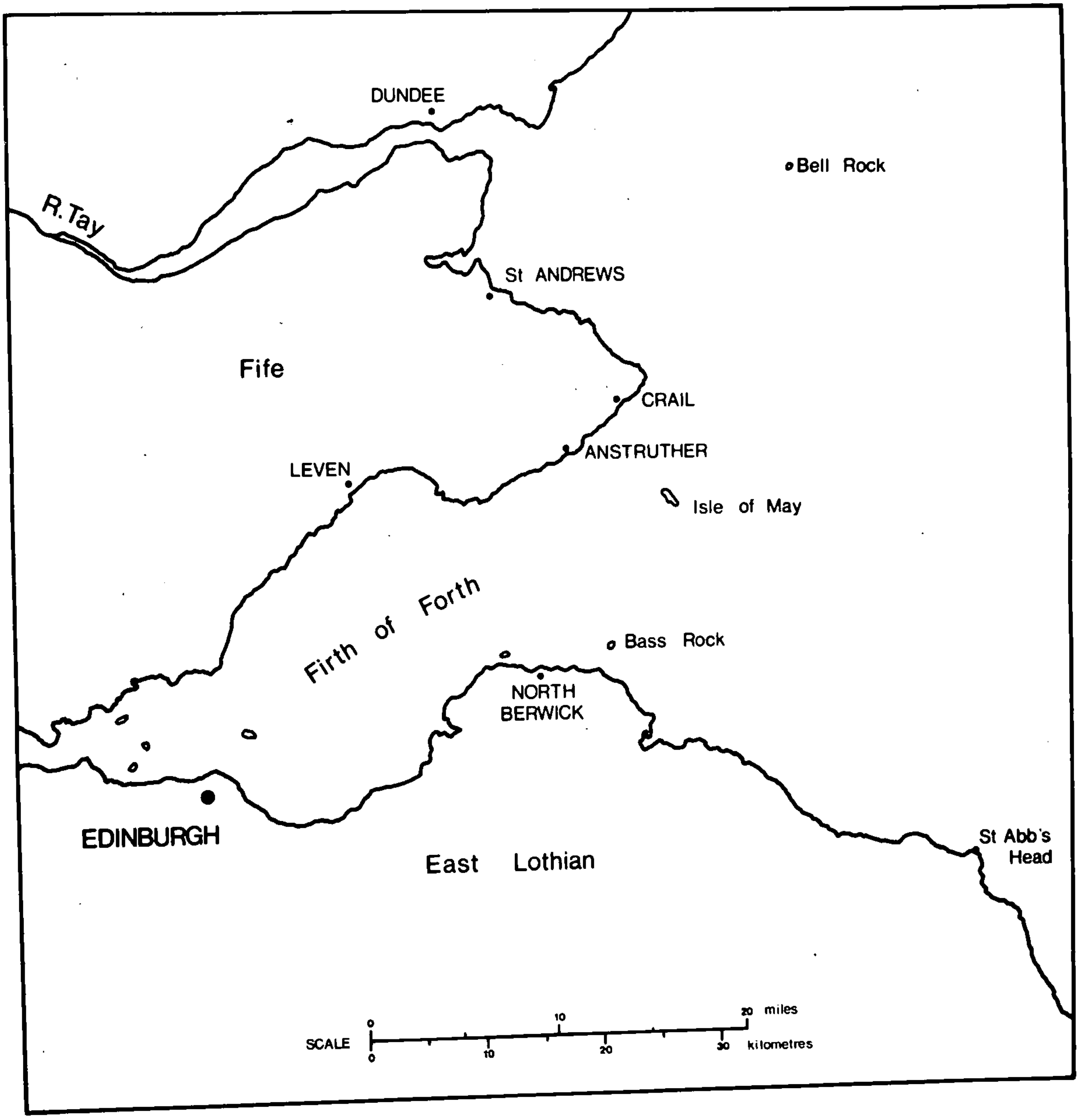
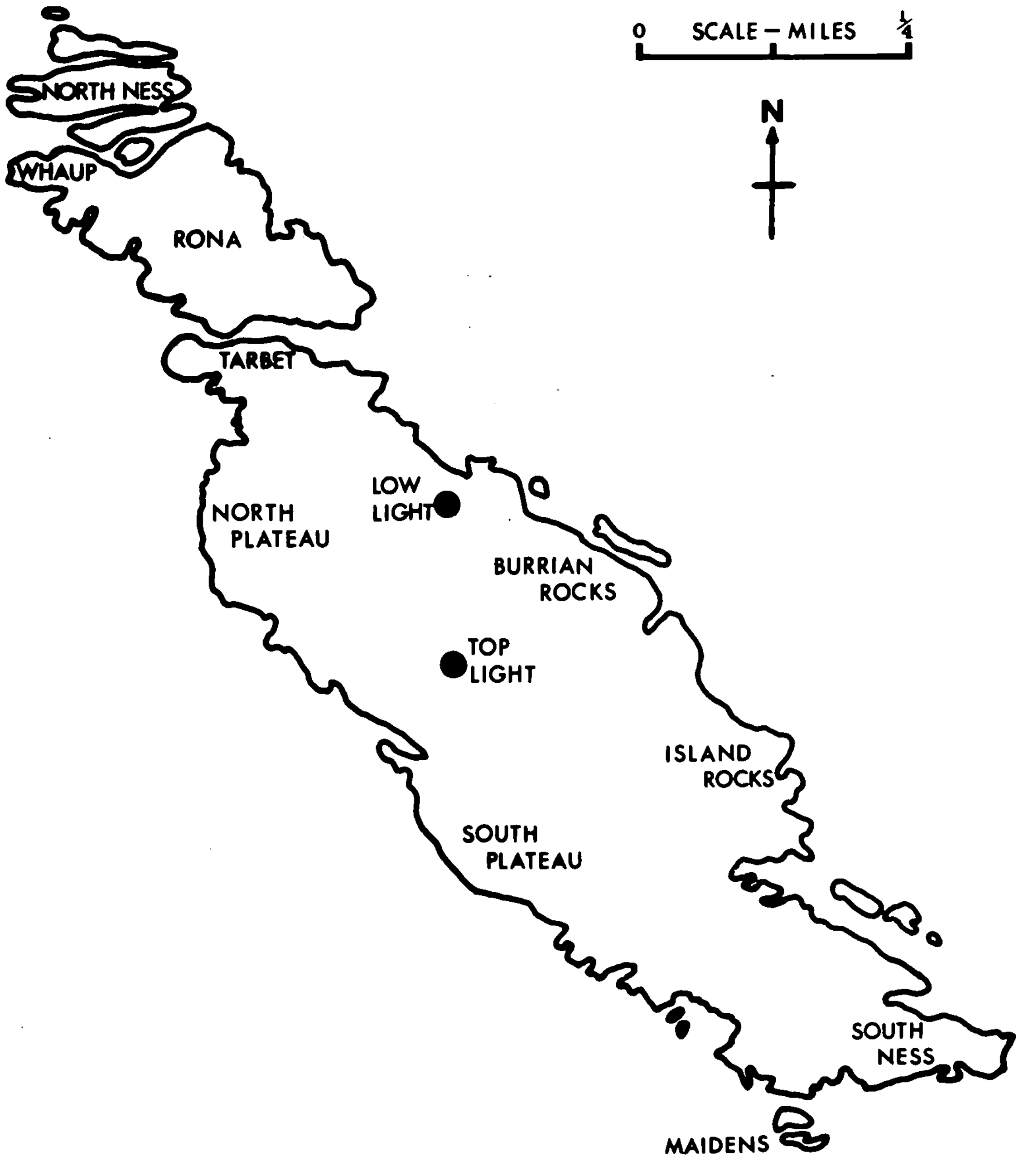

DUNDEE
R. Tay
Bell Rock
St ANDREWS
Fife
CRAIL
ANSTRUTHER
LEVEN
Isle of May
Firth of Forth
Bass Rock
NORTH BERWICK
EDINBURGH
East Lothian
St Abb's Head
SCALE
0
10
20 miles
0
10
20
30 kilometres

Figure 2.

The Isle of May

ISLE OF MAY


0 SCALE – MILES 1/4
N
NORTH NESS
WHAUP
RONA
TARBET
LOW LIGHT
NORTH PLATEAU
BURRIAN ROCKS
TOP LIGHT
ISLAND ROCKS
SOUTH PLATEAU
SOUTH NESS
MAIDENS

central vegetated region and now occupy 65% of the total area of the island. The Lesser Black-backed Gulls are less numerous, totaling 1,500 pairs and forming semi-discrete colonies inland of the Herring Gull nests. Apart from the cliff dwelling Kittiwake, the only other breeding gull is the Greater Black-back whose numbers rose from three (1966-68) to four pairs in 1969.

Several east-west faults cross the island which divide it into convenient working areas. In general the study was restricted to the less vegetated regions. Here, very few Lesser Black-backed Gulls nest, and almost pure Herring Gull colonies are found. A deep fault isolates nearly 22 acres to the north of the island. This area incorporates two regions called North Ness and Rhona (Fig.2, Plate 2), and is reached by a bridge. Therefore, access to it can be somewhat restricted and the nests consequently less disturbed by visitors than elsewhere on the island.

The Isle of May is the property of the Commissioners of Northern Lighthouses. The Bird Observatory and Field Station was established in 1934 and in 1956 the island was declared a National Nature Reserve. Visitors manning the Bird Observatory travel by boat from Anstruther and live in the Low Light. This fixed light, built in 1843-44, ceased to operate when the North Carr Lightship was positioned off Fife Ness. From then onwards it provided accommodation, initially for one of the lighthouse keepers and later for ornithologists.

PLATE 2a. Central area of North Ness sub-colony showing nest sites.

PLATE 2b. View from the north of the Isle of May, showing North Ness control area in the foreground.

2.2 General methods

Marking nests and eggs

All nests in the areas studied were marked with 12 x 1 x 1/4 inch stakes, and numbered by waterproof black felt pens. These pens are the most permanent and serviceable of those tried, and they are also useful for marking eggs (Plate 3). Despite the blotched brown, olive, and dark green colour of the shells, black indelible ink can still be legible at the end of incubation. First, second and third eggs in a brood were numbered before the next egg in the clutch was laid. This increased the accuracy of clutch size measurements. If a solitary unmarked egg is found in a nest which previously contained a marked first egg, it signifies that the first egg was robbed and a second egg laid. Had the first egg been unmarked, no such conclusion could be drawn.

The lengths and breadths of eggs were measured to 0.01mm using vernier calipers, and the fate of clutches under study was followed through to hatching.

Catching Adults

It was necessary to have a reasonable sample of marked adults, to study in particular site tenacity, adult survival and the effects, if any, of continual egg removal. Catching adult gulls is time consuming and it is often difficult to capture specific individuals. The following methods were employed :

PLATE 3a. Clutch of eggs marked according to the sequence of laying.

PLATE 3b. Brood of three chicks soon after hatching.

(i) Dazzling

Large numbers of gulls were dazzled, especially on dark misty nights. However, this operation was restricted to the pre-laying period to avoid breakages and disturbance. The disturbance it causes prevents concentration of ringing to any one area. Perhaps ten gulls can be caught in an area of a thousand pairs before all the birds panic to the sea. Quite soon they learn to leave the island at the flash of a torch.

(ii) Trapping

Funnel-entrance wire traps placed over the incubated nests is a successful means of catching adults. The gull can walk into and out of the cage but, when alarmed, it usually opens its wings thereby preventing its own exit. Such a trap needs to be staked firmly to the ground, an easy procedure on good soil, but almost impossible on rocky areas. The method has other disadvantages, being both laborious and restricted to the incubation period.

(iii) Drugging

Capturing gulls with anaesthetic drugs has advantages over the previous methods described. Firstly, selected individuals can be caught; and, secondly, the degree of alarm caused in the colony is less. Patterson (1965) describes how he successfully used the drug Avertin (tribromoethanol) for catching Black-headed Gulls. As it is a distasteful substance, it was contained in small gelatin capsules which were concealed in pellets of bread and fat.

The recommended dosage of 400-500mg of Avertin per Kg of body weight was in general too small for the Herring Gull. Although there was much variation in the way individuals reacted to a specific dose, 1000mg appeared the most effective quantity. Initially this method was employed late in the season when adults were feeding chicks. This led to the retention, rather than absorption, of the bait and often to the failure of the drug to be effective. When used the following year, just prior to egg-laying, more successful results were obtained.

The baited pellets were placed near particular nests and in this way a small concentration of breeding pairs was caught. The reaction time of the drug varied from 5 to 15 minutes, and the birds remained unconscious for 1 - 4 hours. During this period they were kept warm and constant care was taken to prevent the gull from choking on regurgitated food.

Drugged birds were occasionally mobbed by their neighbours. An unconscious bird would be unmolested, whilst a bird acting strangely would frequently be attacked. Whether chivvied or not, these half drugged adults sometimes flew out to sea, where the drug would complete its effect. For this reason, drugging resulted in a mortality rate as high as 10 per cent.

Marking chicks and adults

All birds caught during this study were ringed with the B.T.O. monel rings (11mm diameter, size G).

In addition, they were marked with colour rings. The latter were used either to distinguish various year classes or to allow identification of individuals from a distance (plate 4).

Colour rings were made from I.C.I. Darvic as described by Coulson (1963). During the four years none of the colours was seen to fade appreciably. All adults caught were marked as individuals, with two colour rings on one leg, and a colour ring over the monel on the other leg. For these, tall Darvic rings were used, made from strips 16 x 75mm.

Chicks were marked with a year class colour only : Red-1966, Yellow-1967, Blue-1968, Black-1969. Various combinations of the monel and colour ring or rings signified the time of hatching in the season. For these, 12 x 95mm strips were cut from the Darvic sheet (1/32 inch thick). Colours used did not overlap with existing ringing schemes on Herring Gulls within 200 miles. Only one colour was employed each year for the chicks. It was felt that mortality based on the finding of rings, often with little carcass remaining, would hold a bias if different colours were used according to the time of hatching. For example, a red ring can attract one's attention more quickly and frequently than a green one.

Marking newly hatched chicks

In most cases, monel rings would not stay on newly hatched chicks until their legs had grown for at least five days. It was imperative to mark chicks at hatching, for a large percentage of pre-fledgling mortality

PLATE 4a. Adult Herring Gull on nest.

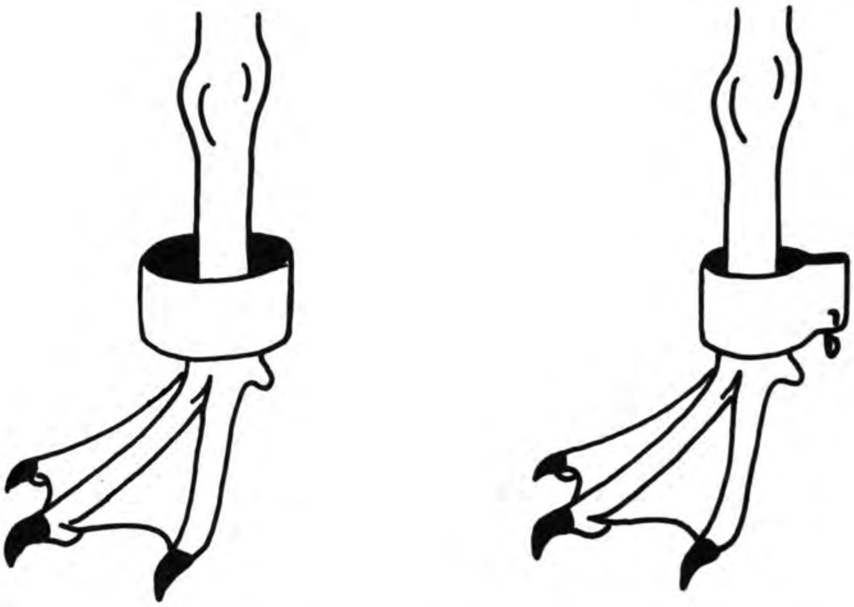
PLATE 4b. Colour-ringed adult Herring Gull.

occurs in the first week; and also it was necessary to differentiate between first, second, and third chicks in a brood. Marshall (pers.comm.) effected a means of marking Eider ducklings by using rings cut from insulating tubing. Although the same internal diameter as the monel ring, they could be slipped over the leg and temporarily held in place with a staple pinching one edge together (fig.3). These rings could later be cut off and replaced by the monel and Darvic rings. If left, the staple quickly rusted and would be pulled apart by the growing leg. The tube would then open to the full diameter without injury or constriction to the bird's leg.

Radio Spares offer a good range of coloured insulating tubing of various diameters, whilst a Bambi stapler was quite strong enough to push through the plastic. It was found that the nest numbers, and other information, could be written on yellow or white tubing by using fine-pointed red felt pens. These figures did not wear off quickly and could even be read on a ring swallowed and regurgitated by a cannibalistic Herring Gull. Therefore, the fate of newly hatched chicks could be followed through to fledging.

Figure 3.

Method of ringing chicks at hatching using insulating tube and staples; and photograph of this method being applied to a Herring Gull chick



METHOD OF RINGING 0-6 DAY OLD CHICKS USING STAPLED INSULATING TUBE

2.3 Delaying the breeding season

Introduction

The Herring Gull is a useful bird to study. It is common to the extent of becoming a pest; and so its eggs can be removed, nests destroyed and the breeding bird generally disturbed without undue public reaction. Furthermore, as a species capable of re-laying after a lost clutch, it lends itself to research on the effects of delayed breeding.

A study of the effects of the season on breeding success should aim to satisfy at least two criteria. Firstly, the length of the breeding season should be maximal. Secondly, any seasonal variability inherent with differences in the age composition of the breeding birds should be eliminated if possible. For instance, a definite correlation is found between the age of the adults and the time of laying in the Kittiwake (Coulson & White 1958b), and many other species. As the Herring Gull also conformed to this pattern (Drost et al 1961), then seasonal variability might only reflect the age structure of the population.

Delaying the breeding season by egg robbing results in the early breeding adults relaying at the same time as the later breeding younger birds. In addition it spreads over a longer period than the three or four weeks recorded in undisturbed conditions, and therefore exaggerates the time factor and perhaps its effects.

Method

In 1967 the island was divided into five experimental areas and three controls, each containing over 500 nests. The breeding season was progressively delayed in the experimental areas by selective removal of eggs (see section 7). The following year, to reach a happy medium between quantity and quality, a single control area was compared with one experimentally delayed area. At the same time, over half of the total nests on the island were robbed generally to delay the breeding season.

Egg removal was obviously a crude method to employ, albeit the only practical one. It presented a number of problems that required studying :

i) The overall ability of the Herring Gull to re-lay.

ii) The percentage re-laying according to the length of time incubating when the clutch was removed.
An inability to re-lay would have caused a reduction in breeding density and its possible effect on chick or egg mortality; furthermore, it would have increased the percentage of natural (unrobbed) late layers in the area under study.

iii) The variation in clutch size with re-laying.

iv) The possible reduction in egg weights or yolk content in re-laid clutches.

SECTION THREE

THE POPULATION

3.1 Population Increase

Introduction

The term population has a broad meaning; islands conveniently lay down their own natural limits and, at the same time, colonial behaviour facilitates the definition of these limits. On the Isle of May, Herring Gulls first bred on the North Ness and the more recent colonisation was at the South Ness. However, despite the spread of gulls from colony to colony and the development of sub-colonies, the May population refers to the breeding pairs in toto.

The measurement of population growth most commonly used is the intrinsic rate of natural increase, $\underline{r}$. It is calculated in terms of absolute time, rather than the length of a generation. Also, exponent $\underline{r}$ is applicable to a population which is expanding at an exponential rate, without density dependent checks. As such it indicates the potential power of increase under the particular regime of mortality and birth rate, within which the measurements are made. Once such a figure is obtained, it is possible to investigate reasons why the regime encourages this degree of growth, what factors contribute most towards it and, if necessary, the control methods most likely to discourage the increase.

Growth of the May population

Various population estimates have been recorded since the first pair were seen to breed on the Isle of May in 1907 (Baxter & Rintoul 1925). Unfortunately, many of these totals are of only certain parts of the island, whilst others fail to state clearly whether nests, pairs of birds, or individuals were counted. Nevertheless, the estimates reproduced in Fig.4 clearly show a geometrical increase resulting in a population of approximately 12,000 pairs in 1967. This value was assessed by counting all the nests in the northern area (over 5,000), and estimating the total by comparison. Furthermore, the ratio of marked to unmarked fledglings was 1:1 near the end of the season at a time when fledging success was calculated to be about 1.0 chicks per pair. Since 6,000 chicks had been ringed, it follows that there was a total of more or less 12,000 pairs of Herring Gulls breeding that year.

Plotting log no. pairs against years (fig.5)

$$y = 0.054x + 0.43$$

when

$$\frac{P_t}{P_o} = (1 + r)^t$$

P1 = No. pairs at time t1
P2 = No. pairs at time t2
t = No. years t2 - t1
r = rate of population increase

the rate of increase of the breeding population on the island is calculated to be 13.3% per year. Although no complete census was attempted in 1968 or 1969, all evidence suggests that this rate of increase has continued. Subjectively, gulls were seen to nest in new areas, encroaching towards the centre of the island. Furthermore, the nests in the study areas grew more dense in both years at a rate comparable to the calculated exponent (Table 1).

The population increase of Herring Gulls breeding on the Isle of May

?

Estimates taken from Eggeling (1960), "Special Notes" - Isle of May Bird Observatory library, and from this study.

Figure 4.

Estimates of the number of breeding pairs

1907 - 1969

Figure 5.

Log. number of breeding pairs

1907 - 1969

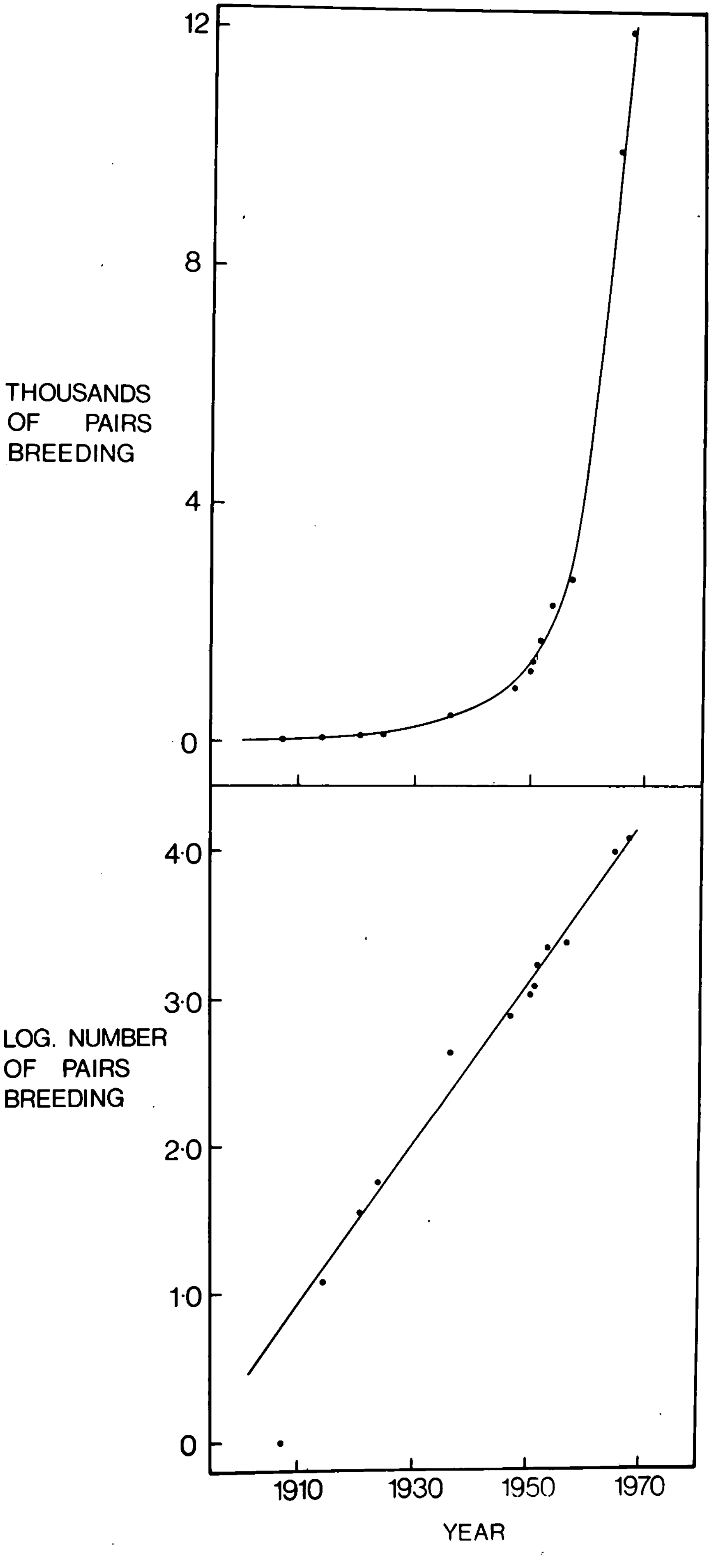

12
8
THOUSANDS OF PAIRS BREEDING
4
0
4·0
3·0
LOG. NUMBER OF PAIRS BREEDING
2·0
1·0
0
1910
1930
1950
1970
YEAR

Table 1. Number of nests in areas of North Ness 1967-1969 and the percentage annual increase

		No. nests	% increase
AREA A	1967	670	
	1968	810	20%
AREA B	1968	186	
	1969	210	13%

Similar records of the breeding pairs of Lesser Black-backed Gulls taken from Eggeling (1960), when plotted on a log scale, show the same increase over more recent years. The rapid rise in numbers from the first pair in 1931 steadied down to a rate of 13% per year, which resulted in a 1969 estimate of approximately 1,500 pairs. This would suggest that the overall conditions are similar for both species despite their behavioural differences.

Comparison with other studies

The Isle of May Herring Gulls, therefore, double their breeding numbers in about six years. Harris (1963) records the numbers of the *Larus* gulls breeding on the Pembrokeshire islands. An analysis of his censuses shows that the Herring Gulls on Skomer and Skokholm up to 1962 had doubled their numbers in 20-25 years. This is a much slower growth rate than either the May or the New England Herring Gull population. In the latter, this species has increased at about 6% per year, doubling every 12-15 years (Kadlec & Drury 1968). It is notable that a comparable average yearly increase of 5.5% is recorded for the Glaucous-winged Gull breeding on Mandrate Island, British Columbia (Vermeer 1963). To summarise, all these populations appear to be increasing. On the May, the rate of 13.3% per year represents the highest growth rate, whilst two species of gulls in Canada are both increasing annually at about 6%. On the west coast, the gull colonies on the Pembrokeshire islands were increasing at 3-4 per cent per year. Over the last ten years this rate has more than doubled to 8-10 per cent (Harris pers.comm.) which is comparable to the 9.5 per cent recorded for both the Herring and Lesser Black-backed Gulls in the Walney colonies (Brown 1967).

Quite how much of these increases is due to immigration is difficult to estimate. Certainly a large contribution is made this way to small, newly developing colonies. The Herring Gull population at Wilhelmshaven rose from 2 pairs in 1948 to 132 pairs in 1957, at a rate of over 30% per year (Drost et al 1961). Only in 1953 did birds previously born in the colony return to breed, adding less than 5% to the population. The remainder were all immigrants. Brown accounts for the sharp build-up of the Walney gulls by postulating a massive immigration in the early 1950s.

The other large, more stable populations probably recruit the majority of new breeders from within their own ranks. Gulls are known to show a strong site tenacity (see Section 4), and tend to breed where they have been raised (Tinbergen 1953); these factors are indicative of a non-immigratory population growth. Certainly there have been no reports of diminishing Herring Gull colonies along the Scottish east coast.

The breeding numbers of several other species of sea-birds have built up in recent years along the north-east coast of Britain. For example, the Kittiwakes at North Shields (Coulson pers.comm.), and the Shags on the Farne Islands (Potts 1969) have both increased at an overall rate of 11% per year. On the Isle of May itself, the censuses of nearly all the breeding sea-birds have shown a marked increase over the last decade, except for the tern species.

3.2 Causes of Increase

Introduction

Two factors have been cited as the cause of this population increase; firstly, the availability of the food supply and, secondly, the relaxation of predation.

Tinbergen (1953) quotes an example where declining numbers of foxes, followed by protection against egg robbing by humans, were both responsible. Similarly Kadlec et al. (1968) ascribe the growth of the New England Herring Gull population to diminishing pressure from humans living along the Maine coast. It may be noted that the lowest rate of increase in Britain was at Skomer (8%). On this island, Harris (1964) states that the Greater Black-backed Gull is a very important predator of gull chicks. Since this form of predation does not occur on the Isle of May, nor in the other colonies, it could have a limiting effect on Skomer.

Although the Herring Gull is a competent fisher in its own right, it has fully made use of the food source provided by human waste. This source is unique, for it is reasonably constant and, more important, it is available during the winter months. Possibly, this improved feeding led to a decrease in mortality during the winter (Hickling 1967, Vemeer 1963), and subsequent increase in the survival and numbers of the species. An analysis of Herring Gull recoveries (Harris 1963) shows a large post-fledging mortality of first-year birds, particularly in September and October. The main mortality of older birds occurs in the summer months and neither category appears to suffer to any extent in mid-winter. The Isle of May recoveries will be discussed in Section 9. One final piece of evidence on the importance of human waste may be obtained from Fordham's (1967) work on the Dominican Gull. The population in New Zealand grew rapidly in the last quarter century; and, more interesting, the colonies with the fastest rate of increase are near man-made food sources.

Several studies have been made of the stomach contents of Herring Gulls. The results vary considerably from place to place and also through the year. The main foods can be categorised as follows :

(i) Fish and Fish Offal

It was previously stated that the Herring Gull is competent at catching fish. The stomach contents of some Herring Gulls on inland waters showed 77% contained river fish caught naturally by the birds (Mendal 1939). In general, though, analysis shows unsaleable fish and fish offal the most frequent form of this food. Boswall (1960) witnessed the wastage of over two hundred weight of liver and entrails, and seven hundred weight of unsaleable fish on a seine-net fishing trip. Studies by Collinge (1924-27), Deusing (1939), Otterlind (1948), Spark (1951), Belopol'skii (1957), and Harris (1965) all conclude that fish and fish offal were the commonest food items.

(ii) Agricultural material

Herring Gulls are frequently seen on agricultural land especially during the non-summer months. Cereals, corn and vegetable matter have been found in most of these analytical studies and, in a few, cereals were recorded as the major food (Florence 1912-15, Ward 1914, Davis 1956). Gulls feed on newly sown grain in March and April and also on turnips during hard weather (Lloyd 1969). They congregate round piggeries and forage on the pig food, causing a nuisance to farmers.

(iii) Human Waste

With an increase in human population, and the standard of living, comes a corresponding increase in refuse. Formerly, waste food was often burnt either in fires at home or in destructors at the refuse disposal units. In recent years it has been dealt with by controlled open tipping (Hickling 1967) whilst, in the home, fires are now restricted to smokeless fuel. Refuse, a quick and easy food supply, has been fully exploited by gulls. Hickling suggests that this form of feeding is further encouraged by the local availability of safe winter roosts, namely, city reservoirs. Both Harris (1965) and Brown (1967) note the predominance of waste food in their respective studies.

(iv) Invertebrates

Several other types of food form a considerable part of the Herring Gull's prey. Beetles, limpets, crabs and earthworms are among the main species, although Focke's (1959) analysis showed that molluscs (especially *Cardium*) were most frequently taken.

The variation in food preferences analysed by these studies probably reflects the local situation. Moreover, it points to a versatility in the diet of this species, which is the key to its success.

Food Source for the Isle of May Gulls

Individual gulls often have their own food preferences. For example, some eat large numbers of earthworms, others restrict themselves somewhat to garbage.

More striking is the annual occurrence of cannibalism, with the same individuals consistently changing to a diet of young gull chicks in June and early July (see section 8).

Despite these singular choices, the Herring Gull is capable of adjusting to different food sources according to the prevailing conditions. Table 2 shows an analysis of food regurgitated by the young Herring Gull chicks during July. Normally, fish and fish offal predominate in the diet. This is collected from the many seine-netters based on the Fife fishing towns. However, there are some days when the boats remain in harbour; for instance, during gales, or over the weekend. Food regurgitated on Sundays has a much more variable composition, with fish one of the less frequent meals.

Table 2. Crude analysis of food regurgitated by Herring Gull chicks on a normal weekday, and on a Sunday

	Weekday		Sunday	
Food item	No.samples	% total	No.samples	% total
Fish	39	78	3	5
Worms	6	12	16	25
Meat (not fish)	2	4	13	21
Grain	1	2	20	32
Bread	2	4	11	17

Difference in fish content between weekday and Sunday

$P < 0.001 \quad (X^2 = 64.0)$

In conclusion, it seems that there has been an increase in the actual amount of food, and of its availability, followed by a change in behaviour of the gulls to exploit these food sources fully. Together, these factors would encourage the sort of population increase that has been witnessed.

3.3 Herring Gull - the pest

Two questions derive from the details of population increase. Firstly, whether Herring Gull numbers have reached pest levels; and, secondly, what type of nuisance does the species cause.

i. Wildlife conservation

Some species have been seriously affected by the increase in Herring Gulls. Although terns, particularly Sandwich Terns, are notoriously unpredictable birds, their absence from the Isle of May can be blamed entirely on Herring and Lesser Black-backed Gulls. Up to the early 1950s several thousand terns of four species bred regularly on the island. They were progressively deprived of their breeding areas by the gulls, so that since 1960 none has nested (Eggeling 1960). Other species, including Shag, Fulmar, Oystercatcher and Eider Duck suffer high egg and chick losses to the gulls. Also, small passerine migrants are occasionally taken and eaten.

Not only do the animals suffer, for the vegetation on the island is also changing rapidly. The adults tear up grass for nesting material, while the vast amount of guano encourages specialised plants, at the same time discouraging many less hardy species. In some parts of the May (e.g. the Maidens) serious erosion problems are resulting from these circumstances.

It would appear that the Herring Gull has become a pest on this Nature Reserve. Admittedly, conservation often allows nature to take its course, but when the human race is responsible for upsetting the balance of nature, control methods should be employed to alter the imbalance that has resulted.

ii. Air strikes

Reports of collisions between aircraft and birds are infrequent, and few fatalities to man occur. However, the annual cost to the Royal Air Force has been estimated at approximately £1 million sterling and, in Britain, one half of the reported bird strikes involve gulls (Brough 1969). Statistics such as these reveal a problem when new airfields are being considered in areas known to be large gull roosts, e.g. Foulness.

iii. Infection

Gulls have been implicated as the carriers of several types of infection. For example, Brough (1969) states that they were probably vectors of avian tuberculosis which recently struck a herd of cattle. Tubercle bacilli have been found in several species which are common in Britain, whilst abroad, bovine cysticerosis has been associated with gulls.

Various Salmonella sp. have been isolated in Herring Gulls (Wilson & Macdonald 1967), including

Salmonella typhimurium from fully grown chicks from the Isle of May 1968. In that year several fledglings died in the late summer (see section 8), and of six carcasses analysed at Lasswade, four contained this organism. Although the laboratory report did not suggest that the Salmonella caused death, it suggested that death was accelerated in these weak and under-weight chicks.

The gulls probably pick up the infections from refuse tips or sewage outlets. Their habit of roosting on freshwater reservoirs causes concern, for in this way they could pollute the water with these infections.

iv. General Pest

The numbers of imputations against gulls increases every year. They range from accusations of Herring Gulls stealing food from the hands of babies (Torquay town councillor, pers.comm.), to complaints of gulls nesting on chimney pots and roof tops. The latter is mainly a recent habit, becoming more common, especially on the east coast of England. The people one would imagine most plagued by gulls are the last to complain. Several fishermen have been asked how troublesome these birds are, but none have labelled them as pests.

Taken collectively, these points advocate that the Herring Gull population should be prevented from further increase and, in many cases, should be actively encouraged to decrease.

Possible methods of control will be examined in section 10.

SECTION FOUR

ONSET OF LAYING

4.1 Site Tenacity

Return to the same territory

The Herring Gull is known to be one of the many species of birds, all of whom are faithful to their nest site over several seasons (philopatry) (Tinbergen 1953, Drost et al 1961). Of 99 colour ringed adults known to return to the May in consecutive years, only five nested away from the close vicinity of their previous territories. None of these five moved more than 100yds from their old sites.

Perhaps more interesting was the return of an additional 21 marked adults who were prevented from breeding in 1968 when their eggs were continually removed. With the exception of one bird, they were all breeding on their old nesting sites in 1969. This represents a 5% failure to conform to the general principal of philopatry which, as a percentage, is no different from the occurrence in undisturbed birds (5/99 = c.5%). However, over more years than one, continual interference could possibly reduce site tenacity.

Return to the colony of birth

Since colour-ringing of chicks only started on the Isle of May in 1966, it was too early to see the extent to which these young gulls restrict their subsequent breeding to their birthplace. Several of these red ringed (1966) birds were seen in the colonies when only three years old, and many more roosted around the perimeter of the island. These roosts also included one- and two-year old Herring Gulls, and the occasional two-year old Lesser Black-backed Gull.

Of greater interest was the tendency for these birds to return to that part of the island from which they fledged. This was at first sight a subjective conclusion, based on the sightings of red-ringed gulls in those areas where ringing took place in 1966. More definite evidence was obtained from three shot birds and ten whose ring numbers were read through a telescope. All thirteen were found in the sub-colonies of their birth-places, well demarcated areas of no more than 4 - 5 acres. These records, admittedly few, point towards a marked trend of young gulls to return, not merely to their general fledging grounds, but more specifically to sub-colonies from which they were reared.

The importance of a strong attachment to the birth-place, and to faithfulness to the nest site, has been pointed out by Tinbergen (1953) : "It means that a species may be composed of many populations which, though they are often mixing outside the breeding season, interbreed scarcely, if at all. They may be reproductively isolated from each other .... allowing them to lead to differences between populations. Mayr has characterised the situation wittily by saying that birds have got their wings not so much for the purpose of getting away to places, but rather for the purpose of getting back to their territories".

4.2 The Laying Period

Onset and duration of normal laying

In 1967 the first eggs were found on 26 April, whereas in the following two years it was on 28 April that eggs were first laid. During the laying period the study areas were visited regularly every two days (in 1968-69) and nests staked as soon as the first egg appeared. In the control areas, 903 and 400 nests were marked in these years respectively. It was not possible to visit the nests so frequently in 1967 and so the build up of laying and the nest contents were less closely observed in the 2,339 nests staked in the control areas that year.

A more comparable measure of the laying period is the median, the date at which 50% of laying has taken place, for it is less affected by the extremes than is the mean. Using this value, it was noticeable that the seasonal distribution of laying was remarkably constant through the years. Discounting repeat layers, 50% of the total laying took place by 17 May (1968) and 16 May (1969). Similar results were obtained for 1966 (17 May), and 1967 (18 May), by working back from the hatching data. The details of the dates of laying in the control areas (1968-69), and the accumulative build up of clutches are shown in Appendix I.

Geographical variation in laying dates

Variation in the laying dates of gulls from one place to another was noted by Harris (1964), who commented on the considerable difference between Paludan's (1951) studies and his own. The Danish colonies started laying as early as 11 April (1943-44), whilst the Skomer gulls began on 22 April (1962) where Harris suggested that the difference was linked with day length rather than temperature. However, traditional theories on day length would hold that north European birds breed later than those in Britain (Lack 1954), and so the Herring Gulls studied by Paludan (1951) at 55½° latitude would be expected to breed later, not eleven days earlier, than those studied by Harris at 51½° latitude.

A more complete picture of the geographical variation in laying dates can now be attempted in the light of recent studies by Drent (1967), and Barth (1967). The mean, rather than the median, was more frequently cited, and so the mean dates of laying the first eggs in all nests were listed in Table 3 for these studies.

If the results of the Scandinavian studies are taken separately, then a correlation with latitude seems apparent. The most northerly colony at Troms was the last to lay, the most southerly colony at Graesholm the first. Barth (1967) explains the results in terms of climate, but adds that "the particularly early dates on Graesholm are not easily explained."

This correlation with latitude seems far less valid when the laying dates in Holland and Britain are considered. On their own they seem to substantiate the above conclusion. The southerly Skomer colonies breed earlier than those on the Isle of May, although the particularly late dates in Drent's (1967) studies present an exception.

An examination of all the data indicate that neither day length nor climate have an overriding effect, otherwise the Scandinavian Gulls would be expected to breed later than the British colonies (Table 3). Marshall (1959) stated that no single overall factor is responsible for the timing of avian breeding seasons, and that the mutual behaviour essential to reproduction will not occur until the environment presents the pair with its species requirement. The local situation therefore bears more relevance to the onset of laying than to the general parameters of day length and temperature, though these will also be important accelerators of the sexual cycle.

Table 3. The mean laying date of all a - eggs for various studies on the Herring Gull, shown with the latitude of the study areas

Study area	Latitude	Mean date of laying	Year	Authority
Troms, Norway	70°	16 May	1959-66	Barth (1967)
Trava, Norway	64°	5 May	1953-56	Barth (1967)
Kristand, Norway	58°	4 May	1948-54	Barth (1967)
Graesholm, Denmark	55½°	24 April	1943-44	Paludan (1951)
Schiermonmkoog, Holland	53½°	19 May	1963-65	Drent (1967)
Priest Island, W. Scotland	58°	15 May	1937	Darling (1938)
Isle of May, E. Scotland	56°	18 May	1966-69	This study
Skomer Island, Wales	51½°	5 May	1962	Harris (1964)

Timing and spacing of nests

Whilst visiting nests during the laying period, it became obvious that some synchronisation of laying was taking place. For example, the sub-colony and control area North Ness appeared as a series of smaller units, although the final nesting pattern gave no indication of such aggregations. Within each unit, which would contain about 10 to 20 nests, eggs were laid at a similar time in the season.

This impression was investigated by gridding North Ness into 10ft squares, and plotting the nests. An analysis was made of 52 sample areas, each 20ft square (400 sq.ft.), within which the number of nests with newly laid clutches was recorded every two days through the laying period (fig.6). The accumulation of these data gave the final nesting density, although it did not account for the three dimensional spacing of territories.

It is generally known that gull's nests are distributed uniformly within the colony, as a consequence of territorial behaviour (Tinbergen 1956, 1957). Distribution patterns may be numerically illustrated by the coefficient of dispersion which, for random distributions, is unity :

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

Mean no. nests per 400 sq.ft. sample = 16.8

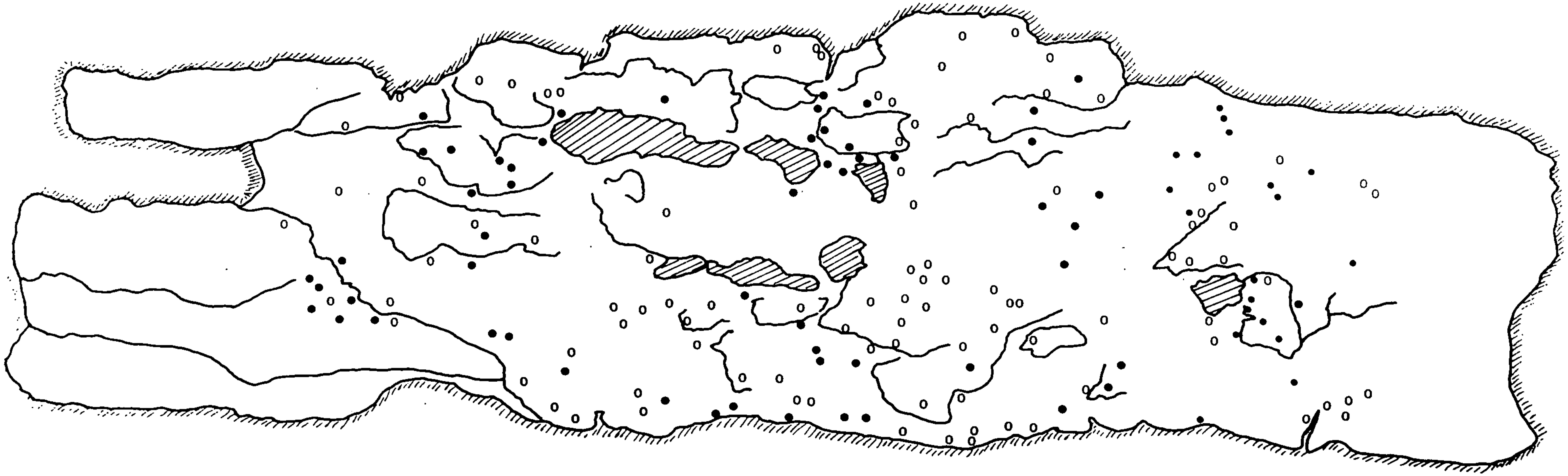
Varience = 14.8

No. samples = 52

Coefficient of dispersion = 0.88

Figure 6.

Synchronisation of laying in areas of North Ness 1968. Nests plotted on a scale diagram of North Ness according to the date of laying a-eggs (i.e. 20 and 24 May)



NORTH NESS 1968

A-EGG LAID ON: ○ 20 may ● 24 may

The 0.05 probability level of significant difference from a random distribution is given by unity $\pm 2x\sqrt{\frac{2}{N-1}} = 1 \pm 0.40$. For this particular analysis, the coefficient of dispersion was within the limits 0.60 - 1.40, and the suggested uniform distribution therefore not significant. However, a more exact analysis was made of the number of nests within a 7.5ft radius of each nest (Table 4). A significant ($p < 0.05$) divergence from a random distribution would be given by a coefficient of dispersion outside the limits 0.78 - 1.22 ($N = 171$). With a coefficient of 0.71, the nests were distributed uniformly at a significance level of 2 per cent. This was further checked by a comparison with the expected number of nests (Poisson prediction, $X^2 = 11.2$ with 3 degrees of freedom, $p < 0.02$).

Table 4. The observed and expected number of nests within a 7.5ft radius of a random sample of nests (N = 171). (Nest site numbers selected from Fisher & Yates' (1963) random number table, and expected frequency calculated by Poisson prediction).

	No. nests					
	0	1	2	3	4	
Observed	56	71	40	3	1	Mean 0.96, Variance 0.68,
Expected	66	63	30	10	2	Coefficient of dispersion 0.71

$X^2 = 11.2$ with 3 degrees of freedom $p < 0.02$

Table 5. To examine whether laying at any time in the season takes place at random throughout the colony, or in synchronised groups within the colony. The observed and expected number of nests containing newly laid clutches in each of the 52 sample areas (400 sq.ft.) through the laying period at two day intervals

	No. newly laid clutches/sample/two day period								
	0	1	2	3	4	5	6	7	
Observed	243	296	121	62	32	15	5	2	Mean = 1.29
Expected	187	240	154	66	21	6	1	0	

$X^2 = 70.1 \quad p < 0.001$

Despite this overall spacing pattern, the onset of laying did not occur randomly or uniformly through the sub-colony. Instead, small groups showed synchronised laying, for when the extent of laying within each sample area was analysed for two day periods, the laying was aggregated (Table 5). The mean number of newly laid clutches per sample per two day period was 1.29 with a significantly aggregated coefficient of dispersion of 1.48 ($p < 0.05$). It is possible that not only laying, but also the initial selection of territories and building of nests occurs in this synchronised manner, and that the cause is social stimulation at the onset of the breeding season.

One final observation was forthcoming during the laying period. Clutches that were laid late in the season were commonly situated on the edge of the sub-colony in the more exposed areas. North Ness was therefore divided into three sections; the perimeter, the centre, and between these two an area called for convenience the boundary. The percentage of laying that occurred in these three areas through the season was recorded (Table 6).

Table 6. Variation in laying dates in nests from three arbitrary areas of North Ness

Laying date	No. of nests	Percentage of laying			Difference between centre and perimeter
		Perimeter	Boundary	Centre	
up to 10 May	188	25%	37%	38%	$p < 0.05$
10-18 May	284	37%	38%	25%	$p < 0.02$
20-24 May	254	43%	38%	19%	$p < 0.001$
after 24 May	170	55%	30%	15%	$p < 0.001$

The result showed that progressively more and more laying took place on the perimeter as the season advanced, whereas in the centre of the sub-colony most of the laying occurred early in the season. The relationship between density and nesting area, and subsequent breeding success will be dealt with in Section 7.

SECTION FIVE

THE PATTERN OF LAYING

5.1 Normal laying

To avoid confusion, the first egg laid by a gull will be referred to as the a-egg; the second egg is therefore the b-egg and so on. Also, a clutch of two eggs will be written c/2 and a clutch of three c/3.

Normal interval between eggs

Before assessing the effects of experimentation on egg laying, it was important to consider the normal rather than the abnormal condition.

The clutch size of the Herring Gull consists of three eggs in the vast majority of cases (see section 7). Data collected from 85 nests visited every twelve hours during the laying period show that the average interval between a and b-eggs, and between b and c-eggs was 48.85 ± 0.44 hours (Table 7). This value was on a par with that given by Drent (1967), 48.72 ± 0.48 hours. Nor was there any difference between the first and second intervals (a-b eggs, and b-c eggs respectively).

Normal interval between repeat layings

If a Herring Gull loses its eggs after incubation has started, it can usually produce a substitute clutch after a fairly well defined interval. In some birds this interval varies according to the length of time spent incubating the first clutch. The histogram of re-laying in the delayed areas on the Isle of May (section 7, fig.27) shows that although eggs were removed in various stages of incubation, re-laying occurred generally within a fortnight, i.e. irrespective of the incubation time. This corroborates Paludan's (1951) conclusion based on the destruction of clutches by a late snow storm in 1944.

The time taken for 160 Herring Gulls to re-lay was measured from the removal of the first clutch, to the arrival of the a-egg of the repeat clutch. The average interval was 13.23 ± 0.12 days. However, the data were analysed to investigate which factor caused the greatest variability or delay. Firstly, the amount of time spent incubating before the loss of the eggs; secondly, the time of the season that re-laying took place, in case the adults found greater difficulty re-laying as the summer progressed (Table 8).

The lack of variation in the results is more interesting than the disparity between the means, for there is only a two day difference between the extremes (i.e. 12.62 and 14.71 days). Nevertheless, it appears that the time in the season exerts a slightly greater effect than does the incubation factor, so that the female takes somewhat longer to re-lay as the season advances. This, of course, becomes critical at the stage when no more re-laying takes place.

Table 7. Showing the mean interval between the layings of eggs in a normal clutch, and also the interval between c and d-eggs when a fourth egg is laid

	Laying interval between eggs in hours							
Interval	24	36	48	60	72	Total	Mean	Standard error
a-b eggs	1	6	67	10	1	85	48.56	0.69
b-c eggs	0	3	72	9	1	85	49.13	0.55
c-d eggs	0	0	24	10	3	37	53.19	1.26

Table 8. Number of days between the removal of the first clutch and the laying of the a-egg of the repeat clutch, according to the time in the season, and the state of incubation at the time of robbing. Number in sample given in brackets. Mean interval in days ± one standard error

	State of incubation at removal of eggs		
Time in the season of laying first clutch	Directly after laying c-egg		15 days incubation
before 25 May	12.62 ± 0.22 (37)	p-NS	13.04 ± 0.14 (77)
	$p < 0.05$		$p < 0.001$
after 25 May	13.48 ± 0.35 (25)		14.71 ± 0.36 (21)
		$p < 0.02$	

Ability of Herring Gulls to re-lay

If a Herring Gull re-lays, it apparently does so within nearly a fortnight. This conclusion fails to account for the percentage of birds that actually do re-lay. An estimate of this value was obtained from records of laying in the delayed areas, though it was not possible to separate the variation due to the incubation interval, and to the seasonal effect as above. These two factors are treated together in Table 9, relating the percentage re-laying to both the progress of the season and to the interval between laying and removal of the first clutch. These data concern only those birds that re-laid in, or near, their first nests and is therefore a minimal figure. Nevertheless, the disturbance of egg robbing does not often encourage the adults to move territory (section 7).

Naturally, not all birds are capable of re-laying, and this inability increases as the season advances, so that by late June no more eggs are found. It will be shown later that this is more a result of a diminishing behavioural and sexual drive, rather than physical exhaustion of the female gull.

Table 9. Numbers of re-laid clutches in relation to the progress of the season and the time interval between laying the first clutch and its removal

Approximate date of removal	17 May		27 May	7 June	
Incubation period before removal in days	0-4	6-8	10-14	16-20	22-24
Number robbed	84	37	67	47	21
Number re-laid	59	18	29	18	7
Percentage re-laid	70%	49%	43%	38%	33%

5.2 Determinate or indeterminate laying

Introduction

Although birds generally lay a fairly definite number of eggs in a clutch, characteristic of their individual species, the mechanism controlling this phenomenon is thought to function in one of two ways. Some birds will lay a set number of eggs irrespective of how many eggs are in the nest; others will continue to lay until their nest contains a definite number of eggs.

Those birds that compensate for a loss of eggs during laying are called indeterminate layers. For example, the Flicker is known to have laid 71 eggs when an egg was taken daily from the nest (Phillips 1887). It is believed that an external stimulus, either visual or tactile, is necessary to stop the production of eggs by the ovary.

On the other hand, some species will lay a definite clutch regardless of the removal or addition of eggs. These determinate layers have an inflexible hypophyseal-ovarian mechanism, so that the numbers of follicles entering the final stage of growth correspond to the size of the clutch. They therefore cannot add to the clutch if one or more eggs are lost during laying.

Despite these well defined categories of laying, the Herring Gull has been claimed by Davis (1942) and Tinbergen (1953) to be a determinate layer, whilst extensive experiments by Paludan (1951) indicated it was an indeterminate layer.

Davis (1942) performed several egg removal experiments and concluded that the birds were not inclined to lay more than the usual three eggs. In three cases where a fourth egg was present in the nest they were interpreted as abnormalities - "the bird may have stolen the eggs from nearby nests". The research took place over a period of six days and, since the Herring Gull requires five days to lay a complete clutch, it is hardly surprising that no more than three eggs were usually found.

Tinbergen (1953) does not give any details of his egg robbing experiments, except to say that "in general neither the taking nor the addition of eggs at whatever stage, and in whatever way or sequence it is done, changes in any way the fixed number of three in a clutch". Instead the bird would start a new clutch after a period of nearly a fortnight (repeat laying) if the first clutch was removed.

Quite contrary to these conclusions, Paludan (1951) showed that indeed a fourth egg can be laid and, under certain circumstances, protracted laying will also occur. Previously, Salomonsen (1939) had induced Herring Gulls to lay a series of eggs, in one case 16 eggs in 39 days; whilst more recently Harris (1964) and Laughlin (pers.comm.) managed to get layings of up to eight eggs in a nest. It is important, however, that to qualify as a protracted laying, this continuation of the clutch should involve regular intervals between successive eggs characteristic of normal laying.

Although Weidmann (1956) achieved this pattern in experiments with the Black-headed Gull, Paludan's results were less convincing. His continuous egg removal experiment involved four pairs of Herring Gulls, of which only two laid eggs at intervals of less than four days.

It seemed worthwhile repeating these experiments using larger samples to investigate the following :

i) whether the production of a fourth egg was normal or exceptional

ii) whether the pattern of protracted laying was regular, or concealed a repetitive quality similar to, though possibly not as long as, true repeat laying

iii) whether the pattern of laying, and in particular the onset of incubation, affected the size and yolk content of the eggs.

Experimental investigation of the control of clutch and egg size

Methods

A total of 280 nests were visited every 12 hours during a period of six weeks. Various egg removal or addition experiments were carried out and the lengths and breadths of eggs measured. All eggs removed were weighed (to .01g), hard boiled, and separated into shell, yolk and albumen, which were likewise weighed. Since 24 of the Herring Gulls nesting in the area were colour-ringed it was possible to observe the effects, if any, of continuous egg removal.

Calculation of egg volume and shape

As eggs were not all removed from the field it was often necessary to use the egg volume rather than the egg weight as a proportional measure of the egg size. This value was especially useful for comparative studies between eggs and clutches in the control areas.

The volume of an egg was calculated from the formula :

$$V = k.B.L^2$$

which is derived from the volume of an ellipsoid, when V is the volume, B the breadth, L the length, and k a constant.

Several values of k have been cited, each based on particular specific gravity determinations of the Herring Gull egg. Paludan quoted (1951) 0.519, Harris (1964) 0.476 and Barth (1967) 0.5084. Throughout this study the figure of 0.476 has been used.

To check the correlation between weight and calculated volume, a graph of these co-ordinates was plotted (Fig.7), and correlation coefficient (r) evaluated = +0.9854 $p < 0.001$.

$$V = 0.8869W - 0.2482$$

$$W = 1.1018V + 2.2878$$

when the standard error of the estimate is given by

$$S_V = \partial_V\sqrt{1 - r^2}$$

$$S_W = \partial_W\sqrt{1 - r^2}$$

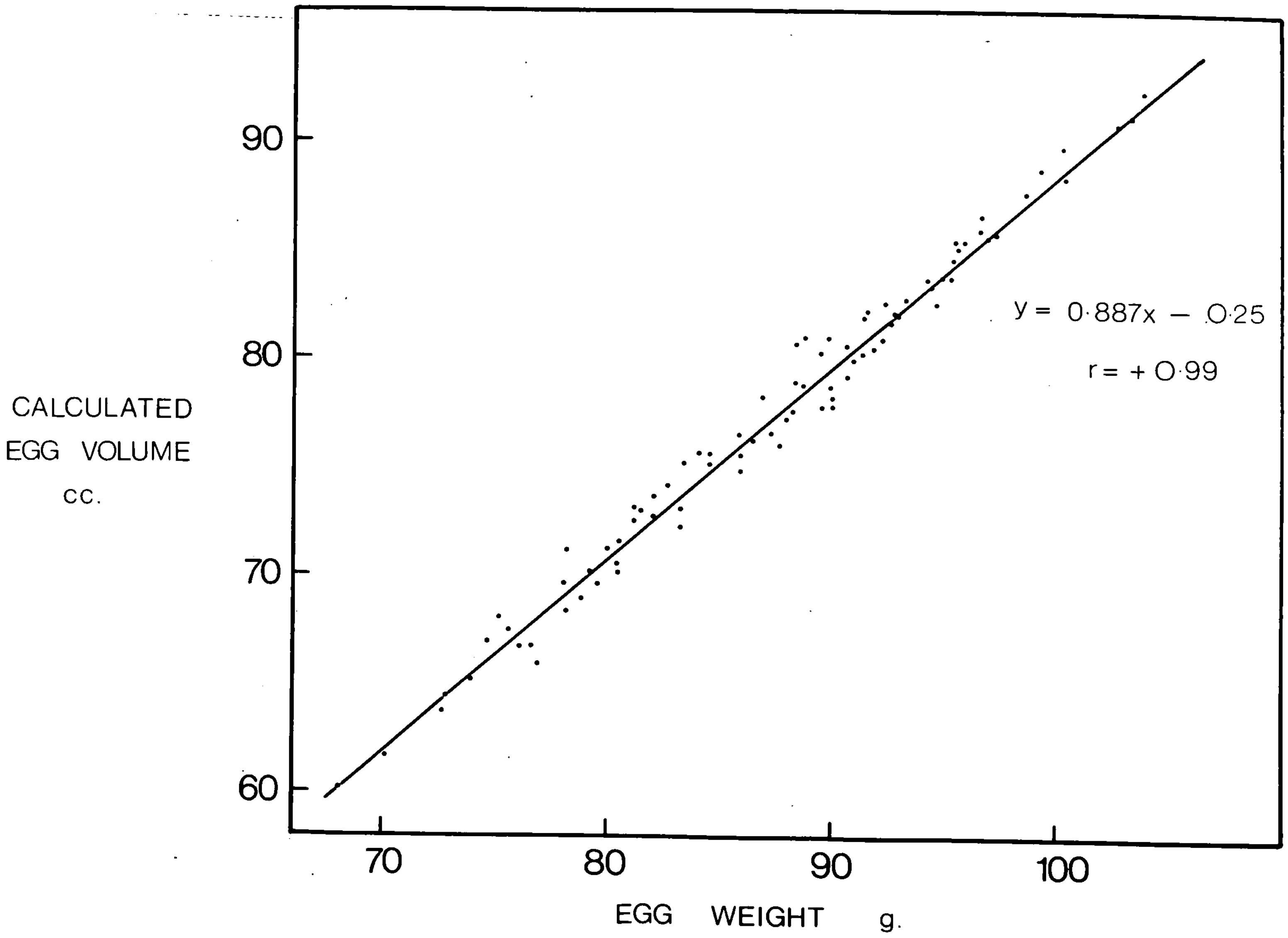
and ∂ = standard deviation.

Then $S_V = 0.11$ and $S_W = 0.13$.

For the purposes of this study, calculations of egg volume based on the axial lengths therefore seem quite adequate. For the

Figure 7.

Regression line of calculated egg volume on egg weight



CALCULATED
EGG VOLUME
cc.
90
80
70
60
70
80
90
100
EGG WEIGHT g.
y = 0·887x − 0·25
r = + 0·99

variability in egg shape, the shape index was calculated as follows (Coulson 1963) :

$$\text{Shape index} = \frac{100 \times \text{breadth}}{\text{length}}$$

Experiment to produce a fourth egg

Occasionally gull nests were found with four-egg clutches, though the frequency was never greater than 1 in 500 (0.2%). The colour and laying interval of these eggs suggested they were from the same female. Moreover, a d-egg was laid in 9 out of 16 nests when the a-egg disappeared in the control areas.

To investigate the ability of gulls to produce this extra egg, the a-egg was removed within 12 hours of being laid in 79 nests. Subsequent eggs were left in the nest and, in 47 cases, the d-egg was laid. This experimental result closely resembles the natural occurrence in the control areas (59% : 57% respectively). The mean interval between laying of the c-egg and d-egg was 53.19 ± 1.26 hours (Table 7), which was significantly longer than the normal laying interval ($p < 0.002$), but was still a continuation of the same clutch. It was also noticed that, discounting repeat layers, fewer birds were capable of laying a d-egg later in the season (Table 10) ($p < 0.05$).

On three occasions, both the first two eggs were removed, each as they were laid. In all three cases, a d-egg was followed by an e-egg at the same interval (48, 48, and 72 hours). The d-egg is much less frequently laid when the first two eggs

Table 10. Comparing the ability of Herring Gulls to lay a d-egg at different times in the season

Total number of eggs laid	Time of laying a-egg before 19 May	 after 19 May
4 (d-egg)	28	19
3 (no d-egg)	11	21
% laid d-egg	72%	48%

$X^2 = 4.84$, $p < 0.05$

Table 11. The number of eggs laid by each pair during the continuous removal experiment

	No. of eggs laid 1-3	 4	 5	 6	 7	 8	 9	 10	 11	 12
Number of nests	13	8	13	20	19	17	6	4	1	1

are not taken until after the b-egg has been laid. From 110 nests studied in this manner, 89 produced only a c-egg, 20 a d-egg, and only one an e-egg.

These experiments imply that the Herring Gull is quite capable of supplementing the loss of its a-egg, by laying a further three eggs to build the clutch up to the normal size. However, although it is a common occurrence, it is by no means the rule, as suggested by Paludan (1951), especially as the season advances.

If the a-egg remained in the nest during the laying period, then no additional d-eggs appeared, even when both the b and c eggs were removed. Similarly, in the majority of cases, the d-egg was withheld when the eggs were removed after the laying of the b-egg. Paludan (1951) states that this happens if the egg removal occurs later than 24 hours after the appearance of the b-egg.

In the field, the a-egg is usually the most vulnerable. Evidence from the control areas shows that within the first week of laying, egg loss frequently involves the a-egg. From 800 clutches of three eggs, the disappearance of the eggs was as follows :

a-egg	34	
		$p < 0.01$
b-egg	15	
		p - NS
c-egg	8	

Predation is the normal cause of egg loss at this stage, before steady incubation has set in. Also, if heavy rain follows the laying of an a-egg, the adult gull will sometimes cover its own egg with new nest material in an attempt to make a dry nest. This happened six times in the same area of 800 nests and, on each occasion, to the a-egg, which was buried and subsequently not incubated.

In situations such as these, the Herring Gull can raise the clutch to the normal size, depending on the time at which the a-egg disappears. However, not once was the production of an e-egg witnessed in the field.

Continuous egg removal experiments

Eggs were repeatedly taken from 102 nests, each egg as soon as it was laid or within 12 hours of laying. Of these, only 13 failed to lay more than the usual three eggs, and none of the 24 colour-ringed adults changed territory throughout the experiment.

It can be seen from Table 11 that in 68 cases (66%), six or more eggs were laid, the equivalent of a second clutch. More important is the pattern of laying and, in particular, whether the intervals between eggs are consistent with repeat laying, or with protracted laying.

In general, the laying patterns fell into five categories. These were based on the position of the longest interval between the laying of consecutive eggs as follows :

i) between the c and d eggs, giving the appearance of a c/3 followed by subsequent eggs (29 nests)

ii) between the d and e eggs, similar to the production of an initial c/4 (39 nests)

iii) between the e and f eggs, so that the longest interval seemed to separate a c/5 from later eggs, even though this interval was quite small (11 nests)

iv) those nests in which a c/4 (5 nests), or a c/3 (5 nests), or even fewer (8 nests) was all that was laid

v) a miscellaneous group which fitted neither of these categories (5 nests).

When the patterns were grouped in this manner, the mean interval between the laying of the a-egg and each of the following eggs was calculated, to give the average pattern for that category. This could then be compared with the normal re-laying situation (Table 12).

Table 12. Patterns of laying after continual egg removal

Category	N.	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Normal repeat laying	63	o		o		o ←						12.65 ± 0.16						→ o		o		o		
i) "c/3".. interval	29	o		o		o ←					8.43 ± 0.49					→ o		o			o			
ii) "c/4".. interval	39	o		o		o		o ←					7.18 ± 0.43			→ o			o		o		o	
iii) "c/5".. interval	11	o		o		o		o				o ←		4.64 ± 0.37			→ o		o			o		o
Individual patterns :																								
Nest no.																								
5		o		o		o		o			o				o			o			o		o	
4		o			o			o		o			o			o				o				o
83		o		o		o			o							o			o			o		
12		o		o		o		o		o						o		o		o		o		o
695		o		o		o			o			o			o				o					o
113		o		o			o	o	o				o				o			o				
43		o			o			o		o			o				o			o			o	

Days after laying the a-egg

In all three major patterns (i, ii, iii), the longest interval between eggs was significantly shorter than that expected by repeat laying ($p < 0.001$). Nevertheless, the groups that initially laid clutches of three (i) and four (ii) eggs, resembled an abbreviated form of re-laying, rather than the theoretical expression of protracted laying. Only in the third group (iii) was a more continuous production of eggs witnessed. In these 11 nests each egg followed its predecessor after a period similar to that of normal laying and could therefore be classified as protracted laying.

It was interesting to note that, of the 102 pairs studied, 57 (39+11+5+2) of them produced at least four eggs in succession. Thus, the laying of the d-egg occurred in the same frequency as in the previous experiment (56%).

Not only do these results contradict the classification of the Herring Gull as a determinate layer, but they also illustrate the variability in possible laying patterns. This may be explained by a lack of uniformity in experimental conditions and also by a difference in the way individual gulls react to the same conditions. On this assumption, some females would be capable of laying larger, and more, eggs than others.

With this in mind, the average weights of a, b, and c-eggs from the different laying categories were compared (Appendix II). The eggs laid as an initial c/3 (pattern i) were consistently though not significantly, lighter than those laid as a c/4 (pattern ii) ($p < 0.1$). The same result was also true for the mean volumes of eggs in the previous experiment. Those eggs produced by females which laid a d-egg, were on average larger than those which only laid a c/3.

Moreover, the eggs of the protracted layers (pattern iii) were significantly heavier than those laid as a c/3 ($p < 0.01$).

Although the normal clutch size in the field is three eggs, some gulls only lay two. The difference between these eggs confirms the above results, for the first two eggs of the normal clutches had a larger calculated volume than those of the 2 egg clutches ($p < 0.01$).

To summarise, the Herring Gulls which, either in the control or in the experimental conditions, laid smaller clutches, also tended to lay lighter eggs. This would indicate that the females conforming to pattern (i) for example, were physiologically incapable of protracted laying and required the interval of 8 days before laying a d-egg.

Table 13. The average number of eggs laid in a nest, for each of the laying categories

Pattern	No. of nests	Mean no. eggs laid per nest
(i) c/3 followed by ..... 2.86 eggs*	29	5.86 ± 0.26
		$p < 0.001$
(ii) c/4 followed by ..... 3.18 eggs	39	7.18 ± 0.17
		$p < 0.001$
(iii) c/5 followed by ..... 4.09 eggs*	11	9.09 ± 0.43

* difference between (i) and (iii) = $p < 0.05$

There is further evidence of a dissimilar fitness between the females in each laying category. Using pattern (i) as an example again, they not only laid lighter eggs, but the total number of eggs each gull produced was also significantly less than in the other categories (Table 13. $p < 0.001$). Even when the initial clutch is disregarded (i.e. 5 eggs in pattern (iii), and 3 eggs in pattern (i)), those that least resembled repeat laying laid more eggs ($p < 0.05$ - pattern iii : pattern i).

Experiments to reduce the clutch size

These results have shown that the Herring Gull will, under certain conditions, lay more than three eggs. To complete an investigation of the control of laying it was desirable to find out whether the reverse situation could be induced. Eggs were added to nests before and during laying, not merely to see if the clutch size could be reduced, but more especially to record whether such experiments affected the size of the c-egg. This was particularly important in lieu of the weight difference between the first two eggs and the c-egg, and the mortality difference between the chicks hatching from these eggs (see section 6).

An extra egg was placed in 54 nests as soon as the a-egg was laid. This had no effect on the total number of eggs laid by the female, for in 48 nests the usual c/3 was laid, whilst in the remainder only one further egg was recorded (c/2). The average clutch size was therefore 2.89, which was the same as that in the control areas; nor did the addition of more than one foreign egg make any difference (87 nests).

When eggs were added to 22 nests before the beginning of laying, the clutch size was reduced, and in at least three cases completely suppressed. In the latter, these additional eggs were incubated for several weeks though they were eventually found to be addled. On six occasions the eggs were rejected by the adults, which left 16 nests with a mean clutch size of 1.81 eggs laid per nest. This was significantly smaller than the expected clutch size ($p < 0.001$).

Paludan (1951), who records a similar result, states that the introduced eggs are accepted about 9 days before laying the a-egg, which corresponds to the time when the follicles start their final growth phase. Prior to this time the foreign eggs are eaten or removed from the nest.

Since the developing follicles can be suppressed by the brooding of foreign eggs, then the same physiological response may contribute to the variation in egg sizes within a clutch. To investigate this, measurements of eggs and of the onset of incubation were analysed.

5.3 The control of laying

Follicle development

During these experiments, observations either record the presence or absence of eggs and, although much can be inferred from the results, an understanding of the ultimate mechanisms involved requires a knowledge of the internal state of the adult female gull. Paludan (1951) examined the ovaries of Herring Gulls during the laying period and similar dissections were performed by Weidmann (1956) on the Black-headed Gull.

Paludan showed that the first ovulation occurs about two days before the laying of the a-egg. At this time four follicles have entered the final stage of growth and, after the a-egg has been laid, the fourth follicle starts to degenerate. It is therefore believed that contact between the a-egg and the brood patches causes this degeneration, but only in the fourth follicle. The development of the b and c-follicles has reached such a stage that they are ovulated regardless of an increasing drive to incubate the a-egg. Without this contact, the hypophyseal-ovarian feedback allows further growth of the fourth follicle, which undergoes ovulation to give rise to a d-egg.

However, it has been shown that the d-egg is not always laid under these circumstances. This would suggest that either broodiness in some adults starts before the a-egg is laid, or that the d-follicle does not always reach the final growth phase. The latter seems more feasible, for if broodiness encouraged degeneration before the laying of the a-egg, then it would also be expected to affect the c-follicle, resulting in a more common occurrence of c/2s.

Ideally, constant removal of eggs would precipitate a steady production of follicles, regimentally arranged to facilitate protracted layings at regular intervals. This rarely occurs, either because the Herring Gull as a species is not adapted for continual egg production, or because such laying places too many demands on the physical abilities of the female. Since some individuals were capable of protracted laying, it was not a genetic impossibility. Instead, it would seem that the repeated laying of about 85g of egg material can only be achieved by a minority of the population. The remainder require an interval in which to build up material, if eggs of a reasonably constant size are to be laid.

Broodiness and incubation during the laying period

The previous experiments indicated that follicles can be encouraged to degenerate; normally this involves the d-follicle, though addition of eggs at a crucial stage prior to laying will affect some or all of the developing eggs. Broodiness is regarded as the cause, which consequently results in a failure of an egg to be laid. However, it is possible that a reduction in egg size is the more subtle effect, whilst the ultimate response is the non-appearance of the egg. Harris (1964) stated that "effective incubation probably does not start until the laying of the third egg". Contrary to this, Paludan (1951) had suggested that the incubating process at the beginning of laying was probably responsible for the smaller size of the c-egg. It therefore seemed worthwhile examining the effectiveness of incubation during the laying period, since the physical intensity of broodiness should be related to the hormonal responses that occur with the onset of incubation.

The interval between the laying and the hatching of eggs is given in Table 14.

Since the eggs are laid at intervals of two days, then on average the b-egg hatches just after the a-egg, followed one day later by the hatching of the c-egg. Similar incubation times were recorded by Paludan (1951)

Table 14. The mean intervals in days between the laying and hatching of eggs ± one standard error

Laying sequence	No. nests	No.days between laying and hatching	No.days between laying a-egg and hatching
a-egg	31	29.96 ± 0.29	29.96
b-egg	28	28.30 ± 0.21	30.30
c-egg	27	27.00 ± 0.26	31.00

and Drent (1967) who concluded that incubation during the laying period was rather ineffectual. In terms of the developing embryo this may be correct, but these intervals do show that incubation does take place before the c-egg is laid, otherwise all the eggs would hatch on the same day. Therefore, in terms of the hormonal mechanisms involved, this early broodiness heralds an important behavioural change in the adult gull.

Paludan (1951) examined embryonic development at stages varying from three days after the termination of laying until the first young were hatched. The embryo weights showed that some development took place in the a-eggs before the b-eggs were laid.

It seemed necessary to obtain a more precise measurement of the very early growth of the embryoes. This had previously been lacking, as the young embryoes were too small to weigh. Within the first two days of incubation the primordial heart of a chick becomes connected to a network of blood vessels established in the area vasculosa.

This appears as a disc of radiating capillaries, situated on the yolk surface, and terminated by a distinct boundary (the sinus terminalis). The vascular system increases in size, so that by the fifth day of incubation it completely covers the yolk. It could therefore be recorded as an alternative measure of incubation.

Eggs of 172 clutches were marked during the laying period, and clutches removed at various 12 hour intervals measured from the time that the c-egg was laid. Each egg was carefully broken into a petri-dish and the average diameter of the area vasculosa recorded (see Plate 5).

The results, expressed in Fig.8, clearly demonstrate that incubation is effective even before the b-egg is laid. The a-egg embryo was at all times significantly more advanced than that of the b-egg ($p < 0.001$), on average by a laying interval of 12 hours. Likewise the development of the c-egg lagged behind the b-egg by about 32 hours. This is somewhat longer than the hatching interval between these eggs, which is possibly due to the smaller c-egg having a shorter overall incubation period (see section 6).

The effects of broodiness on egg size

These investigations have been aimed at not merely understanding the control of egg laying in the Herring Gull, but also accounting for the size differences between eggs.

Although similar in size, the a-egg is generally larger than the b-egg ($p < 0.001$) especially later in the season (see section 6). Measurements from 455 clutches showed this to be the case in 299 nests (66%), whilst in 156 nests the b-egg

Figure 8

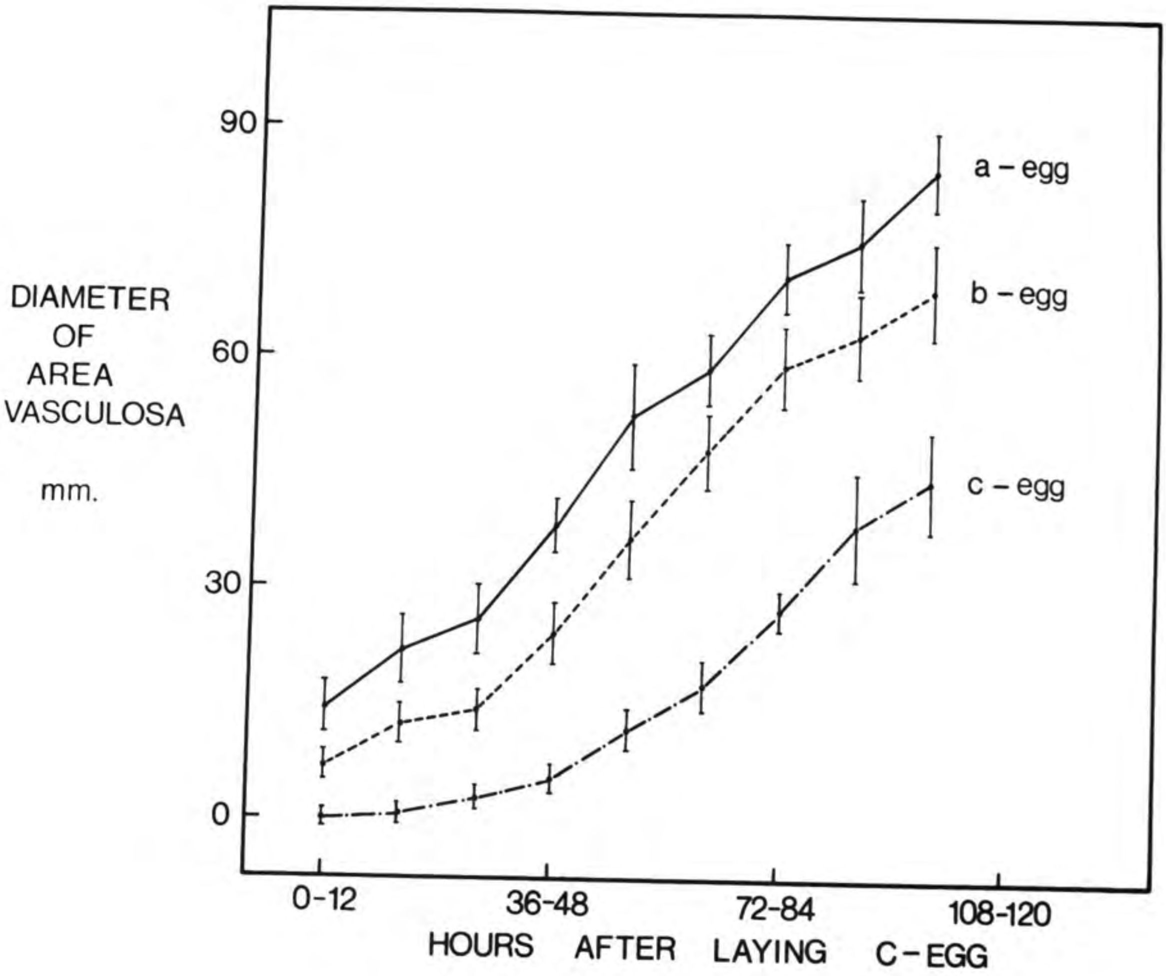
The onset of incubation according to the laying sequence. Mean diameter of the area vasculosa (± 2 standard errors) at various times after laying of the c-egg.

Plate 5a and b

Photographs of the area vasculosae of clutches taken :

(a) 48 - 60 hours after laying of c-egg (above)
(b) 96 - 108 hours after laying of c-egg (below)

(Diameter of area vasculosa given beneath each egg).


DIAMETER OF AREA VASCULOSA mm.
90
60
30
0
a – egg
b – egg
c – egg
0-12
36-48
72-84
108-120
HOURS AFTER LAYING C – EGG

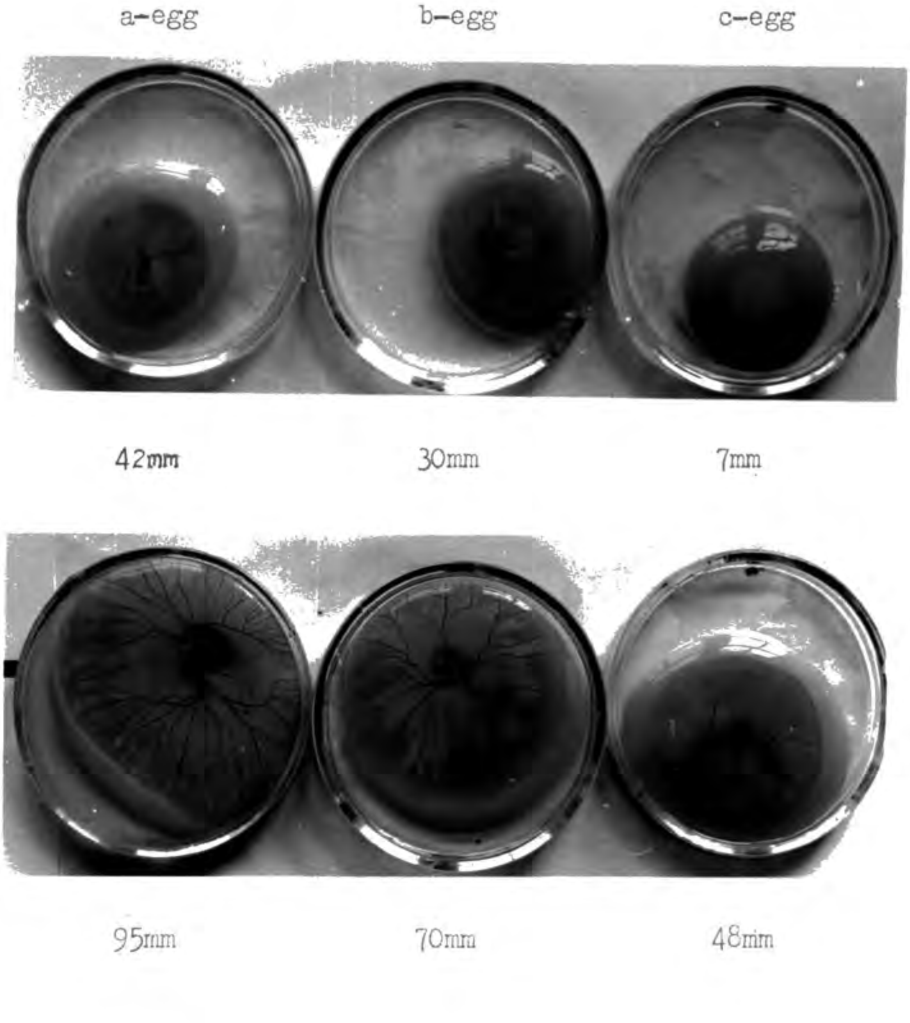

a–egg
b–egg
c–egg
42mm
30mm
7mm
95mm
70mm
48mm

Table 15. Comparing calculated egg volumes (± one standard error) of eggs in normal layings, and eggs produced under various experimental conditions

	N. clutches	a-egg		b-egg		c-egg		d-egg	% difference a : c egg
Normal laying	50	78.80±1.02		78.14±0.96	← $p < 0.001$ →	70.58±1.04			10.4%
		↕ NS		↕ NS		↕ $p < 0.02$	↖ NS ↘		
a-egg removed d-egg laid	38	79.03±0.98		77.58±1.01	← NS →	74.95±0.96	← $p < 0.001$ →	68.69±0.98	5.2%
		↕ NS		↕ NS		↕ NS		↕ $p < 0.001$	
All eggs removed when laid	27	79.95±1.03		77.73±1.02	← NS →	75.54±1.01	← NS →	75.48±1.08	5.5%
One extra egg added when a-egg laid	47	75.53±1.00		74.59±0.88		68.29±0.83			9.6%

was larger. The volume difference is rarely more than 2 per cent, whereas the c-egg is consistently smaller than the a-egg by a factor of over 9 per cent (Table 15). This pronounced disparity between the sizes of the c-eggs and of the a or b eggs has been observed in other Laridae (Table 16).

Table 16. The difference between a and c-egg volumes for various species

Species	No. clutches	Percentage difference between a and c-eggs	Authority
Herring Gull	57	9.7%	Paludan (1951)
Herring Gull	310	8.1%	Barth (1967)
Herring Gull	455	11.0%	This study
Lesser Black-backed Gull	62	9.4%	Paludan (1951)
Lesser Black-backed Gull	59	5.7%	Harris (1964)
Greater Black-backed Gull	218	3.8%	Barth (1967)
Laughing Gull	15	7.0%	Preston & Preston (1953)
Kittiwake	33	7.3%	Coulson (1963)
Common Tern	22	5.8%	Gemperle & Preston (1955)
Common Tern	29	6.1%	Dunn (pers.comm.)

This is not always the case, for in the Shag (Coulson et al 1969) the a-eggs are the smallest, but the c-egg is still smaller than the b-egg. Furthermore, in the House Wren, the final egg laid is usually the largest (Kendeigh et al 1956).

In the past, small last laid eggs have been attributed to a deficiency of material, especially in research on the domestic fowl (Romanoff & Romanoff 1949). However, Paludan (1951) pointed out that the eggs of a Herring Gull that produced protracted layings did not show the decrease in volume anticipated by the situation in the c-egg.

In the experiments that led to the production of a d-egg, the gulls were not given the opportunity of incubating the a-egg, for this egg was always removed just after laying. Under these circumstances, the c-egg was only 5.2 per cent smaller than the a-egg. It was also significantly larger than the normal expected size of the c-egg ($p < 0.001$), and not significantly different from the b-egg. Furthermore, the d-egg which was subsequently laid was 13.0 per cent smaller than the a-egg, and no different from the size of the normal c-egg ($t = 1.62$) ($P < 0.3$, Table I5)

Again, in the continuous egg removal experiment, a similar pattern was noticed. In this case, no eggs that would encourage broodiness remained in the nest, and as would be expected the d-egg was not significantly smaller than either the b or c eggs. Moreover the group that laid without interruption (protracted) showed the least difference between a and c eggs :

		Percentage difference a : c eggs
Normal laying		10.40%
Experimental laying		
pattern (i) c/3		5.34%
pattern (ii) c/4		4.96%
pattern(iii) c/5	protracted	2.03%

The addition of an extra egg after the laying of the a-egg did not result in a further reduction in the size of the c-egg, which was as usual 9.6 per cent smaller than the a-egg (Table 15).

These comparisons lead to the conclusion that the onset of incubation is responsible for the relatively smaller size of the c-egg. When the a-egg is not present to stimulate broodiness, the c-egg is no longer significantly smaller than the first two eggs. Instead, the ensuing d-egg shows this volume difference. In three nests, when both the a and b eggs were removed, three further eggs were laid. In this case, the e-egg was 12.6 per cent smaller than the c-egg, whilst the d-egg was the size of the normal b-egg. Finally, when all eggs were removed, the protracted layers showed no significant volume change between consecutively laid eggs. The eggs, however, became progressively smaller, though the ninth egg was only 7.4 per cent smaller than the first egg (Appendix III).

Effects of broodiness on the proportions of yolk and albumen

Variability in the size of eggs does not necessarily reflect a proportionate difference in the relative weights of yolk, albumen, and shell. Harris (1964) stated that "yolks represented the same proportion of the egg weight as in a, b or c eggs", and suggested that the smaller c-egg was merely a scaled down a or b egg. Similarly, Paludan (1951) argued that the depressive action of incubation on the c-follicle was based on the supposition that small eggs correspond to small yolks.

It will be shown later that although there is a general correlation between egg size and yolk weight, the c-egg is not a scaled down a-egg. Instead, it has proportionately more yolk and less albumen than either the a or b eggs (see section 6). For instance, a 90 gram a-egg contains approximately 22.1g of yolk, whereas the yolk of a similar sized c-egg would weigh about 23.5g. However, because the c-egg is smaller, its mean yolk weight is usually, but not significantly, less than that of the a-egg, the major weight difference being in the albumen.

If broodiness affected the c-follicle, the resulting yolk would be expected to be smaller than the a-yolk. Conversely, when broodiness is inhibited, the c-yolk should show an increase in weight corresponding to the ensuing increase in the size of the c-egg. When the normal egg and yolk weights are compared with those obtained from the protracted laying experiments, these expected differences are not apparent (Table 17). The yolk weights remain fairly constant, whilst it is a significant increase in the albumen (plus shell) weight that accounts for the heavier c-egg produced under these conditions ($p < 0.01$). This is illustrated by comparing the ratio of yolk and albumen expressed as a percentage. For the a-egg, this value was the same in both groups. However, the result of the c-egg proportions was 36.14 per cent in the control eggs, and 34.44 per cent for the larger protracted layings ($p < 0.02$).

Table 17. Comparing yolk and albumen weights of control c-eggs, and of c-eggs produced during the continuous egg removal experiment. Weights in grams with one standard error.

	N	c-egg wt.	Albumen + shell wt.	Yolk wt.	% yolk/albumen + shell
Control	45	82.56 ± 1.02	60.74 ± 0.81	21.82 ± 0.26	36.14 ± 0.54
		$p < 0.05$	$p < 0.01$	NS	$p < 0.02$
Expt.	45	85.73 ± 0.97	63.87 ± 0.87	21.87 ± 0.23	34.44 ± 0.47

This suggests that the depressive effect of incubation during the laying period is restricted to the albumen of the c-egg, although it obviously causes complete degeneration of the d-follicle (yolk) under normal conditions.

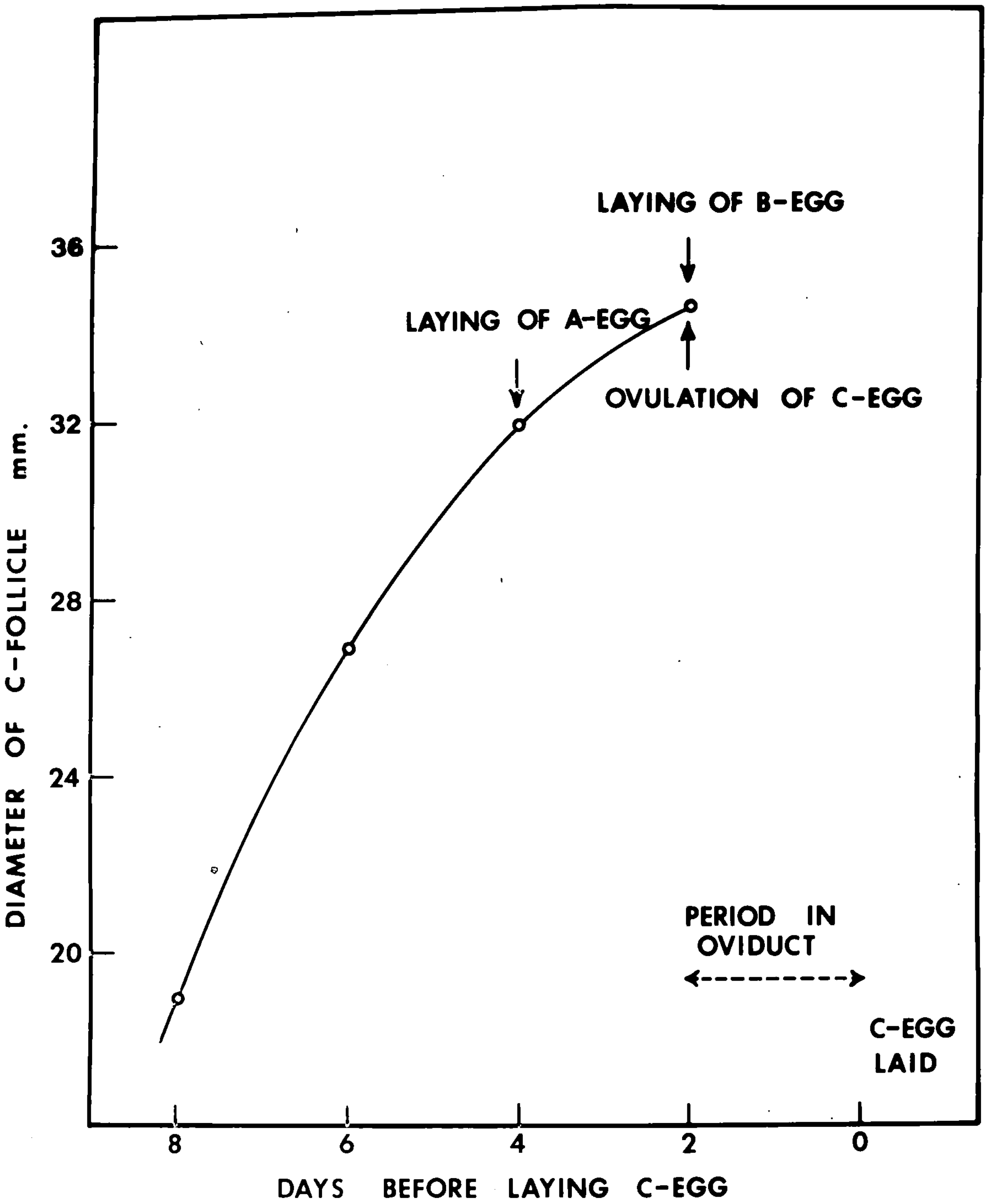
Paludan (1951) examined an ovary just before the first ovulation, and measured the diameters of the four largest follicles. Using these figures, an approximate reconstruction of the events prior to the laying of the c-egg can be attempted (Fig.9).

Ovulation in most birds occurs just after the laying of the previous egg, and so successive ovulations take place at an interval of the same magnitude as that between laid eggs (Sturkie 1954). The ovum (yolk) of the c-egg is therefore released into the body cavity two days before the actual egg is laid, and two days after the laying of the a-egg. At the time that the a-egg is laid the c-follicle has almost attained maximum size, and so unless broodiness elicits an immediate and depressive response, it will have no effect on the ultimate size of this follicle.

It is during the two days after ovulation that fertilisation, and then the secretions of albumen, shell membranes, and shell take place in the oviduct (Sykes 1959). Without chemical analysis of the albumen, it is impossible to conclude whether protein deposition or water uptake or both contribute most to the differences between the albumen weights of these c-eggs. Nor is it easy to understand how the onset of incubation can cause these differences. It is,

Figure 9.

Estimated change in the diameter of the c-follicle prior to laying of the c-egg, illustrating the timing of events during the laying sequence (based on measurements of follicle size from Paludan 1951)


LAYING OF B-EGG
LAYING OF A-EGG
OVULATION OF C-EGG
PERIOD IN OVIDUCT
C-EGG LAID
36
32
28
24
20
DIAMETER OF C-FOLLICLE mm.
8
6
4
2
0
DAYS BEFORE LAYING C-EGG

however, known that in the domestic fowl the oviduct is more sensitive than the ovary to factors adversely affecting egg formation (Romanoff & Romanoff 1949). Also, it is the rapidly growing follicles that maintain the oviduct in a highly functional state, by the secretion of oestrogen. Broodiness is effected by the secretion of an anterior pituitary hormone, prolactin, which also decreases the production of gonad-stimulating hormones. Without the latter, the d-follicle and others degenerate and the ovarian secretion of oestrogen is depressed. This chain of events might account for the slightly less productive oviducal materials laid down for the c-egg in the control conditions. Nevertheless, the more important conclusion is that the c-yolk is relatively constant in size irrespective of the experimental or natural conditions.

A general uniformity in egg and yolk size is a characteristic of these laying patterns. For example, yolk of the j-eggs (10th) laid during protracted laying was only 2 grams lighter than that of the a-egg, and the total egg weights decreased by a similar proportion of 9 per cent (Appendix III). Furthermore, the last egg laid in any cycle appeared to have the same weight and yolk content regardless of the total number of eggs in the cycle. Those adults that laid only five eggs produced an e-egg no larger than the 10th egg of a more prolific layer (Table 18).

This implies that a follicle must attain a certain size before it will undergo ovulation. Instead of laying progressively smaller eggs, this minimum size limits the

Table 18. The mean egg weights of the last egg laid in a series compared with the first egg of the same series

Number of eggs laid	N	Wt. last egg g ± 1 st.error		Wt. a-egg g ± 1 st.error	
5	13	79.64	1.36	85.59	1.50
6	19	82.67	1.06	87.83	0.98
7	18	83.01	1.60	89.96	1.02
8	19	80.62	1.43	90.52	1.15
9	5	78.41	2.50	86.32	2.47
10 & 11	7	81.76	1.29	90.96	2.33

Table 19. The mean and standard error of the volumes of two and three egg clutches (cc.)

	N	a-egg	b-egg	c-egg
C/2	30	75.56 ± 1.34	71.34 ± 1.17	-
		p-NS	$p < 0.001$	
C/3	50	78.80 ± 1.02	78.14 ± 0.96	70.58 ± 1.04

number of eggs a particular individual can lay. An equivalent situation occurs naturally in the field. Some clutches are of only two eggs instead of the usual three. In this case, the volumes of the b-eggs are no different from the volumes of the normal c-eggs (Table 19). A corresponding relationship was shown in the Kittiwake (Coulson 1963), which more frequently lays two egg clutches

(75 per cent). In this species, the volumes and shape indices of single egg clutches, and of the last eggs laid in clutches of two and three, all closely resembled one another.

These figures indicate that the extra eggs required to increase the clutch size to three would be below the minimum size limit for an egg, and are therefore not laid. It would, of course, be interesting to know whether birds that lay one and two egg clutches have several other developing follicles as is characteristic of normal females.

Initially, these investigations were aimed at determining and accounting for the size difference seen in the c-egg, and appreciating its possible effect on the mortality of the third chick. However, although the a and b eggs are similar in weight, it became apparent that there was also a marked difference between these eggs (section 6). The b-yolk was significantly heavier than the a-yolk ($p < 0.001$) by a difference of nearly 1 gram (4%). (Fig.15, Table 29). In the domestic fowl the amount of yolk increases through the first year, but the increments in yolk size gradually become smaller (Romanoff & Romanoff 1949).

The cause of this yolk difference is possibly an increase in physiological efficiency as development progresses from the first follicle to the second. On this assumption, the yolks of protracted layers would be expected at least to remain the same size as the b-yolk. Instead, they decrease in weight.

However, irrelative of the variability in the yolk content, the total egg weight remains the same. For instance, when the b-yolk was 1.16g heavier than the a-yolk, its albumen and shell weight was 1.46g lighter (N=11). The same occurred between the b and c eggs in the protracted layers, although subsequent eggs became smaller.

The ovulated egg spends a major part of its time in the uterus (75%), where it receives the shell, and where water and salts are added to the albumen (Sturkie 1954). It would therefore seem that the oviducal secretions of albumen and shell tend to bring the egg up to a fairly constant size, characteristic of the individual female, or more correctly of the individual uterus.

control nests.

SECTION SIX

THE EGG

The account of the control of laying has in places employed the results of a general investigation of the Herring Gull egg. Notwithstanding this anticipation, the following section describes the variability in egg size and content within a clutch and through the season, both in an attempt to determine the effects of re-laying on egg quality, and of egg size on the subsequent future of the chick.

6.1 Variation in egg size

Variation within the clutch

In the 1968 control area, a total of 455 clutches of three eggs were measured through the season and, as far as could be detected, none of these were re-laid clutches. The mean egg dimensions are shown in Table 20 for a, b, and c-eggs. The length, breadth, and volume of the b-egg were significantly smaller than those of the a-egg ($p < 0.001$), and likewise the c-egg was significantly smaller than the b-egg. However, the volume difference was only 1.8cc between a and b eggs, compared with 8.6cc between b and c-eggs. Conversely, the shape index increased from a to c-eggs ($p < 0.001$). This was somewhat expected, since there is a general inverse relationship between the shape index and the volume :

$$\text{Volume} = L.b^2.K.$$

$$\text{Shape index} = \frac{b}{l}$$

$$= \frac{b^3}{V}.K$$

l = length, b = breadth, V = volume, K = constant

Table 20. Mean egg dimensions of 455 clutches laid on North Ness (control) in 1968 ± one standard error (N.B. does not include repeat clutches)

	length mm	breadth mm	volume cc	shape index
a-egg	69.38±0.14	48.54±0.07	77.92±0.29	70.06±0.16
b-egg	68.48±0.13	48.28±0.07	76.12±0.29	70.59±0.13
c-egg	66.21±0.13	46.85±0.07	69.32±0.30	70.84±0.14

The relationship is complicated since the volume also incorporates the length and breadth of the egg. However, the breadth is a much more stable parameter than the length with coefficients of variation (CV) 3.1 and 4.2 respectively (CV = standard deviation x 100/mean).

So the shape index of small a-eggs (67.5cc. N=40) is 70.27, whilst larger a-eggs (88.3cc.N=57) have an index of only 69.54. Barth (1967) pointed to a similar correlation between species, with the shape index increasing gradually in species that lay smaller eggs (Table 21).

Table 21. Mean volumes and shape indices of eggs of various species of Laridae

Species	Volume cc.	Shape index	
Greater Black-backed Gull	113.4	68.3	Barth (1967)
Herring Gull	94.1	68.9	Barth (1967)
Lesser Black-backed Gull	74.9	70.3	Barth (1967)
Common Gull	51.9	71.9	Barth (1967)
Kittiwake	43.2	73.3	Coulson (1963)
Common Tern	17.1	74.1	Dunn (pers.comm.

Although the eggs of the Herring Gull, Lesser Black-backed Gull, and Greater Black-backed Gull conform to this pattern of increasing shape index with decreasing volume, the Kittiwake (Coulson 1963) and the Common Gull (Barth 1967) c-eggs have both the smallest shape index and the smallest volume.

In the previous section, it was concluded that oviducal secretions tend to bring eggs up to a size characteristic of the individual female gull. It would follow that gulls laying large a-eggs should also lay large b and c eggs, and conversely gulls laying small a-eggs should lay small b and c eggs. This is generally correct, for when volumes of 455 a-eggs were correlated against those of b and c eggs, the resulting correlation coefficients (+0.764 and +0.651 respectively) were highly significant ($p < 0.001$).

The difference between egg volumes of clutches of three and clutches of two eggs has already been mentioned (section 5).

Seasonal variation

Egg size has been shown in the Kittiwake (Coulson 1963), the Shag (Coulson et al 1969), and the Gannet (Nelson 1966) to decrease as the breeding season progresses. In addition it is known in these species that older females tend to breed earlier and also lay larger eggs than younger birds. However, Coulson et al (1969) have recently separated both the age and the seasonal effects, and have concluded that females of the same age lay larger eggs earlier in the season, whilst at the same time in the season young females lay smaller eggs than older birds. In other words, both these effects contribute towards the 10-11 per cent change in mean egg volume recorded through the season for the Kittiwake and the Shag.

Although Barth (1967) divided his Herring Gull measurements into early and late laid eggs and showed a corresponding decrease in volume, his late clutches were mainly re-layings. Harris (1969) measured 100 clutches but found no change in egg or clutch volume through the season. The Isle of May data, discounting re-laid clutches, were therefore analysed for volume change through the season (Appendix IV).

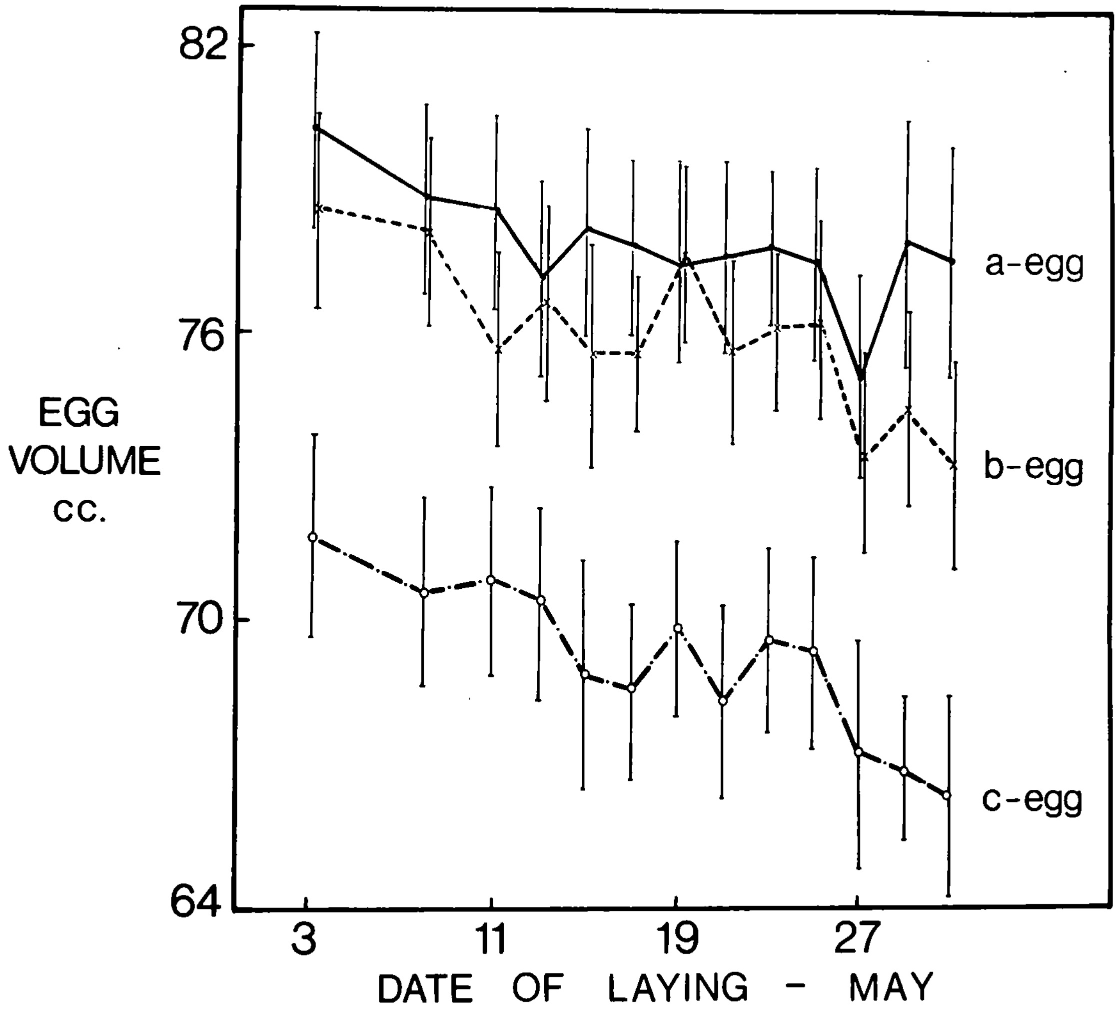
There is a progressive decrease in the mean volumes of a, b, and c-eggs through the season (Fig.10), and when the measurements are divided into five time groups, the decrease becomes significant between layings separated by more than 15 days. Between the extremes of laying dates, the difference is highly significant ($p < 0.001$) except in the a-egg. In fact egg volume decreases least in the a-egg and most in the c-egg. From the calculated regression lines of egg volume against laying date, the average decrease in egg volume from 3 May to 31 May was as follows :

Figure 10.

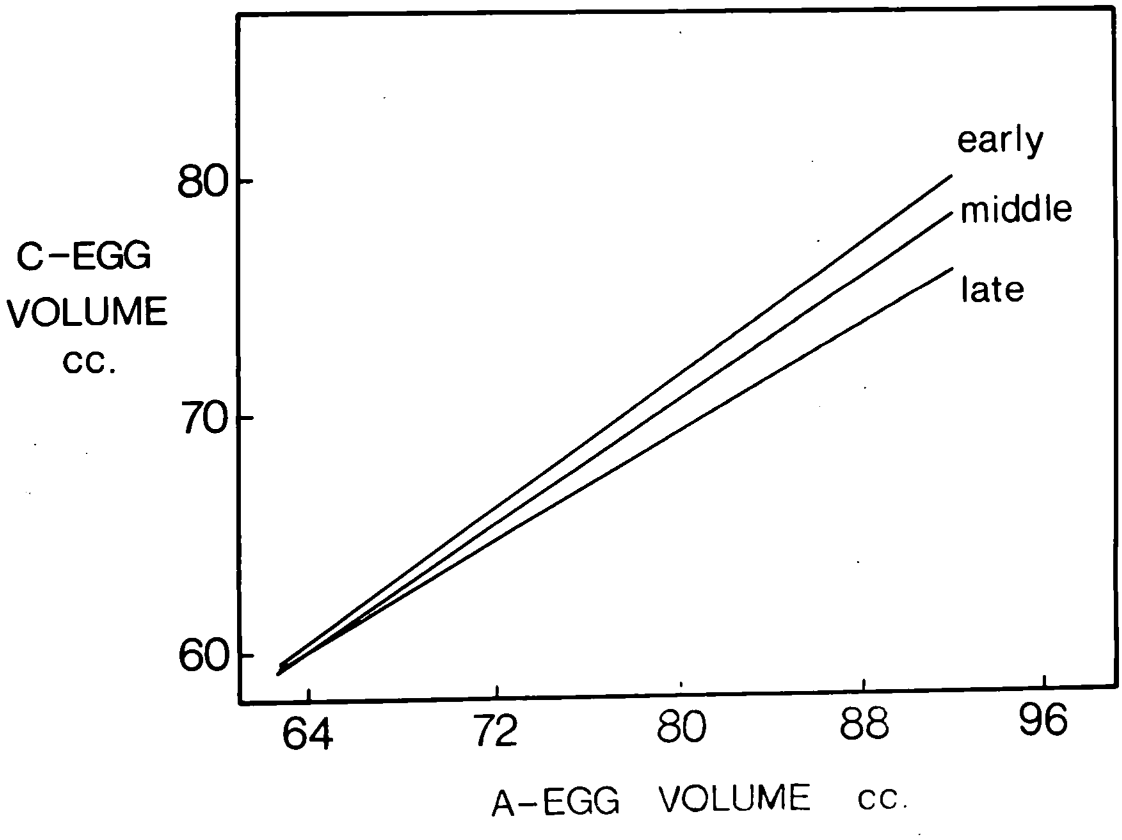
Variation in the mean volume of a, b and c-eggs (± 2 standard errors) through the season for c/3 only, excluding repeat layings - North Ness control area 1968

Figure 11.

Regression lines of c-egg volume on a-egg volume for clutches laid early (up to 9 May), middle (9 - 17 May), and late (after 17 May) in the season on the North Ness control area 1968



82
76
70
64
EGG
VOLUME
cc.
a-egg
b-egg
c-egg
3
11
19
27
DATE OF LAYING - MAY



80
70
60
C-EGG
VOLUME
cc.
early
middle
late
64
72
80
88
96
A-EGG VOLUME cc.

Seasonal decrease in egg volume calculated from Fig.10

	decrease in volume cc	Percentage decrease
a-egg	2.5	3.2%
b-egg	4.2	5.4%
c-egg	4.8	6.6%

This means that the difference already noted between the a and c-eggs is exaggerated through the season in normal laying and is as much as 14.5 per cent at the end of May, compared with 10 per cent at the beginning of laying. When a-egg volumes are correlated against c-egg volumes at various times in the season, the same result is obtained (Fig.11).

The trend for the c-egg to show the greatest volume decrease was contrary to Barth's (1967) results, which suggested the opposite to be the case. Again, in the Kittiwake the c-egg was the least variable with season. This could be predicted, since in the Kittiwake (Coulson 1963) and also in the Herring Gull (Andersen 1957) the c-egg becomes more and more different from the first two as the age of the female increases, and therefore as the laying date becomes earlier in the season. However, although the age effect should result in a less variable c-egg, the season itself may in this case exert an overriding effect to produce the differences shown in this study. One final explanation can be offered for an interpretation of Barth's results. The difference between the mean a and b egg volumes and the c-egg volume in 54 first clutches was compared with the same difference in their subsequently re-laid clutches and found to be 7.42 per cent and 6.11 per cent respectively. Therefore, under these circumstances the decrease was least in the re-laid eggs, and Barth's late laying group were mainly repeat clutches.

Returning to the normal clutches, the results indicate that if the third chick suffers a higher mortality due to the c-egg volume difference, then there would be a trend for this differential mortality to increase through the season.

Variation with re-laying

In any experimental investigation it is important to determine and separate the factors that are directly and indirectly related to the experimentation. Egg size has been shown to decrease with the progress of the breeding season, due both to the age of the females and to the time of laying in the season. Delaying the breeding season by egg removal could directly affect the eggs and exaggerate the size decrease owing to the physical stress of producing a second clutch. Indirectly, re-laying could merely result in an extrapolation of the seasonal effect; conversely, an older bird re-laying later in the season may lay eggs of a greater volume than that expected for the delayed laying date.

The eggs of 97 clutches were measured before removal, and the same measurements taken for the clutches re-laid in these nests. Using mean egg volumes obtained from the graph of normal laying in the control areas, it was possible to compare re-laying with the expected results.

The loss in total egg volume between clutches laid at different times in the season will vary according to the interval between the laying of these clutches. This loss was calculated for three time intervals in the control layers, and compared with the decrease observed in the re-laid clutches (Table 22). Although the rate of decrease was similar in both cases (0.4 and 0.5cc/day respectively), the total volume loss was always greater in the re-laid clutches, suggesting that the seasonal effect was not the only influence on egg size in repeat clutches.

Table 22. The decrease in total egg volume for clutches of three eggs during re-laying according to the interval between the laying of the first and repeat clutches.

Observed (O) and expected (E) results compared

Interval between clutches	No.clutches	Decrease in total egg volume			
		cc.		%	
		O	E	O	E
17 days	17	8.5	7.5	3.7%	3.4%
25 days	15	12.8	10.4	5.5%	4.6%
38 days	11	20.5	16.0	8.8%	7.0%

Table 23. Observed (repeat clutches) and expected (normal clutches) decrease in the volumes of a, b, and c eggs from 17 May - 4 June (18 days) calculated in regression lines in Fig.12

	Volume decrease cc.	
	Re-laid clutches	Normal Expected
a-egg	4.5	1.6
b-egg	3.2	2.8
c-egg	0.7	3.1

When the volume decrease is divided into the a, b, and c egg components, it becomes apparent that the first two eggs are contributing far more than the c-egg to the difference (Table 23). This is most noticeable when the mean egg volumes are plotted against the laying dates of the repeat clutches (Fig.12). The calculated regression lines appear as a continuation of the control data, but differ markedly in two respects. Firstly, the decrease in egg volume as the season advances is not so prominent; secondly, the difference in size between the first and repeat clutches is mainly the result of a smaller a-egg, rather than an exaggerated seasonal effect.

The volume of the c-egg is particularly constant with time, at a level of 68 ± 6cc (one standard deviation). This volume corresponds closely with that of the last laid eggs in the protracted laying experiment (approx. 69cc), and with the volumes of the control c-eggs near the end of the normal laying period, at a time when c/2 are frequently laid. It is therefore suggested that there is a minimal size for the c-egg, below which it is re-absorbed and not laid, and that the c-egg regression line represents a level not far above this minimum.

It has already been mentioned that in normal clutches the first two eggs of c/2 are smaller than those of c/3 (Section 5). The same significant difference is seen in the repeat clutches, especially between the b-eggs (Table 24, $p < 0.01$), and can be represented graphically by the regression lines of the combined a and b egg volumes (Fig.13).

Assuming that only females laying b-eggs larger than 72cc will lay a c-egg, this prediction can be tested with the original

Figure 12.

Regression lines of the variation in a, b and c-egg volume with the date of laying (1968) for first and repeat clutches.

Figure 13.

Regression lines of the variation in combined a and b-egg volume for repeat clutches according to clutch-size and date of laying (1968)

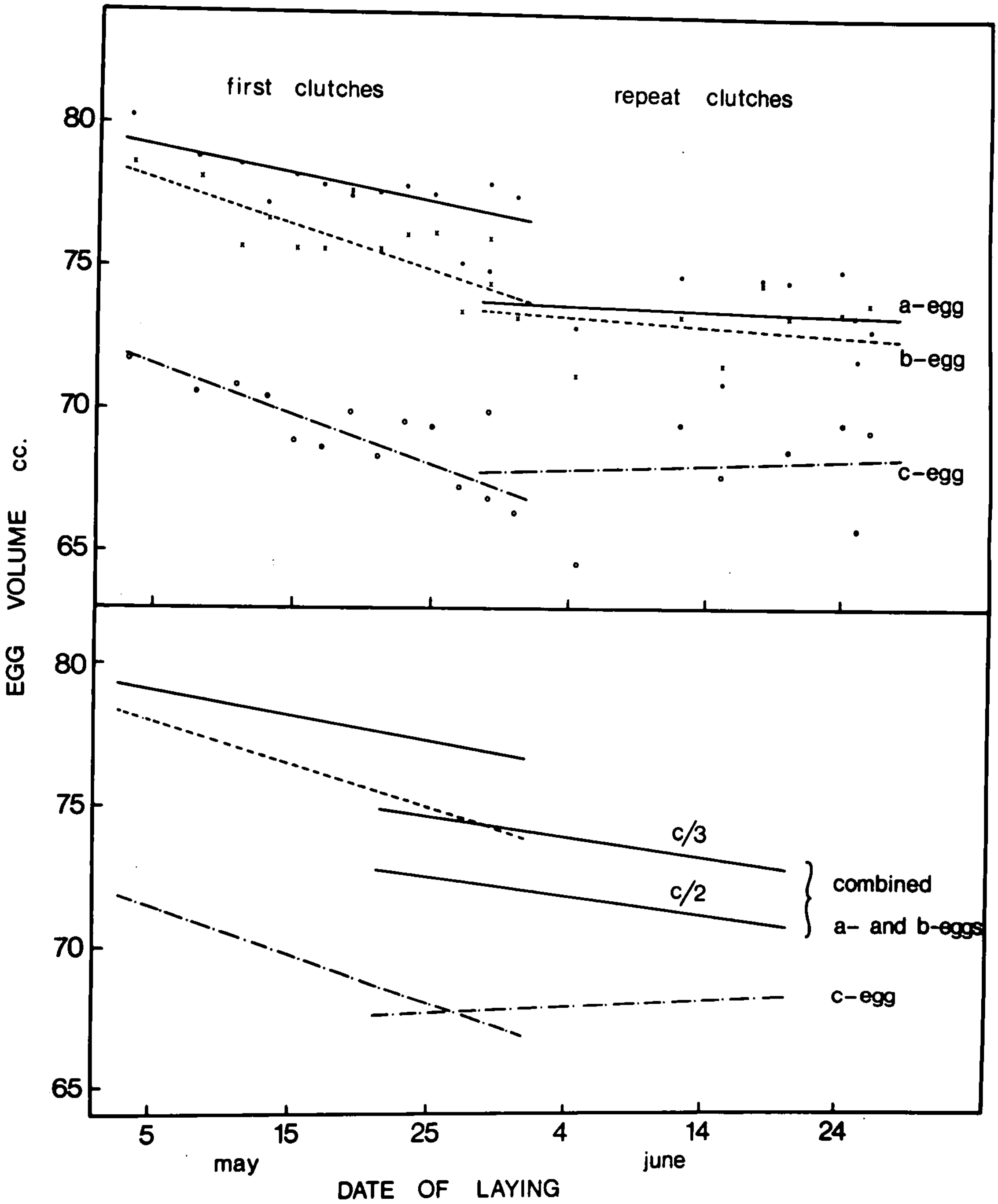

first clutches
repeat clutches
80
75
70
65
a–egg
b–egg
c–egg
EGG VOLUME cc.
c/3
c/2
combined
a- and b-eggs
c–egg
5
15
25
4
14
24
may
june
DATE OF LAYING

Table 24. Volumes of a and b eggs of repeat clutches, to show the difference between C/2 and C/3

	N	Volume cc ± 1 st.error a-egg	b-egg
C/3	104	74.12 ± 0.63	74.07 ± 0.68
		NS	$p < 0.01$
C/2	69	73.02 ± 0.61	70.98 ± 0.76

field measurements (Table 25). From 165 clutches, it was found to be 70 per cent correct, at a significance level of $p < 0.001$. Therefore, it seems that when the a and b eggs fall below a certain level, no third egg is laid. The relationship between the decline in egg volume and the seasonal changes in clutch size will be referred to in Section 7.

Table 25. Predicting whether a c-egg will be laid according to the size of the b-egg (72cc) - i.e.

Volume > 72cc - C/3 laid

Volume < 72cc - C/2 laid

Predicted clutch size	Prediction incorrect	correct	Total	Percentage correct	X^2 p.
C/3	21	46	67	69%	$p < 0.002$
C/2	29	69	98	70%	$p < 0.001$
Total	50	115	165	70%	$p < 0.001$

Variation within the colony

There is evidence in the Kittiwake (Coulson 1968) and the Shag (Coulson et al 1969) that birds nesting on the periphery of expanding colonies are mainly young birds, whilst those in the centre are predominantly older. Differences in the breeding biology of Herring Gulls in various parts of the colony indicate that a similar situation is manifest in this species (see Section 7).

Since gulls on the edge of the colony breed later, then the difference in mean egg volumes between edge and centre groups is quite expected. However, when eggs laid at the same time in the season are compared, all three eggs of the peripheral group are consistently, but not significantly, smaller than those from the centre (Table 26). It is possibly a result of young birds on the edge breeding at the same time as the older birds, or even a difference in the quality of birds of the same age nesting at the edge and the centre of the colony.

Table 26. Egg volumes of clutches laid at the same time in nests at the edge (N = 40) and in the centre of of the colony

	Volume cc.		
	a-egg	b-egg	c-egg
centre	77.79 ± 0.84	76.59 ± 0.91	70.28 ± 0.90
edge	76.96 ± 0.93	76.41 ± 0.86	68.90 ± 0.88

6.2 Component parts of eggs

Method

Separation of the egg into shell, yolk and albumen by hard boiling is only effective in fresh eggs. It has already been demonstrated (Section 5) that incubation of the a and b-eggs commences before the laying of the c-egg. The division between yolk and albumen breaks down during the early stages of incubation, rendering the separation of these constituents by hard boiling an impossible task. It was therefore necessary to remove each egg of a clutch as soon as it was laid, that is, before any incubation had taken place. In order to avoid disturbance to the normal laying pattern, other eggs were substituted when a and b-eggs were removed. Egg recognition does not develop immediately, if at all, and none of the replacement eggs were rejected.

A total of 273 clutches were collected in this way through the season. Of these, 154 were normal clutches separated into early, middle, and late layers, whilst the remaining 119 were re-laid clutches. Yolks were retained for fat analysis and, as before, shells, yolks and albumens were weighed to 0.01g.

Proportions of yolk, albumen and shell

Romanoff & Romanoff (1949) showed that birds' eggs can be grouped into two classes according to their relative amounts of yolk and albumen. Nidifugous birds, such as the domestic hen, lay eggs with a higher percentage of yolk in the egg (30-40 per cent) than nidicolous species, as for example the Laridae (25 per cent) (Table 27). A relatively large yolk assures a fairly advanced stage of development in the young at hatching, whereas chicks from small yolked eggs are helpless during the post-hatching period. Although the Herring Gull belongs to the latter group, its nestlings are comparatively more independent at hatching than many altrical species (e.g. Doves, Pigeons, with 18 per cent yolk).

Table 27. Proportional composition of average eggs of the Herring Gull and the domestic hen (Romanoff & Romanoff 1949)

	Herring Gull		Domestic Hen	
	wt.g.	% wt.	wt.g.	% wt.
Albumen	59.8	67.3	32.9	55.8
Yolk	22.3	25.1	18.7	31.9
Shell	6.8	7.6	6.4	12.3
Total egg	88.9	100.0	58.0	100.0

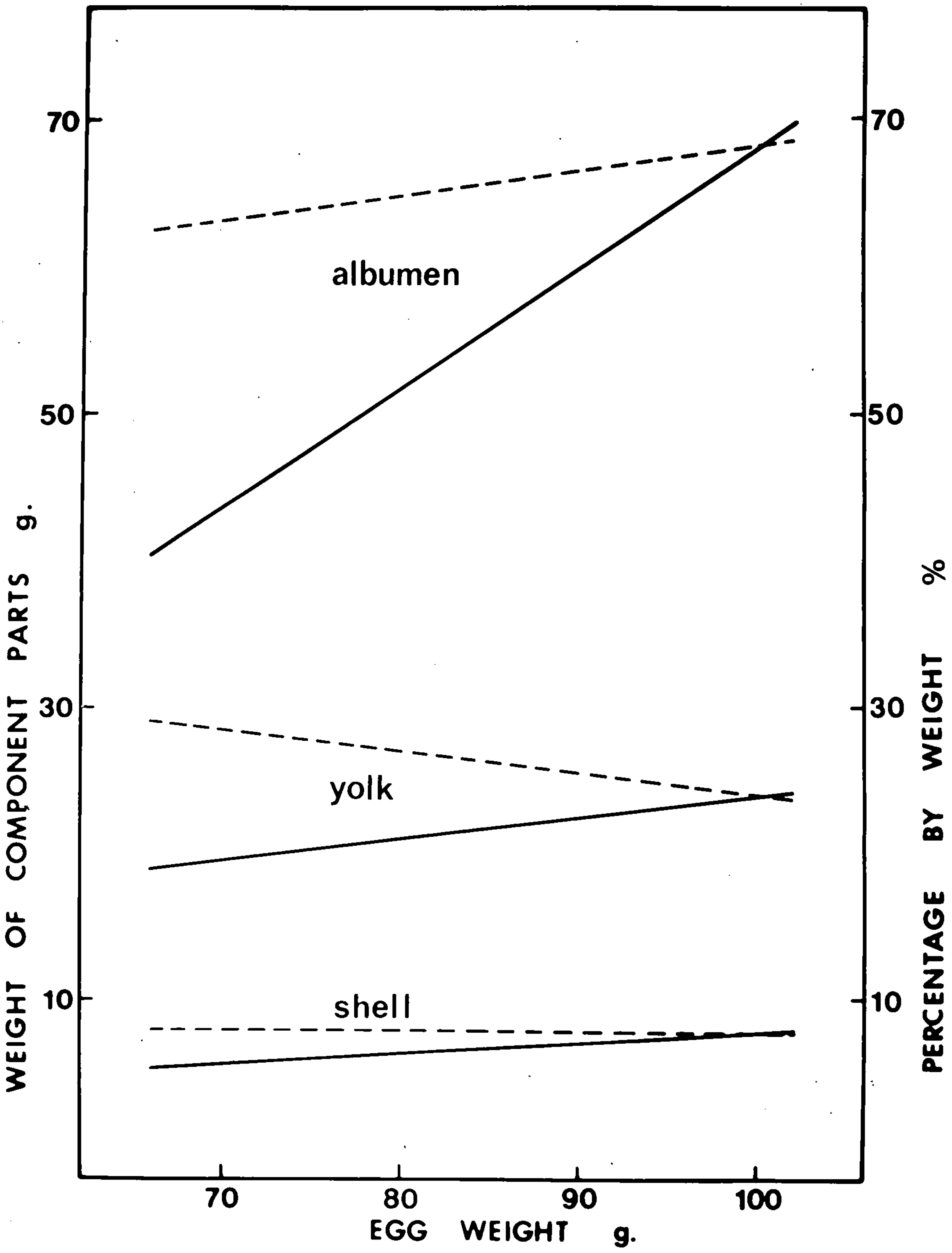
Table 28. Regressions of yolk, albumen, and shell weight on egg weight

	N	Mean weight gm.	Slope	Correlation coefficient - r
Yolk	125	22.32	+ 0.187	0.721
Albumen	210	57.29	+ 0.813	0.932
Shell	160	6.68	+ 0.067	0.770

The relative proportions of yolk and albumen and shell vary with the size of the egg. Larger gull eggs contain relatively less yolk and more albumen than smaller eggs (Fig.14), although the actual weight of the yolk does increase with egg size. There is a significant positive correlation between yolk, albumen, and shell weights and total egg weight (Table 28), but the yolk and shell are the least variable components. Between the extremes of egg size, the albumen varies from 40-70g (42 per cent), whilst the yolk only increases from 17-25g (30 per cent). Similarly, by listing eggs of various species by size, the yolk constitutes an ever larger proportion of the total egg weight as the egg size decreases (Romanoff & Romanoff 1949).

Figure 14.

The component parts of eggs. Regression lines of the variation in weight (continuous line) and percentage composition (dotted line) of shell, albumen and yolk of eggs of various sizes


70
50
30
10
70
50
30
10
albumen
yolk
shell
WEIGHT OF COMPONENT PARTS g.
PERCENTAGE BY WEIGHT %
70
80
90
100
EGG WEIGHT g.

Variation within the clutch

The regression of yolk weight on egg weight (Fig.15) shows a trend, though not significant, for the a-egg to contain relatively less yolk than the other two eggs (Table 29). At any stage in the season the mean yolk weight for the c-egg is no different from that of the a-egg, even though the total egg weight is significantly lighter ($p < 0.001$). It is the albumen which accounts for this difference (Table 29). The importance of this phenomenon in the understanding of egg laying and post-hatching mortality will be referred to later.

Variation through the season and with re-laying

It has previously been shown that egg size decreases both through the season and with re-laying, and this effect was obviously evident in the weights of yolk (Table 30) and albumen. However, in order to investigate whether the proportion of these components remained the same under varying conditions, the regressions of egg weight against yolk weight were compared (Appendix V). Eggs of the same size had a similar composition early and late in the season, whereas in the middle of the laying period there was relatively more yolk in larger eggs ($p < 0.001$, Fig.16). Whether this represents the optimum environmental conditions for egg laying is not known. The percentage of yolk in re-laid eggs was no different from normal clutches.

Figure 15

Regression lines of yolk weight on egg weight according to the sequence of laying.

Figure 16

Regression lines of yolk weight on egg weight for clutches laid early (up to 9 May), middle (9 - 17 May) and late (after 17 May) in the season

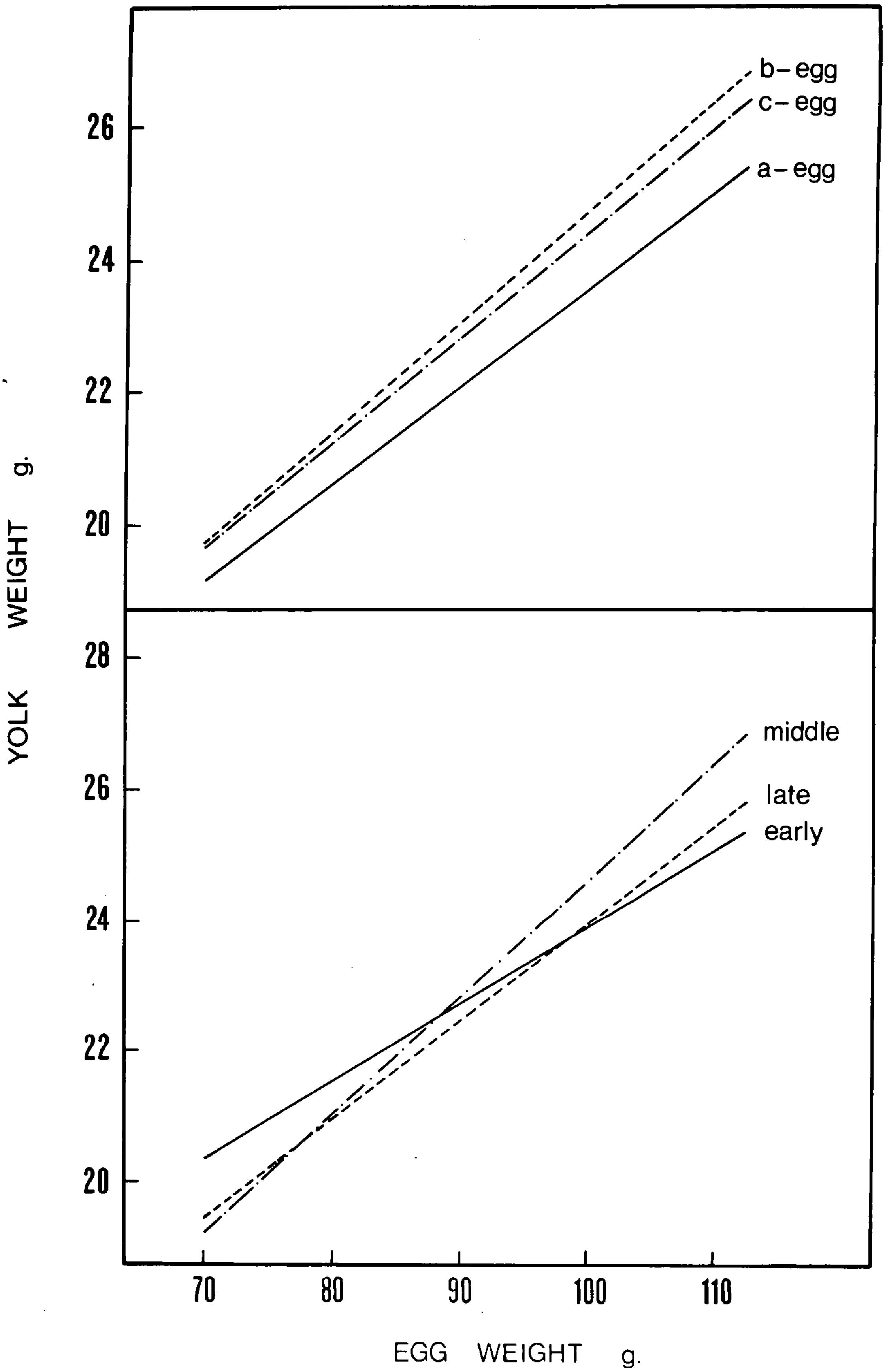

b- egg
c- egg
a- egg
middle
late
early
YOLK WEIGHT g.
26
24
22
20
28
26
24
22
20
70
80
90
100
110
EGG WEIGHT g.

Table 29. The relationship between egg weight, yolk weight, and albumen weight for eggs
according to laying sequence
± one standard error

YOLK

Laying sequence	N	Mean egg wt.g.	Mean yolk wt.g.	% Yolk	Correlating yolk wt. on egg wt. Slope	Intercept.	coeff.-r.
a-egg	121	90.64±0.73	22.25±0.17	24.5%	+0.146±0.018	9.01	+0.63
b-egg	118	89.98±0.68	23.11±0.18	25.7%	+0.168±0.019	7.98	+0.62
c-egg	109	83.88±0.65	21.92±0.17	26.1%	+0.162±0.020	8.51	+0.61

ALBUMEN

			Mean albumen wt.g.	% albumen	Correlating albumen wt. on egg wt. Slope	Intercept.	coeff.-r.
a-egg	105	88.79±0.53	58.97±0.49	66.4%	+0.830	-14.68	+0.90
b-egg	70	87.00±0.78	56.78±0.68	65.3%	+0.806	-13.37	+0.91
c-egg	35	81.46±1.44	53.27±1.21	65.4%	+0.807	-12.44	+0.93

Table 30. Mean Yolk and Egg weights through the season ± one standard error

		Date of Laying			
		Early (up to 9/5)	Middle (9/5-17/5)	Late (after 17/5)	Re-layers
	N	50	42	20	71
egg wt.	a-egg	91.34±0.97	89.91±1.26	90.13±2.15	85.62±0.67
	b-egg	89.84±0.94	90.30±1.22	89.73±1.69	86.92± 0.67
	c-egg	84.40±0.88	83.77±1.18	82.91±1.55	80.63±0.64
yolk wt.	a-egg	22.40±0.23	22.16±0.32	22.03±0.35	20.94±0.17
	b-egg	23.23±0.25	23.06±0.34	22.85±0.39	22.11±0.20
	c-egg	22.32±0.23	21.71±0.31	21.39±0.36	20.94±0.19

6.3 Yolk lipid content

Lipids form the largest part of the organic solid matter in the yolk (Romanoff & Romanoff 1949), and are indispensable to the life and growth of the chick embryo. Variations in the lipid content are therefore of considerable biological importance. The albumen contains virtually no lipids, and so only the yolks were retained for lipid analysis.

Method

The hard-boiled yolks were dried in a vacuum oven to constant weight, and the soluble lipids extracted with a petroleum-ether mixture, using a modified soxhlet technique (after Evans pers.comm.).

Table 31. Relationship between egg weight, yolk weight, and soluble lipid weight (dry)

Regression x	Regression y	N	mean x gm.	mean y gm.	slope y on x	correlation coefficient
Egg wt :	yolk wt	42	88.90	22.62	+0.30	+0.88
Yolk wt dry:	yolk lipid	42	11.45	6.92	+0.62	+0.95
Egg wt :	yolk lipid	42	88.90	6.92	+0.09	+0.81

Table 32. Lipid extraction of 15 clutches to show relationship between egg weight, yolk weight, and soluble lipid content

	mean egg wt.	mean yolk wt. (wet)	per cent yolk	mean yolk wt. (dry)	mean lipid wt.	lipid x 100 dry yolk wt.	lipid x 100 egg wt.
a-egg	92.15	23.00	25.0%	11.61	6.92	59.6%	7.5%
b-egg	91.19	23.00	25.2%	11.61	7.02	60.5%	7.7%
c-egg	83.96	21.76	25.9%	11.10	6.75	60.8%	8.0%

Results

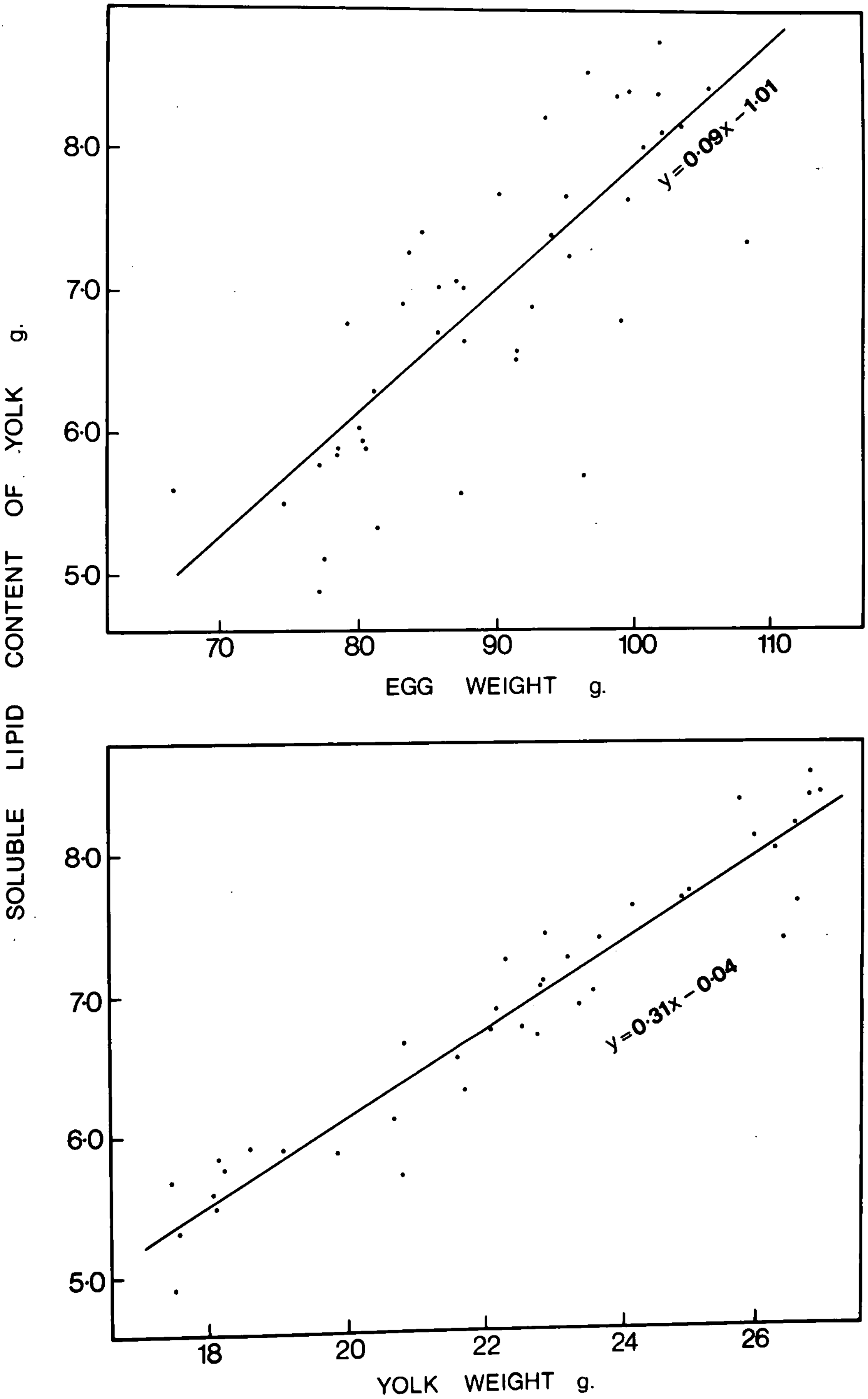
The soluble lipid content represented about 60 per cent of the dry yolk weight. There were significant positive correlations between lipid weight and egg weight and between yolk weight and egg weight (Table 31), which would indicate that egg size is an appropriate guide to the energy available to the chick embryo. Yolk lipid weight ranged from 5.0-8.5gm between small and large eggs (Figs.17 & 18).

Figure 17

Regression of soluble lipid content of yolk on egg weight

Figure 18

Regression of soluble lipid content of yolk on yolk weight


SOLUBLE LIPID CONTENT OF YOLK g.
8·0
7·0
6·0
5·0
y=0·09x-1·01
70
80
90
100
110
EGG WEIGHT g.
8·0
7·0
6·0
5·0
y=0·31x-0·04
18
20
22
24
26
YOLK WEIGHT g.

The total lipid extracted from the c-eggs was invariably less than that present in the a or b-eggs, although it represented a higher percentage of the total egg weight (Table 32). This emphasised the situation already noted with the yolk weights, where the b-egg was seen to contain the most yolk, and therefore lipid, of the eggs.

6.4 Relationships with egg size

Egg size and incubation period

In general, incubation and egg laying take longer in larger birds with larger eggs (Vemeer 1967), and this can be demonstrated within the Laridae family (Table 33). This is understandable, since the energy requirement for incubation is related to the surface area and weight of the eggs.

Table 33. Egg volumes and incubation periods of various Larus species, incubation measured from the laying to the hatching of the c-egg (k = 0.476 for volume index)

Species	N	vol.cc	incubation period days	
Black-headed Gull	624	32	22.8	Ytreberg (1956)
Common Gull	100	48	25.9	Barth (1955) and Witherby et al (1941)
Herring Gull	30	70	27.0	This study
Greater Black-backed Gull	35	94	29.0	Harris (1964)

Incubation periods of 134 a-eggs were analysed to investigate whether the same principle could be detected within the same species. The larger eggs ($>$76cc) took significantly longer to hatch than the smaller ones ($<$76cc) ($p < 0.001$), with an average difference of 16 hours for a 10cc increase in volume (Table 34). This would indicate that the incubation period of the smaller c-egg is less than that of the a and b eggs. Furthermore, it could explain why the initial difference of 32 hours between the development of the b and c eggs is reduced to approximately 18 hours at hatching.

Table 34. Incubation period for large and small a-eggs

Size of a-egg	N	Incubation period	
76cc (mean 82cc)	67	29.98 ± 0.08 days	
			$p < 0.001$
76cc (mean 71cc)	67	29.31 ± 0.11 days	

For the same reason, incubation takes less time later in the season when the egg size is decreasing (Table 35). It is noticeable that the shortening of the incubation period (20 hours) is greater than expected for a volume decrease of about 4cc, and it is therefore probable that in this case egg volume is not the only factor contributing to the shorter period. It is possible that as the season progresses, the onset of incubation follows more rapidly after laying.

Table 35. Incubation periods early (before 10 May) and late (after 24 May) in the season for a, b, and c eggs (sample number in brackets)

	a-egg	b-egg	c-egg
early	29.96 ± 0.19 (28)	28.43 ± 0.19 (28)	27.52 ± 0.18 (26)
	$p < 0.001$	$p < 0.002$	$p < 0.001$
late	29.08 ± 0.11 (79)	27.74 ± 0.12 (75)	26.70 ± 0.14 (41)

N.B. Incubation period is measured from the laying to the hatching of the egg

Egg size and hatching success

Egg removal as a method of delaying the breeding season produces its own effects which should be separated from any influence the time of laying may have on the breeding biology. Re-laid eggs show size differences, albeit marginal, from eggs of first clutches laid at the same time. It was therefore necessary to compare hatchability with egg size, so that any experimental effects on hatching success could be isolated.

Eggs were grouped according to egg volume and laying sequence and the percentage of eggs hatching was recorded (Table 36). There was no appreciable difference in the hatching success of a, b, or c-eggs. Hatching success was positively correlated with egg size ($p < 0.05$), although this relationship was reversed for the largest egg grouping of any egg in the laying sequence. It appeared that very small and very large eggs were less likely to hatch than those within the normal range of egg volume. It is possible that small eggs contain inadequate reserves for embryonic development, or are laid by adults less successful at incubation or protection of their clutches. At the other extreme, adults may not be able to provide the required heat exchange for the development of a clutch of very large eggs, since the energy cost of incubation is related to egg size (Drent 1967).

Tindell & Morris (1964) found a highly significant positive trend between egg size, fertility, and hatchability in poultry. It is interesting that the range in hatching success of hen's eggs was similar to the above results, varying from 73 to 82 per cent. A decrease in hatching success was also recorded for the largest egg grouping (Table 38), an effect which was not due to a reduction in the fertility of large eggs, but a result of subsequent incubation.

Table 36. Comparing egg volume with hatching success and laying sequence

		Egg volume cc									
		50-60	60-65	65-70	70-75	75-80	80-85	85-90	Total	X^2	P
	No.laid	-	-	47	111	116	115	60	349		
a-egg	No.hatched	-	-	34	81	93	96	45	449	5.7	NS
	% hatching success	-	-	72.3%	73%	80.2%	83.5%	75%	77.7%		
	No.laid	-	14	61	121	127	89	33	351		
b-egg	No.hatched	-	11	45	90	104	74	27	445	4.5	NS
	% hatching success	-	78.6%	73.8%	79.4%	81.9%	83.1%	81.8%	78.9%		
	No.laid	28	86	132	109	68	20	-	341		
c-egg	No.hatched	18	62	101	91	54	15	-	443	6.2	NS
	% hatching success	64.3%	72.1%	76.5%	83.5%	79.4%	75.0%	-	77.0%		
	No.laid	32	109	246	357	327	223	101	1041		
All eggs	No.hatched	19	79	183	273	265	184	78	1337	15.3	<0.05
	% hatching success	59.4%	72.5%	74.4%	76.5%	81.0%	82.5%	77.2%	77.9%		

Table 37. Comparing egg volume with hatching success for normal and re-laid eggs, and also with the percentage of addled eggs

		Egg volume cc									
		50-60	60-65	65-70	70-75	75-80	80-85	85-90	Total	X^2	P
Normal eggs (total)	No.laid	43	109	246	357	327	223	101	1041		
	No.hatched	19	79	183	273	265	184	78	1337	15.4	<0.05
	% hatching success	59.4%	72.5%	74.4%	76.5%	81.0%	82.5%	77.2%	77.9%		
re-laid eggs	No.laid	6	28	76	68	50	18	-	183		
	No.hatched	4	18	57	53	37	14	-	24.6	1.9	NS
	% hatching success	66.7%	64.3%	75.0%	77.9%	74.0%	77.8%	-	74.4%		
% addled eggs		12.5%	11.9%	6.9%	10.9%	8.6%	7.6%	11.9%	9.3%		

Re-laid eggs showed the same trend between egg size and hatchability (Table 37), and the total hatching success (74.4 per cent) was not significantly different from normal clutches.

Eggs that showed no sign of embryonic development were noted as addled, and these appeared to vary little with egg size (Table 37). Furthermore, all eggs of the laying sequence were equally prone to being addled, although the b-egg was, if anything, slightly less so than its siblings (Table 39). The same pattern occurred in re-laid clutches, where slightly more eggs were recorded as addled (also see Section 7). Any changes in the behaviour that is required for fertilisation of the eggs will be more prevalent at the onset and termination of laying. It is possible that at these times, when the a-eggs and then the c-eggs are being laid, fertilisation is less frequently completed. It must be emphasised, however, that differences seen in the b-egg are not significant.

Table 38. Percentage fertility and hatching success of domestic hen's eggs of various sizes

(Tindell & Morris 1964)

	Egg weight gm.			
	18-20	20-22	22-24	24-26
Percentage fertility	83.4%	86.3%	90.6%	92.6%
Percentage hatching success :				
i) from fertile eggs	88.0%	89.0%	90.6%	87.2%
ii) from all eggs	73.3%	76.8%	82.1%	80.7%

Table 39. Percentage of addled eggs and laying sequence

Sample number in brackets

	normal clutches	re-laid clutches
a-egg	10.0% (449)	12.9% (101)
b-egg	8.5% (445)	12.6% (95)
c-egg	9.0% (443)	13.3% (45)

Egg size and chick weight

Egg volume and chick weight on hatching were positively correlated (corr.coef. r =+0.91, N = 76, Fig.19). Unfortunately, it was not possible to measure the length of time after hatching that chick and egg weights are related. Various studies on poultry have shown a dependence of body weight on egg weight declining with age, having little effect after two weeks (Godfrey et al 1953), or after five weeks (Halbersleben & Mussehl 1922). However, others have claimed that the difference can still be detected as long as eight weeks (O'Neil 1950), and twelve weeks after hatching (Wiley 1950, Skoglund et al 1952, Morris et al 1968).

6.5 Fate of the third chick

Introduction

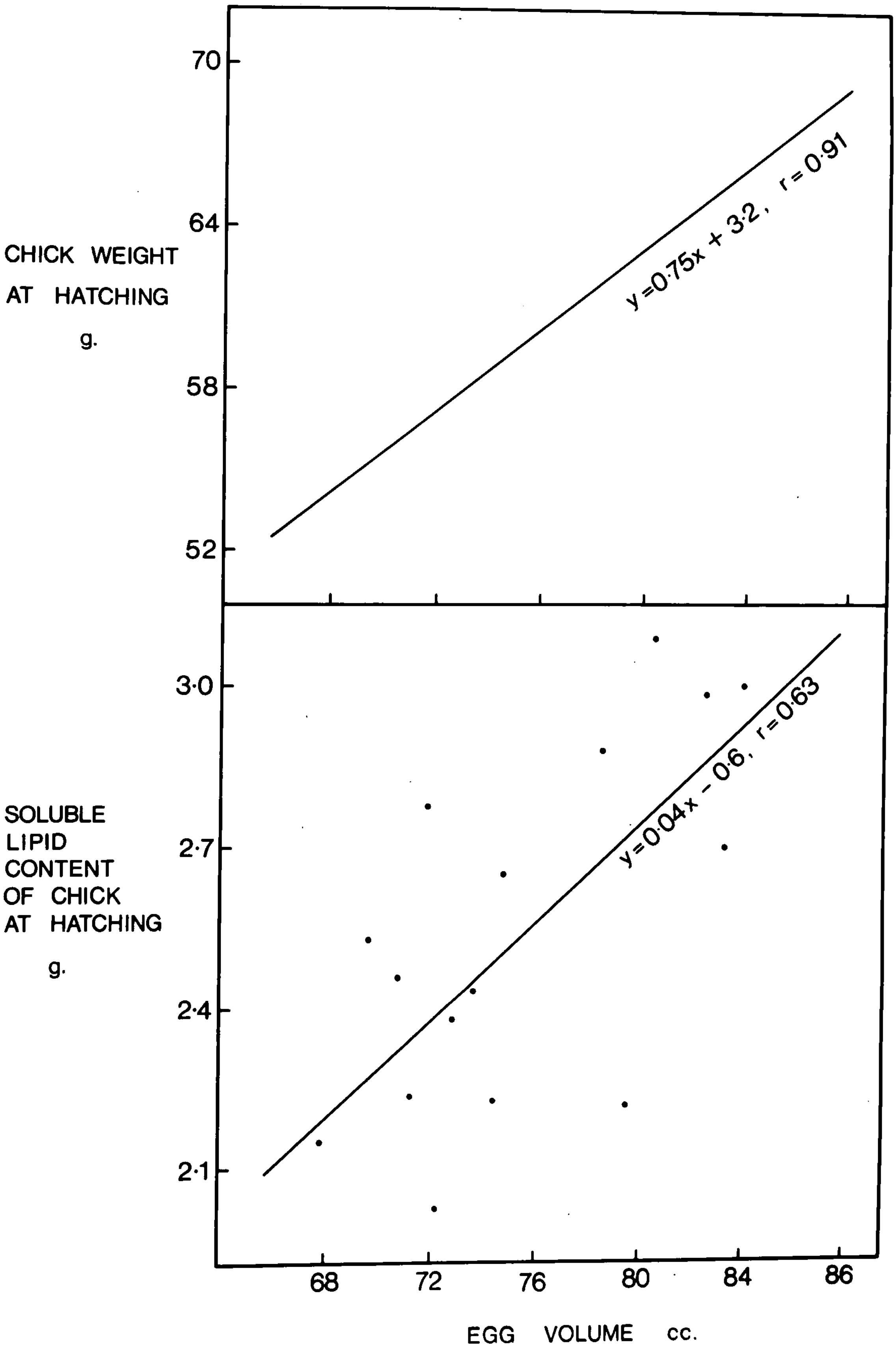
It may appear premature to discuss pre-fledging mortality in a section on egg size. Nevertheless, it is fitting at this point to elaborate on the differences in mortality that may be attributed to egg size, although

Figure 19

Regression lines to show the relationship between egg volume and

(i) chick weight on hatching (upper graph)

(ii) soluble lipid content of chicks on hatching (lower graph)



CHICK WEIGHT AT HATCHING g.
70
64
58
52
y=0·75x + 3·2, r=0·91
SOLUBLE LIPID CONTENT OF CHICK AT HATCHING g.
3·0
2·7
2·4
2·1
y=0·04x – 0·6, r=0·63
68
72
76
80
84
86
EGG VOLUME cc.

general chick mortality will be referred to in Section 8 .

Egg variability has been studied on the assumption that egg size and breeding success bear some degree of correlation. It was important to estimate the extent of this relationship, so that the effects of the laying sequence, experimentation and time of laying on egg size could be evaluated in terms of breeding success.

Laying sequence and post-hatching mortality

Emphasis has repeatedly been placed on the smallness of the c-egg relative to the first two eggs laid in a clutch. It is possibly an adaptation, the smaller c-egg giving rise to a weak and small chick which would perish in unfavourable conditions. It therefore seemed worthwhile examining the nesting success in this study.

It is known that most of the pre-fledging mortality in the Herring Gull occurs soon after hatching, and over half within the first week of life (Paynter 1949, Harris 1964, Kadlec et al 1968 and 1969, this study). Therefore, the mortality has been separated into two groups, namely, the mortality before (post-hatching) and then after the seventh day of life (Table 40). The fate of chicks was grouped according to laying sequence for broods of three chicks, and also for broods of two when one egg failed to hatch (Appendices VI and VII).

In both 1967 and 1968, the third chick, (i.e. the c-chick) suffered a significantly higher post-hatching mortality than its siblings ($p < 0.001$), but this was not apparent after the first week of life. The result contradicts

Table 40. Laying sequence and pre-fledging mortality in broods of three chicks

	Total No. chicks dying	Percentage of total mortality			
		a-chick	b-chick	c-chick	Probability of difference between a- and c-chick mortality
1967	103	16.5%	22.3%	61.2%	$P < 0.001$
1968					
(i) Post-hatching mortality 0-7 day old chicks	267	20.6%	21.7%	57.7%	$P < 0.001$
(ii) Pre-fledging mortality after 7 days old	82	28.0%	35.4%	36.6%	NS

Harris (1964) who found "no evidence to indicate that the third chick either weighed less, or survived less well than the other two chicks." When chicks were weighed on hatching, the c-chick was significantly lighter than its siblings ($p<0.001$, Table 41). This is consistent with the general relationship already shown between egg size and chick weight. Furthermore, this weight difference was increased when the brood was weighed on the day that the c-chick hatched (Table 41).

When more than one chick of the brood died, the b-chick also showed a greater mortality than the a-chick ($p<0.05$, Appendix VI). However, if only two chicks hatched, no significant differences were detected between siblings, although the trend was always for a lower survival of the last chick to hatch and the lack of significance may be due to the small sample sizes. This would indicate that the size disadvantage is not the only factor involved in the differential mortality, since the b-egg and chick are not significantly smaller than the a-egg and chick. Another factor, namely the sequence of hatching, may play an important role in these differences. The b-egg hatches up to twelve hours after the a-egg, and usually the c-egg is chipping for another day before hatching (see earlier). To evaluate the relative importance of these two factors, an egg transfer experiment was carried out.

Egg transfer experiment

An experiment was designed to distinguish between the effects of egg size and hatching sequence on the post-hatching survival of chicks. Eggs were transferred from nest to nest, so that the larger a-eggs hatched last,

Table 41. Comparing the weights of chicks immediately after hatching. ± one standard error

	chick wt.at hatching g. (21 broods)	% difference from a-egg	chick wt.when c-chick hatched (16 broods)	% difference from a-egg
a-chick	64.4±0.88		68.1±2.63	
b-chick	63.8±1.07	-0.9%	66.4±1.88	-2.5%
c-chick	56.6±1.12	-12.1%***	58.0±1.27	-14.8%***

Significance of difference in weight from a-chick weight *** $p < 0.001$

whilst the small c-eggs hatched first. This was achieved by interchanging a-eggs which had just started chipping, with chipping c-eggs from nests in which the first two eggs had already hatched (Fig.20). The normal size difference between a and c-eggs was maintained in these altered nests. Hatching chicks were marked with plastic colour rings according to the following categories :

a-chick hatching last
c-chick hatching first
normal a-chick
normal b-chick
normal c-chick

Nearly a week after hatching, chicks were re-visited, and the plastic rings removed. The number caught and released gave an estimate of survival, whereas those found dead represented the minimal mortality. The number of rings unaccounted for was approximately the same in each category (Table 42), and so it would appear that the method was suitable for comparative analysis.

Figure 20

Egg transfer experiment. Illustration of the exchange between large chipping a-eggs and small chipping c-eggs, resulting in clutches with the a-egg hatching last and the c-egg hatching first

EGG SWAPPING EXPERIMENT – TO INVESTIGATE DIFFERENTIAL MORTALITY BETWEEN THE 1st AND 3rd CHICKS OF A BROOD

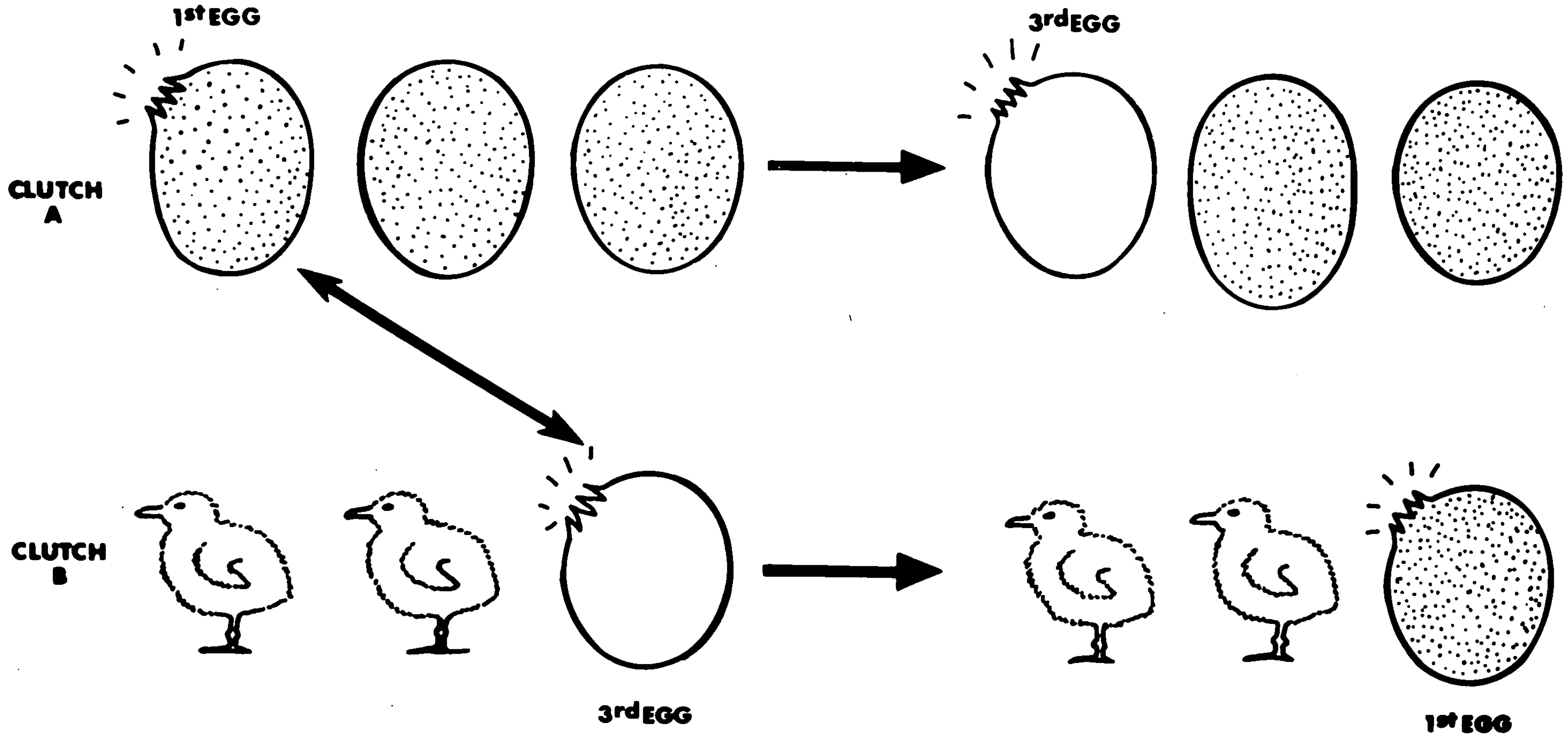


Table 42. Egg transfer experiment. Comparing the post-hatching mortality and survival of normal and substituted eggs when the hatching sequence had been altered

	c-egg hatching first	a-egg hatching last	normal hatching sequence		
			a-egg	b-egg	c-egg
No.ringed	123	152	221	271	46
No.recovered :					
dead	13	28	15	33	13
alive	72	75	143	170	19
Per cent mortality	10.6%	18.5%	8.6%	12.2%	28.3%
Per cent survival	58.5%	49.3%	64.7%	62.7%	41.3%
Per cent accounted for	69.1%	67.8%	73.3%	74.9%	69.6%

It is appreciated that this experiment produces abnormal broods, in which there are those with two a-eggs, and others with two c-eggs. Also, there are further permutations of eggs which would be of equal interest. For example, large c-eggs, hatching in the normal sequence, could be placed in nests with small a and b-eggs. However, the difficulty in finding nests where all three eggs are hatching, and are of the appropriate size and state of chipping, makes such experiments practically infeasible. Interchanging eggs will only be successful if the substitute eggs are not rejected, even at the latter stages of incubation. A trial egg transfer experiment, involving 72 nests, showed no indication of an increase in the mortality of eggs or chicks that had been introduced into foreign nests.

The results show that when the c-egg hatches first, the chick suffers less mortality ($p<0.01$) and has a better survival ($p<0.05$) than in the normal situation (Table 42). Similarly, the survival of a-chicks hatching last decreases ($p<0.01$) and the mortality increases ($p<0.001$). This indicates that the sequence of hatching contributes significantly towards the future of the chick. Asynchronous hatching of young is regarded as an adaptation to a somewhat unpredictable food supply, reducing the brood size to the availability of food without jeopardizing the survival of the older young (Lack 1954). Although the interval between the hatching of consecutive eggs in the Herring Gull is not as marked as in, for example, hawks and owls, there is a difference which contributes to the differential mortality of the third chick. This is perhaps surprising in a species whose food supply is now relatively predictable and rarely in short supply. However, even when hatching last, the a-chick does not suffer as high a mortality as the normal c-chick. Nor indeed does the c-chick hatching first survive as well as its siblings. It would therefore appear that the egg size, irrespective of the sequence of hatching, may also have an effect on post-hatching survival.

Egg size and post-hatching survival

To investigate this problem further, a detailed study was made of the post-hatching survival of chicks from eggs of known volume. Age is known to influence the breeding success in the Kittiwake (Coulson 1966), and Herring Gulls breeding for the first time rear fewer chicks than older birds (Drost et al 1961). Therefore a general correlation between egg size and breeding success might merely reflect the age structure of the population, since young gulls breed later, and lay smaller eggs which subsequently give rise to fewer fledged chicks. However, by analysing eggs laid at the same time in the season, this problem could be avoided.

Over 1400 eggs were measured in the field, and their volumes calculated. The survival of the chicks was again followed by leg banding on hatching. The fate of chicks were grouped according to egg volume and sequence of laying (Table 43, Fig.21).

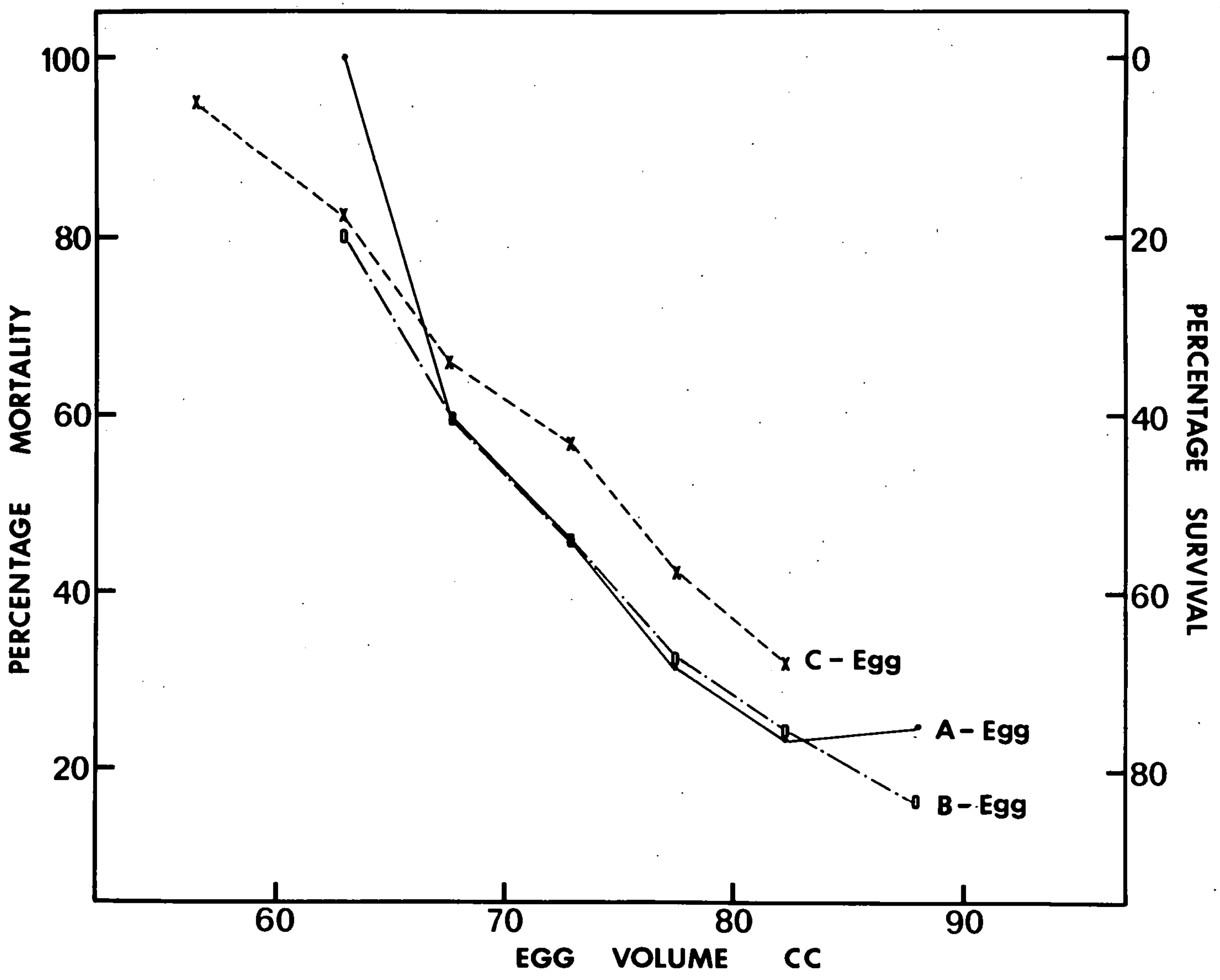
In each instance there is a marked correlation between egg size and chick survival ($p<0.001$), giving a range from approximately 80 per cent to 10 per cent survival. The relationship between survival and egg volume for the first two eggs in a clutch is not significantly different, but although the slope is the same for the c-egg, the survival is over 10 per cent lower for eggs of the same size ($p<0.001$). Thus the survival of the c-chick is lower than would be expected from its size, and is presumably a result of the sequence of hatching. Nevertheless, egg volume is a most important factor in determining post-hatching survival, and nearly all the chicks from eggs smaller than 65cc died soon after hatching. Only 8 per cent of all eggs laid were below this size and 89 per cent of these

Table 43. Comparing chick mortality within a week of hatching and calculated egg volume

		Egg volume cc.									
		50-60	60-65	65-70	70-75	75-80	80-85	85-95	Total	X^2	P
	No.hatched	-	4	32	79	86	94	40	335		
a-egg	No.died	-	4	19	36	27	22	10	118	23.5	0.001
	% mortality	-	100%	59.4%	45.6%	31.4%	23.4%	25%	35%		
	No.hatched	-	10	42	87	96	78	25	338		
b-egg	No.died	-	8	25	40	31	19	4	127	27.1	0.001
	% mortality	-	80%	59.5%	46.0%	32.3%	24.4%	16.0%	37.6%		
	No.hatched	18	60	95	92	55	16	-	336		
c-egg	No.died	17	49	62	52	23	5	-	208	36.1	0.001
	% mortality	94.4%	81.7%	65.3%	56.5%	41.8%	31.3%	-	61.9%		
	No.hatched	18	74	169	258	237	188	65	1009		
Total	No.died	17	61	106	128	81	46	14	453	157.4	0.001
	% mortality	94.4%	82.4%	62.7%	49.6%	34.2%	24.5%	21.5%	44.9%		

Figure 21

Comparing the relationship between egg volume and the percentage post-hatching chick mortality/survival for each egg of the laying sequence



100
80
60
40
20
PERCENTAGE MORTALITY
0
20
40
60
80
PERCENTAGE SURVIVAL
60
70
80
90
EGG VOLUME CC
C - Egg
A - Egg
B - Egg

were c-eggs. Neither repeat nor protracted layers continued to lay once their eggs had become as small as 65-70cc. To lay and incubate smaller eggs would be a disadvantage if the chicks have little chance of survival. The actual size of the egg need not be wholly responsible for the future of the chick, for within the same age class, some adults will be more successful at rearing chicks than others, and it is not unlikely that the poorer quality females will lay smaller eggs.

Both egg size and hatching sequence seem to contribute to the differential mortality, and the differences already noted (Table 40) may be anticipated from Fig.21. The mean volumes of a and b-eggs are 77.9 and 76.1cc respectively, whereas that of the c-egg is only 69.2cc. From the slope of the combined a and b-eggs, this would give a differential mortality of 22 per cent due to egg volume alone. A further 11 per cent chick mortality is added owing to the sequence of hatching, giving a total difference in mortality of 33 per cent. In the same way, an increase in the post-hatching mortality due to the seasonal decrease in egg volume may be calculated. For eggs laid in the first and last weeks of May, the difference would be about 7 per cent mortality for the a-eggs and 12 per cent for the c-eggs. Similarly, repeat clutches should show a chick mortality increase of 12 per cent and 2 per cent for the a and c-eggs respectively.

In order to appreciate the advantages conferred on chicks from large eggs, an analysis of chick lipid reserves was carried out using the Soxhlet apparatus.

Egg size and chick lipid reserves

Chicks from eggs of known volume were weighed on hatching and later dried in a vacuum oven. Soluble lipids were extracted using a petroleum ether mixture and the modified soxhlet technique.

Egg size has already been shown to be positively correlated with such factors as yolk weight and lipid (hexane soluble) content. This relationship is still noticeable at hatching, for the weights of chicks and their lipid content were positively correlated with egg volume (Table 44, Figs. 19 and 22). Between the extremes of egg size (65-90cc) the soluble lipid content of the hatching chick may vary by as much as 35 per cent (2.1 - 3.2g respectively).

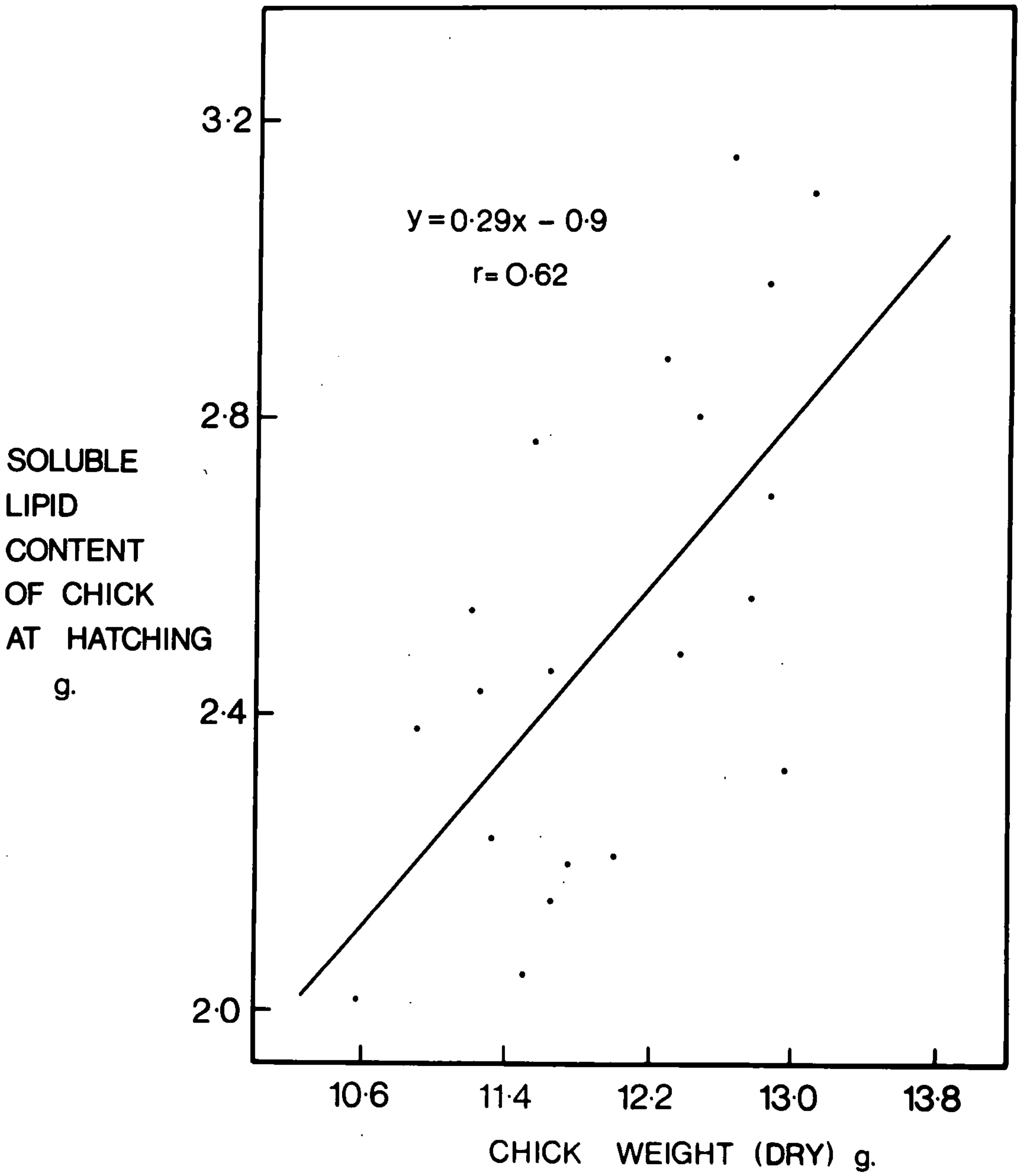
Table 44. Regression analysis of egg volume on chick weight and lipid content

	correlation coefficient -r	slope	N	probability
Egg vol : chick wt.	+0.911	+0.75	76	<0.001
Egg vol : chick lipid wt.	+0.634	+0.04	16	<0.01
Dry chick wt : chick lipid wt	+0.623	+0.29	20	<0.01

Lipid retained in the chick at hatching represents an appreciable percentage (21%) of the total dry weight of the chick. In the precocial, nidifugous, species (Domestic Duck and Fowl) less than half the original fat store is consumed during the development of the embryo, so that upon hatching the young bird can survive for a considerable period without

Figure 22

Regression of the soluble lipid content of chicks at hatching on the dry weight of the chicks


y=0·29x - 0·9
r= 0·62
3·2
2·8
2·4
2·0
SOLUBLE LIPID CONTENT OF CHICK AT HATCHING g.
10·6
11·4
12·2
13·0
13·8
CHICK WEIGHT (DRY) g.

food (Drent 1967). This may be longer than 48 hours in the Mallard (Kear 1965), or as much as 5 days in the Capercaillie (Marcström 1960). Altricial, and nidicolous, species consume nearly all the lipid content in the egg during incubation, so that the hatching chick is entirely dependent on its parents. The precocial, but nidicolous, Herring Gull lies intermediate between these two groups. The mean lipid content of the eggs was shown to be 6.92g. At hatching, the chicks contain an average of 2.58g of soluble lipid, or 37 per cent of the original reserves. This is similar to the figure of 40 per cent estimated by Drent (1967).

An appreciable part of the size difference in newly hatched gulls is therefore caused by the surplus of lipid retained within the chick at hatching. It is suggested that the parent-chick relationship takes some time to develop, and that the food reserve is of considerable importance in assisting the survival and activity of the chick in its first post-hatching days. Chicks from large eggs will have a greater food reserve, and therefore stand more chance of survival during this period than chicks from smaller eggs.

Variation in lipid reserves are clearly relevant to the survival of chicks from eggs of differing sizes, and it would seem at first that the chick from the small c-egg is an obvious example of this relationship. However, it is not so straightforward, for although the c-egg is smaller than the other two, it contains nearly as much yolk as the a-egg (see earlier). Furthermore, the yolk lipid contents are more or less the same for all eggs (Table 32) and yet the c-chick still hatches significantly smaller than its siblings.

A lipid analysis was carried out on five broods taken as each chick hatched (Table 45). The b-chick contained the most lipid, as expected from its yolk lipid content, but the a-egg had the least reserves. It is possible that the a-chick is more advanced on hatching, and has used up more of its original yolk stores. This could occur if social facilitation causes the premature hatching of the c, and perhaps the b chicks. Synchronised hatching in the Bobwhite Quail is produced by the acceleration of embryo development through auditory contact with more advanced members of the clutch (Vince 1964). It has already been mentioned that the initial time difference between the development of the b and c eggs is reduced by half on hatching, which could be explained by premature chipping of the c-egg. In an attempt to verify this supposition, the yolk lipid weight was estimated from the mean egg volumes, and the probable percentages of lipid reserves that remained on hatching were calculated (Table 45). The result indicated that more of the a-egg yolk had been consumed before hatching and during the 48 hours after hatching there will be further reduction in these reserves.

When five broods were taken on the day that the c-chick hatched, the a-chick was heavier than the b-chick even though it had hatched from a smaller egg (Table 45). Meanwhile, the lipid was being progressively consumed.

Table 45. Mean weight and soluble lipid content of chicks and hatching sequence.

i) on hatching ii) on the day that the c-chick hatched

iii) chicks dying in the field

		N	Mean egg vol. cc.	Mean chick wt. g.	Mean dry wt. g.	Mean lipid wt. g.	Estimated percentage of egg lipid left in hatching chick
i) chicks taken on hatching	a-chick	5	81.78	63.81	12.57	2.36	35%
	b-chick	5	82.58	66.00	13.26	2.81	42%
	c-chick	5	74.94	58.36	11.98	2.44	44%
ii) chicks taken when c-chick hatched	a-chick	5	77.16	71.31	15.03	1.99	-
	b-chick	5	79.56	69.81	14.96	2.18	-
	c-chick	5	71.88	55.99	11.85	2.47	-
iii) chicks dying in the field		4	-	48.58	10.33	1.30	(12.6% of dry wt.)

The resources of the yolk sac are drawn on mainly during and just after hatching, when the expenditure of energy is enormous (Kear 1965). Very young chicks found dead in the field were analysed, to find out whether death had been coincident with exhaustion of energy reserves. Marcström (1966) has shown that Mallard Ducklings which had starved to death still contained a basic lipid content. This was 10.6 per cent of the dry weight of the ducklings. Similarly, these Herring Gull chicks, although in a state of emaciation, contained lipids representing 12.6 per cent of the dry body weight (Table 45). Nevertheless, there had been an estimated loss of 50 per cent of the lipids between hatching and death.

To summarise, these results show firstly that egg size and chick mortality are correlated, and secondly that much of this relationship is a result of varying lipid reserves. However, although the importance of these lipids is undeniable, other factors must be involved to explain the relative smallness of the c-chick. The mortality this chick suffers is due partly to egg size, and also to the sequence of hatching. The behavioural mechanisms involved in the change-over from incubation to parenthood are obviously of ultimate importance to the survival of the chicks. Even though there is an abundance of food available to the adults during this period, the major cause of chick mortality is probably exposure (Harris & Plumb 1965) and starvation due to lack of parental care. It would also appear that the Herring Gull has considerable difficulty in forming a further parent-chick bond when there are already two earlier hatched chicks in the nest.

In poultry, a relationship between egg size and subsequent chick mortality would be of economic importance, since pullets lay a high proportion of small eggs (Romanoff & Romanoff 1949). However, although small chickens are less able to withstand rough transport and unfavourable temperature conditions than larger chicks (Skoglund et al 1952), various studies have failed to detect a difference in survival according to egg size (Skoglund & Tomhave 1949, Wiley 1950, Tindell & Morris 1964, Morris et al 1968). It is suggested that the difference in yolk content between the nidiculous Herring Gull and the nidifugous fowl, combined with the higher mortality apparent in a natural and therefore more severe environment, produces a marked correlation between egg size and chick mortality hitherto absent in studies on poultry.

SECTION SEVEN

CLUTCH SIZE AND HATCHING SUCCESS

7.1 Introduction

It is generally accepted that breeding seasons are so timed that offspring are reared during a period of maximum food availability. Furthermore, Lack (1954) argues that clutch size is adapted to correspond with the largest number of young the parents can successfully raise. However, the more recent activities of man appear to have altered the stability of many sea-bird populations. In particular, the Herring Gull is now able to take advantage of a less seasonal, and more abundant, source of food. Vermeer (1963) showed that the Glaucous-winged Gull is capable of rearing broods of four to six young, even though the brood patches limit the clutch size to three eggs. Similar results were obtained for the Lesser Black-backed Gull, but not for the Herring Gull (Harris & Plumb 1965). It was also shown by experiments in gulls fostering chicks of other species that adult gulls can supply enough food for the chicks to grow as quickly as possible (Harris 1964).

To detect whether breeding of the Isle of May Herring Gulls is less dependent on the season, breeding was delayed by egg removal and the subsequent laying, hatching and fledging success recorded.

Delayed breeding

Gull's eggs are commonly removed on the Farne Islands (Northumberland) for human consumption. This practice continues until the beginning of July, and yet repeat layings occur throughout this month. Accordingly, it was hoped in 1967 to progressively delay the incubation period until July on the Isle of May.

Nests were staked in three control areas, and five delayed areas, each containing at least 500 nests. In one of the delayed areas, clutches were continuously removed both in 1967 and in subsequent years, so that no hatching took place. In the remaining four areas, robbing was ceased progressively through the season, and abruptly in mid-June when repeat laying became unexpectedly infrequent (Table 46). Although the Herring Gull is often capable of producing several eggs, as shown by protracted layings, it appears that the nesting and laying behaviour diminishes later in the season, and commonly only one repeat clutch is laid (see also Section 5).

In 1968 the study areas were restricted to a control of 903 nests, and a delayed area with a final total of 358 nests. Again, all eggs were removed from Whaup.

Relaying requires a repetition of the behavioural activities which precede the completion of a clutch. Usually this clutch is laid in the original, but often renovated, nest. However, if this nest were also removed, the necessity to build anew might create an additional strain on the adults. As such, the removal of nests, as well as eggs, may be a more efficient method of control than merely egg robbing. This was investigated by separating the 1968 delayed area into two sections. Both were robbed on the same days, but nests were only removed in one area. In the latter, 84 repeat clutches were laid after 6 June, following the destruction of 238 nests with eggs.

Table 46. Control and experimental areas under study

Area	No.nests	Robbing ceased	No.eggs removed	Mean hatching date
1967				
S. Rona	1092	Control		17 June
N. Ness	677	Control		17 June
Burrian (2)	570	Control		17 June
E. Tarbet	507	26 May	419	20 June
Burrian (1)	-	8 June	1268	25 June
Burrian (3)	-	9 June	1776	2 July
N. Rona	-	15 June	2089	25 June
Whaup	-	continuous robbing (last egg laid 6 July)	2448	-
1968				
N. Ness	903	Control		16 June
E. Tarbet (a)	251 (final)	29 May	1069	8 July
E. Tarbet (b)	107 (final)	29 May	627	8 July
Whaup	-	continuous robbing (last egg laid 14 July)	-	-

The percentage re-laying was therefore 35.3 per cent compared with 50.0 per cent (195 nests) in the less disturbed area. The difference is significant ($p < 0.01$), and indicates the additional stresses involved in rebuilding nests. Observations of colour-ringed individuals showed that the result was due to an inability to re-lay, rather than to an emigration from the area.

Continuous removal of eggs from Whaup had a marked effect on the adults. Photographs taken through the season showed a progressive decrease in the number of gulls resident in the area (Table 47). Also their behaviour to human disturbance changed, so that in early July the near presence of a human would clear the entire area of gulls. However, any long term effect of robbing was not obvious, for there was no discernable difference in either the density or laying period in the two subsequent years (Appendix VIII).

Table 47. The decrease in numbers of adult gulls resident on Whaup through the season

	Herring Gull		Lesser Black-backed Gull	
date	No.adults	% decrease	No.adults	% decrease
20 May	522	-	48	-
23 May	512	2%	39	19%
27 May	419	20%	24	50%
10 June	321	39%	24	50%

7.2 Clutch size and seasonal variation

Although a seasonal decline in clutch size has been recorded for the Kittiwake (Coulson & White 1958a), opinions differ in studies on the Herring Gull. Paynter (1949) and Harris (1969) found no seasonal change in clutch size, whereas Brown (1967) demonstrated a decrease from 2.77 to 2.40 eggs per nest between early and late May.

It was shown in the Kittiwake that the difference was not solely the result of older birds breeding earlier and laying more eggs. The time of laying also influenced the clutch size (Coulson & White 1961). It was hoped that delaying the breeding season of the older Herring Gulls would illustrate the relative importance of either age or season on clutch size.

The mean clutch size in the control areas, excluding repeat clutches, was 2.73 ± 0.018 (1 st.error) eggs. It was similar to that reported by Harris (1964) from Skomer (2.76 ± 0.037), but significantly different from the clutches on Walney (2.56 ± 0.053, $p < 0.01$, Brown 1967) and Graesholm (2.91 ± 0.022, $p < 0.001$, Paludan 1951). However, this may reflect the amount of disturbance during the laying period, and the regularity of visiting nests more than an actual geographical difference in clutch size.

The three brood patches play an important role in limiting the clutch size to three eggs, despite a well developed fourth follicle. Rice & Kenyon (1962) added an extra egg to albatross clutches, but found the albatrosses unable to incubate both eggs. Oversize clutches of four and five Herring Gull eggs were set up, but all showed a poorer hatching success than the controls ($p < 0.001$). Of the 78 clutches, only 37 per cent of the eggs hatched, compared with 65 per cent in normal clutches. Even discounting the additional eggs, the hatching success of 52 per cent was still low ($p < 0.01$). In other words, the adults were unable to successfully incubate more than the normal number of eggs, and the confusion caused by the additional eggs even made this task more difficult.

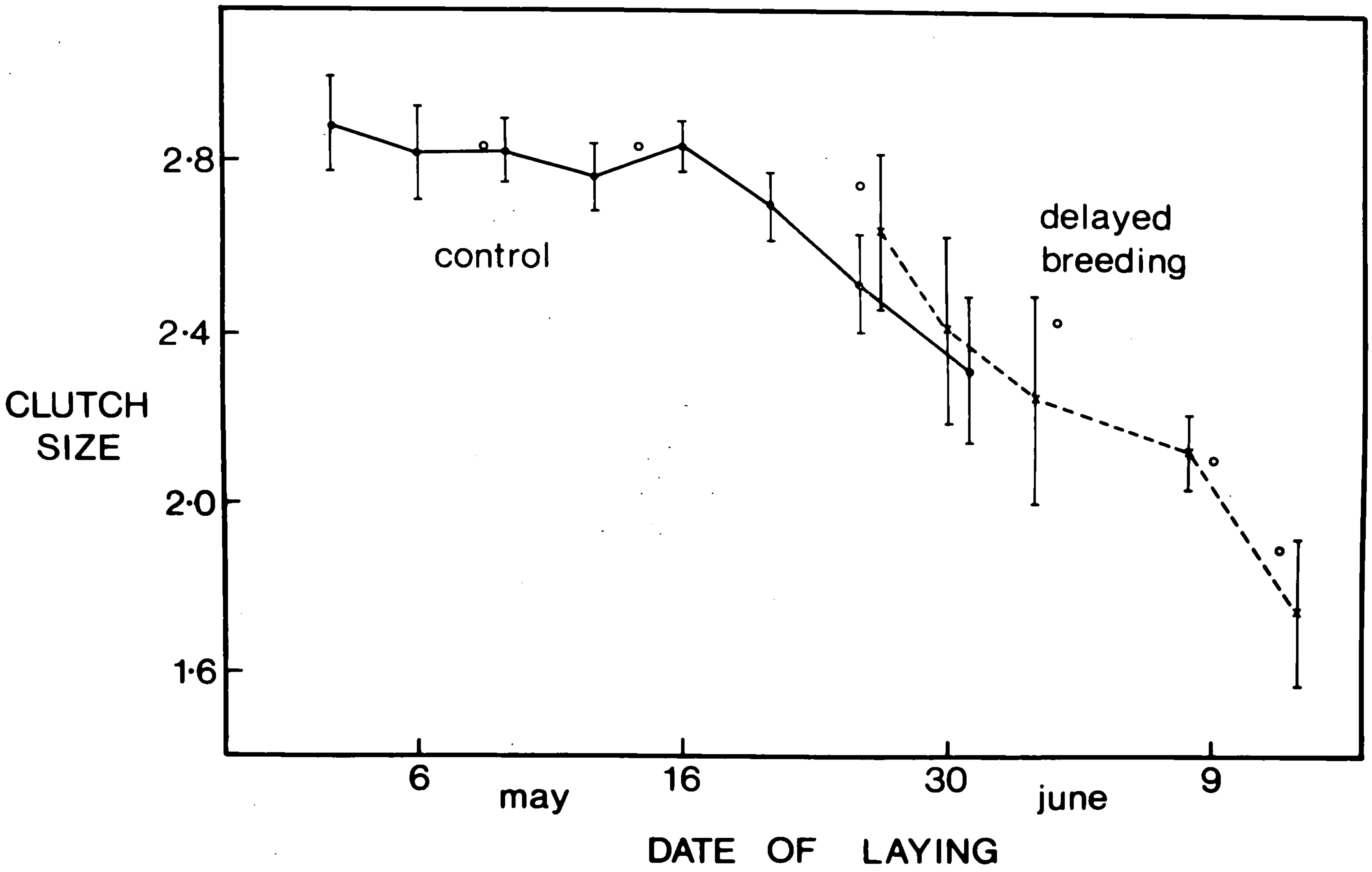
In the control areas, the clutch size varied little until late May, when a significant and continued decrease occurred (Fig.23), even though re-layings were excluded from the analysis. Furthermore, the decrease was maintained in the delayed areas when repeat clutches were laid (also Fig.23). If Herring Gulls behave like Kittiwakes, and show the same age differences in the time of breeding, then the effects on clutch size are less obvious. The older adults, re-laying at the same time as the late laying younger birds, do not on average lay a larger number of eggs. Instead, the time of laying seems to be of prime importance in determining the clutch size.

Egg volume, as well as clutch size, decreases through the season so that the total decline in clutch volume may be considerable. Clutch volume can be represented by the product of mean clutch size and mean egg volume for a particular time period. Between the first week in May and the second week in June, this decreased by 32 per cent, from 216cc to 147cc. Coulson et al (1969) calculated a 10-11 per cent decrease in the egg volume of the Shag, compared with 4.5 per cent in the Kittiwake (Coulson 1963) and 5 per cent in the Herring Gull (this study). However, the seasonal decline in the clutch size of the Kittiwake was far greater than that in the Shag. It was therefore suggested that "an explanation for the relatively small decline in the egg volume of the Kittiwake is probably that the decline in clutch size frees more material to compensate egg volume." A similar argument could be voiced for the Herring Gull.

It is difficult to find a reason for a shortage in materials necessary for egg production during late laying. At this time in the season young are being fed, and there

Figure 23

Variation in mean clutch-size (± 2 standard errors) through the 1968 season in the control (North Ness) and delayed (E. Tarbet) areas. Mean clutch-size during 1967 also shown (open circles)


CLUTCH SIZE
2·8
2·4
2·0
1·6
control
delayed breeding
6
may
16
30
june
9
DATE OF LAYING

is no evidence of a decline in the food supply. Environmental factors appear to be favourable and so a more intrinsic mechanism must be involved. Coulson et al (1969) showed that the interval between nesting and laying is correlated with the clutch volume in the Shag, and suggested that late laying birds have insufficient time for the maximum development and functioning of the reproductive system. The preparatory period prior to re-laying is far shorter than the interval between nest building and normal laying, and probably accounts for the lowering of clutch size.

7.3 Hatching success - variation with clutch size

In the North Ness control area (1968) a total of 1722 chicks hatched from 2463 eggs, with a hatching success of 69.9 per cent. This compares with a hatching success of 64.3 per cent calculated for the 1967 control areas. These are similar to the figures recorded by Harris (1964) for Skomer (64.1%), and by Brown (1967) for Walney (66.6%). Several studies have shown a greater hatching success from clutches of three eggs than from smaller clutches (Paynter 1949, Harris 1964, Brown 1967), although Kadlec & Drury (1968) found no such difference (Table 48). It was suggested that small clutches are laid by young, "careless", and inexperienced birds. A majority of the smaller clutches are laid later in the season, and probably by younger birds, but none of the studies excluded the seasonal and age effect in their analyses. The overall hatching success on the Isle of May showed the same significant differences between clutches ($p < 0.001$, Table 48),

Table 48. The influence of clutch size on hatching success. Number of nests studied given in brackets.

	Per cent hatching success		
	c/3	c/2	c/1
Paynter (1949)	80% (54)	56% (39)	29% (7)
Harris (1964)	67% (180)	50% (27)	0% (13)
Brown (1967)	72% (88)	50% (52)	
Kadlec & Drury (1968)	77% (591)	72% (98)	-
This study :			
i) control area	73% (695)	54% (170)	18% (38)
ii) delayed area	75% (122)	63% (182)	34% (61)

but it was also possible to compare clutches that were laid at the same time in the season (Table 49). Throughout the season, the combined clutches of one and two eggs produced fewer chicks per egg than did the clutches of three eggs. It therefore appears that irrespective of the time of laying, a bird laying less than three eggs will consistently hatch a smaller percentage of eggs. Furthermore, this effect is as likely to be an inherent fault of the individual, as the inexperienced carelessness of a young bird, and in both cases it may be an illustration of the effects of a low reproductive drive.

Brown (1967) and Beer (1961) showed, in the Herring Gull and Black-headed Gull respectively, that more settling movements are performed when incubating smaller clutches, and suggested that these clutches presented inadequate stimuli to the bird. This conclusion is not verified by the above results, for when repeat laying results in clutches of one and two eggs, the subsequent hatching success is significantly higher than in normal laying (c/2 63% : 54%; c/1 33% : 18% $p < 0.02$). On the other hand, there is no significant difference between the hatching success of normal and repeat clutches of three eggs. If the difference was due to inadequate stimulation, then the fate of both normal and repeat small clutches should be the same. Conversely, if the difference was a result of an inherent lower reproductive drive, then those birds that laid a clutch of three eggs, and later a repeat clutch of two eggs, would not be expected to show the same hatching success as their "careless" neighbours.

Seasonal variation in hatching success

i) control areas

A common form of egg loss is predation by neighbouring gulls, and the loss is heaviest during the waxing and waning of parental attentiveness (Drent 1967). This is especially obvious during the first week of incubation. To evaluate whether human disturbance increases egg predation, two areas of 140 nests were selected. One was visited two times each day during incubation, and the other only once every two days. A similar hatching success from both areas (62% : 65% respectively) indicated that this form of disturbance had little effect. A slow walk through the nesting colony causes very few birds to leave their nests.

Patterson (1965) found a significant correlation between breeding success and the degree of nest synchronisation, so that Black-headed Gulls laying at the peak of the season were more successful than early or late layers. A similar trend, though not significant, was noted by Brown (1967) when comparing hatching success and laying date in the Herring Gull, but Harris (1964) concluded that hatching success increased as the season progressed.

In the control area of this study, eggs that were laid during the peak laying period (i.e. 16-20 May) were the most successful (77.9%). Both early (laid before 8 May) and late eggs (laid after 24 May) had a significantly lower hatching success than this middle group ($p < 0.001$, Table 49). The low clutch size and hatching success of eggs laid between 12-16 May can be explained by the weather conditions. Meteorological records showed a period of continuous and heavy rain from 13 to 16 May, with force 4 to 6 S.E. winds. Nests that are not fully incubated are often swamped by such conditions, and the eggs may be chilled or destroyed. The fact that eggs laid during this period had the highest percentage of addled eggs (Table 49) adds weight to the theory that the eggs may have been chilled. "Addled" in this context refers to those eggs that remained unhatched in the nest, and which did not contain a developed, but dead, chick.

Table 49. Comparing hatching success with clutch size through the season (1968)

Number of nests in brackets, and chicks per pair given ± one standard error.

		Laying date - May							
	Clutch size	up to 4	5-8	9-12	13-16	17-20	21.24	25-28	29 onwards
Percentage hatching success	c/3	67% (42)	70% (75)	72% (112)	69% (105)	80% (158)	80% (108)	69% (62)	65% (33)
	c/2	0% (3)	38% (8)	47% (18)	56% (26)	65% (24)	54% (37)	57% (29)	58% (25)
Difference between c/3 and c/2	P	-	0.01	0.01	NS	0.05	0.001	NS	NS
Total hatching success									
No. chicks		84	165	259	246	409	302	162	95
Percentage hatching success		63.2%	67.4%	69.3%	66.5%	77.9%	75.1%	63.8%	59.4%
Percentage "addled" eggs		12.8%	10.6%	9.9%	13.8%	5.5%	8.9%	12.2%	12.5%
Chicks per pair		1.83±0.17	1.90±0.12	1.96±0.09	1.84±0.10	2.21±0.08	2.03±0.08	1.60±0.11	1.38±0.13
Difference in chicks/pair over a one week period	P	←	NS ⇄	NS ⇄	0.05 ⇄	NS ⇄	0.001 ⇄	0.001 →	-

There is a trend for an increase in the number of addled eggs in early and late nests (Table 49), although they do not account for the seasonal variability in hatching success to any marked extent. If these eggs are not included as egg loss, then the shape of the re-plotted hatching success curve (Fig.24) is not radically altered, though the abnormally low figure for the 12-16 May is no longer apparent.

It is possible that this seasonal difference in hatching success is due to young females breeding later, and experiencing the lower breeding success that Coulson & White (1958b) noted in the Kittiwake, although it would not explain the poorer success of early breeders. However, if this were so, then the clutches of two eggs laid later in the season, and probably by these young birds, should show the major part of this reduced hatching success. Instead, the results shown in Fig.25 illustrate that the clutches of three eggs contribute to the late seasonal effect, whereas the hatching success of late laid two egg clutches is less variable.

It appears, therefore, that the age differences are probably of little importance in determining the overall pattern of hatching success. The alternative causes may be the relationship between predation and synchronised laying, and the direct effects of the season. Weather, or perhaps reduced fertility, could conceivably alter with time and should both be manifest by an increasing percentage of addled eggs. However, when such eggs are not included in egg loss, the difference between the hatching success of the middle group and the early and late layers is still

Figure 24

The percentage hatching success (chicks per egg) according to date of laying in the control and delayed areas (1968) including addled eggs (continuous line) and discounting addled eggs (dotted line)

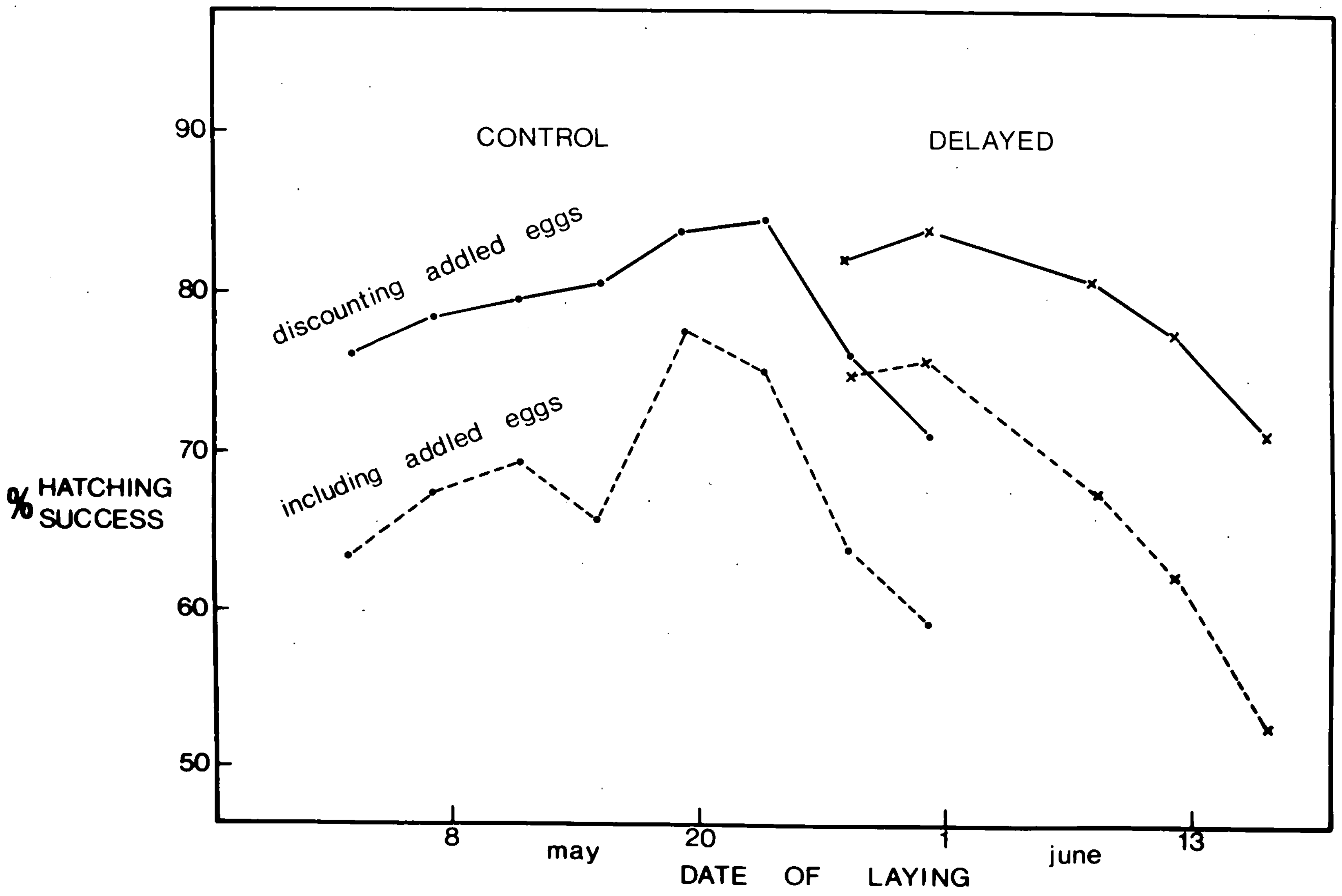

CONTROL
DELAYED
discounting addled eggs
including addled eggs
% HATCHING SUCCESS
90
80
70
60
50
8
may
20
1
june
13
DATE OF LAYING

Figure 25

Comparing the percentage hatching success (chicks per egg) according to date of laying in the control and delayed areas (1968) for c/3 and c/2. Numbers refer to number of nests under study

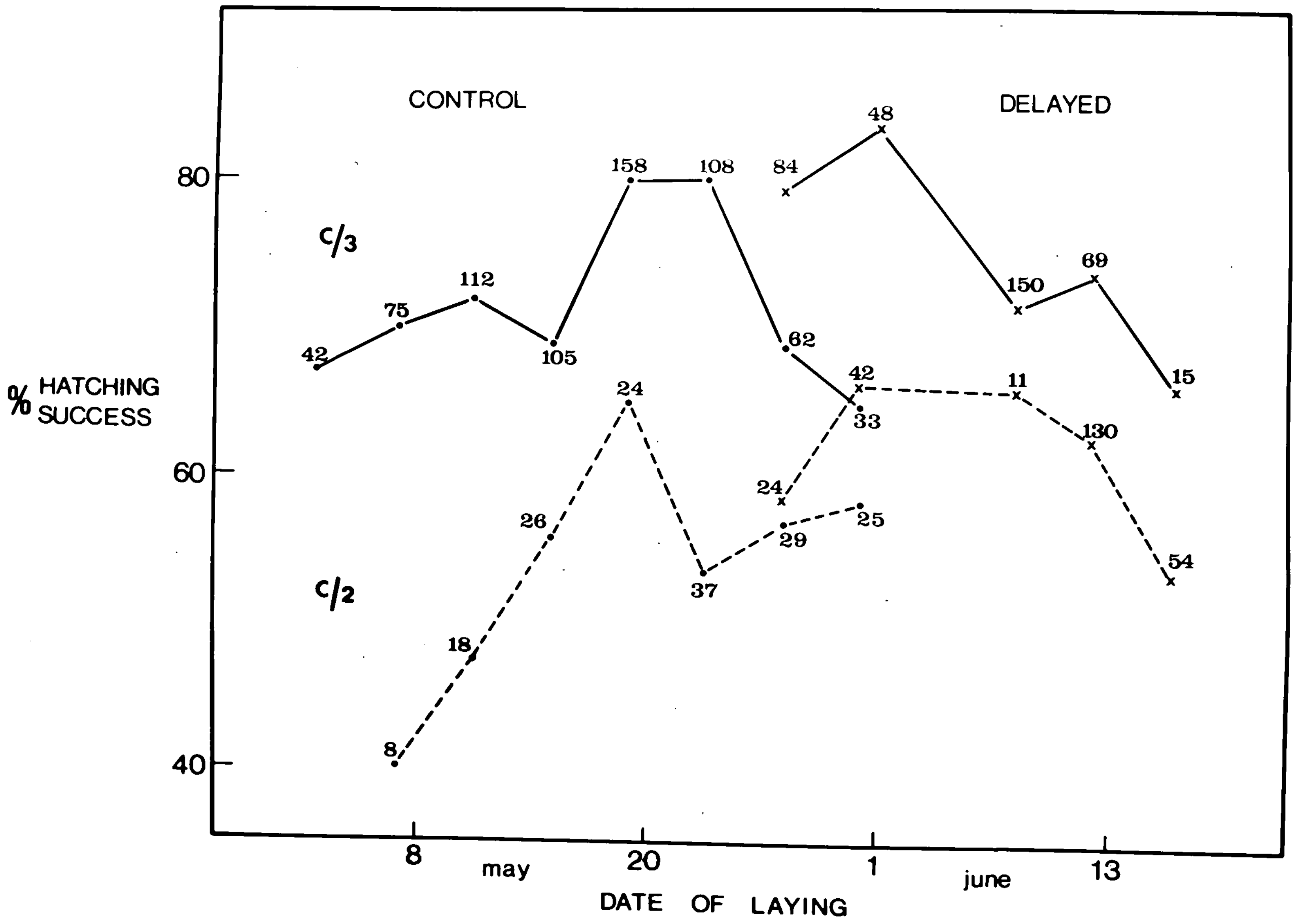

CONTROL
DELAYED
C/3
C/2
% HATCHING SUCCESS
80
60
40
8
may
20
1
june
13
DATE OF LAYING
42
75
112
105
158
108
62
33
84
48
150
69
15
8
18
26
24
37
29
25
24
42
11
130
54

Figure 26

Histograms showing the percentage frequency of hatching during 1967, comparing the control area with various experimentally delayed areas. Mean date of hatching given by dotted line

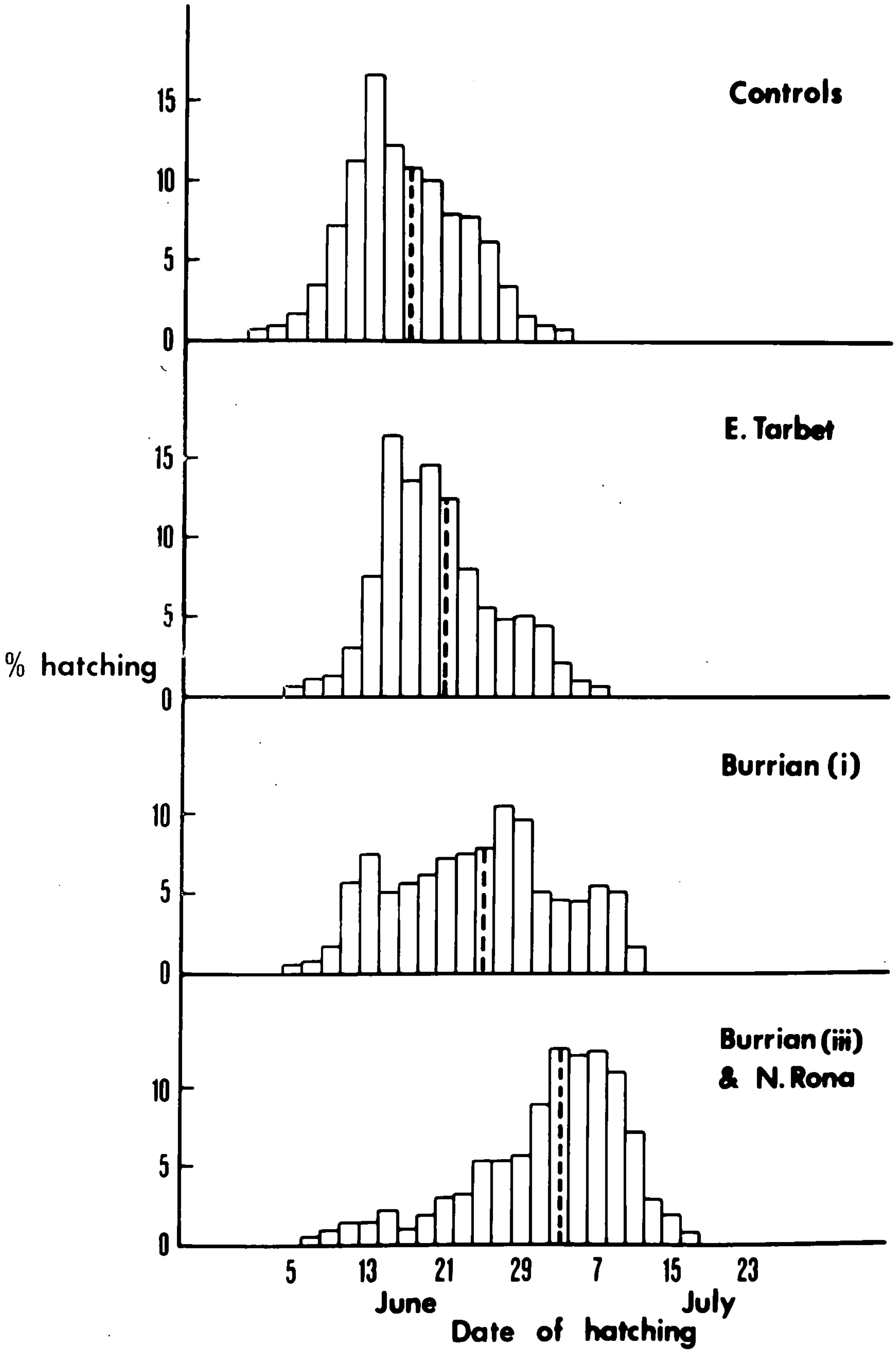
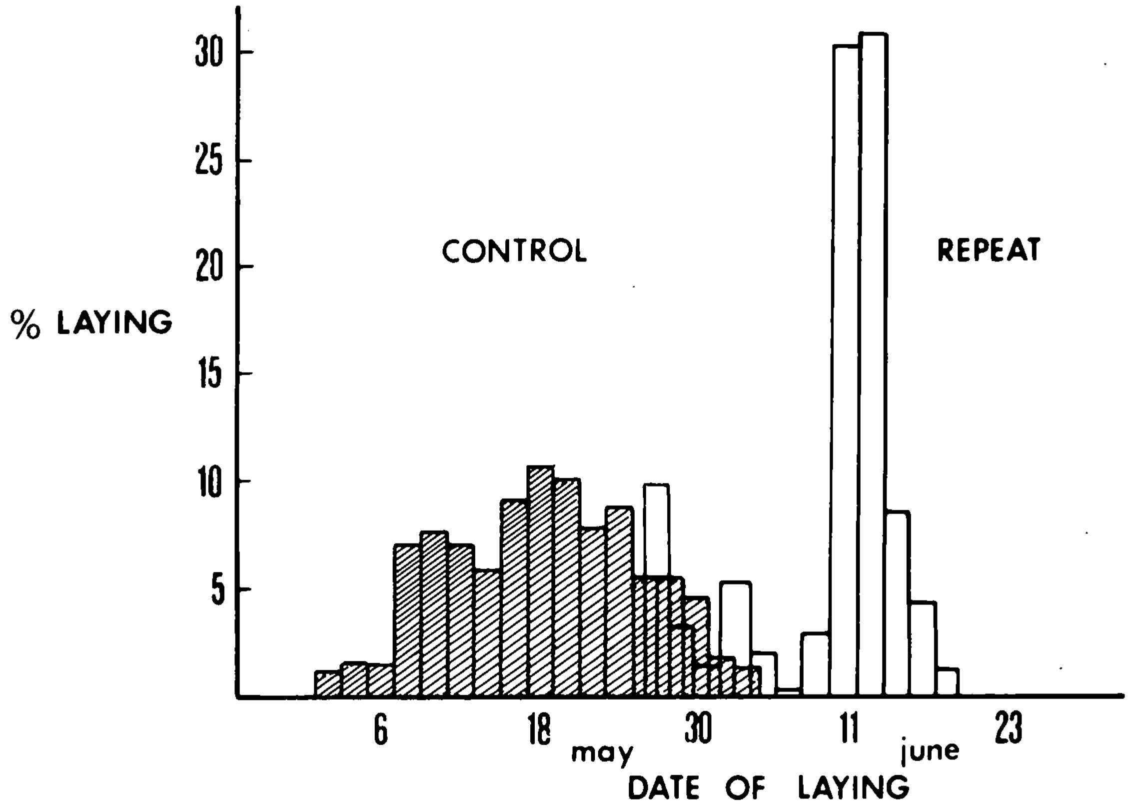
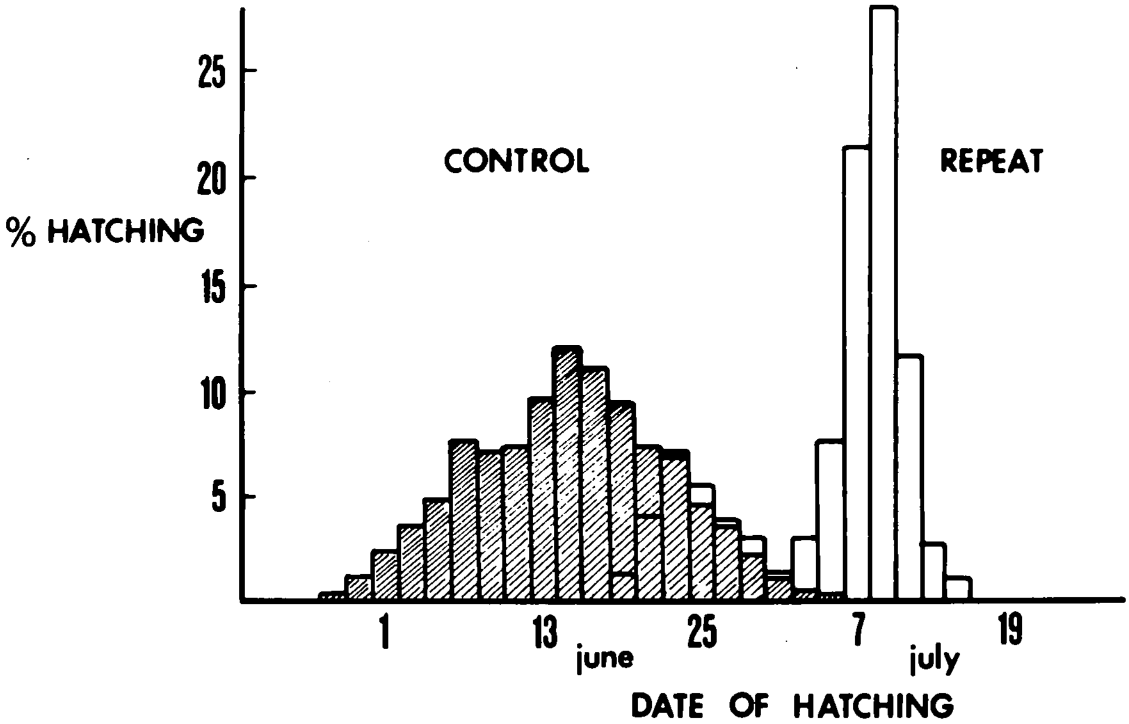

Controls
E. Tarbet
Burrian (i)
Burrian (iii) & N. Rona
% hatching
0
5
10
15
5
13
21
29
7
15
23
June
July
Date of hatching

Figure 27

Histograms showing the percentage frequency of laying and hatching in the control (shaded) and delayed (unshaded) areas during 1968



30
25
20
15
10
5
% LAYING
CONTROL
REPEAT
6
18
may
30
11
june
23
DATE OF LAYING



25
20
15
10
5
% HATCHING
CONTROL
REPEAT
1
13
june
25
7
july
19
DATE OF HATCHING

significant ($p < 0.01$ and $p < 0.001$ respectively). Consequently, predation would seem to be the most likely alternative, and one which could be verified by examining the hatching success of delayed breeders.

ii) Delayed breeding

The effect of egg removal and re-laying on hatching date is illustrated by the frequency distribution of hatching dates in the control and delayed areas for 1967 and 1968 (Figs. 26 and 27). The overall breeding season was extended to cover a period of 7-10 weeks, instead of 4-5 weeks.

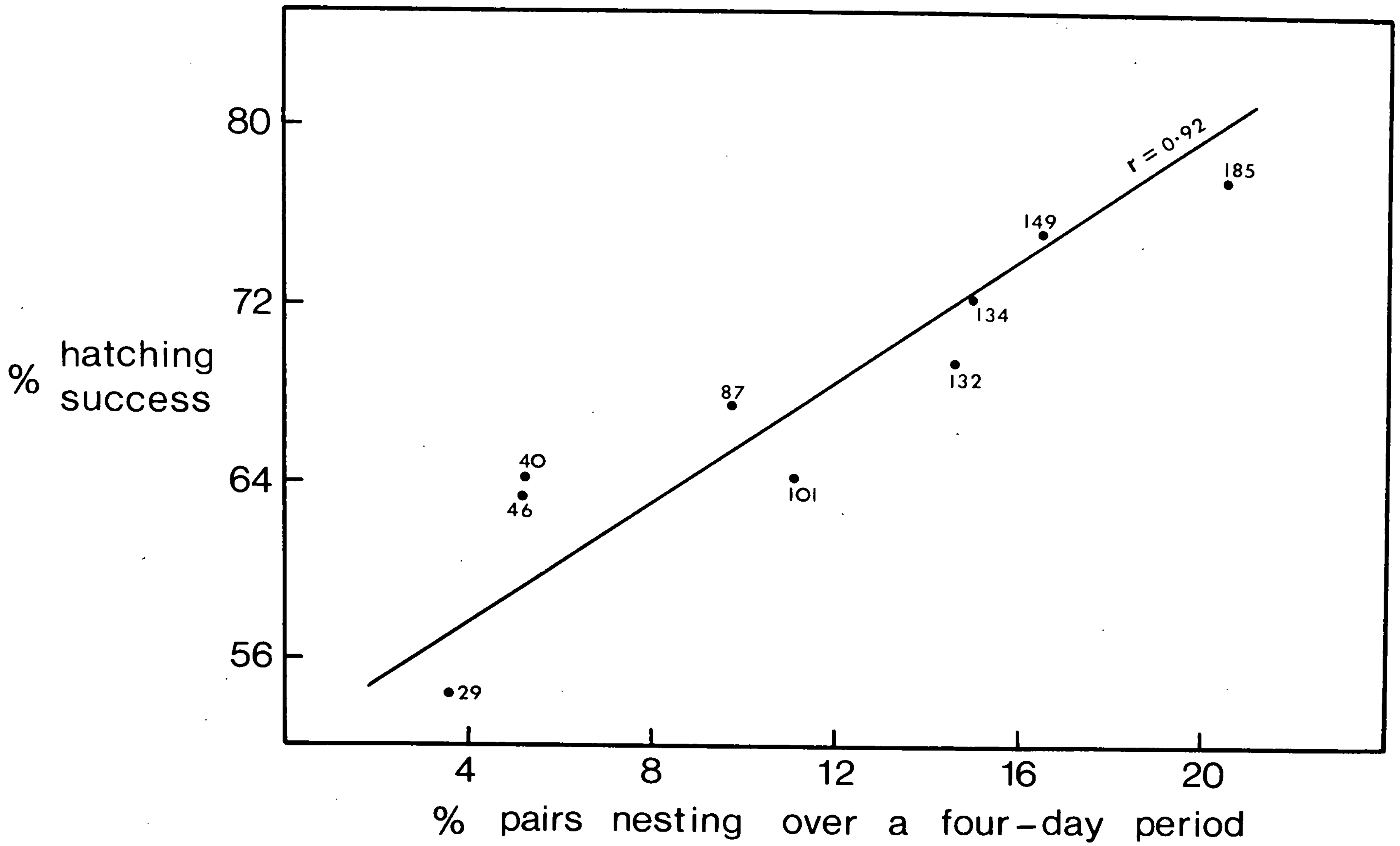
If the decreased hatching success of the late laid clutches was seasonal, then the delayed clutches should show an exaggeration of this effect. Instead, the delayed areas behaved like the controls, but shifted nearly one month later in the season (Figs. 24 and 25). For example, there was the characteristic peak of hatching success, with less successful clutches laid earlier (not significant) and later ($p < 0.05$) in the already delayed season (also Appendix IX). At a time when the hatching success of normal clutches is decreasing, the delayed clutches are more successful ($p < 0.01$), and do not show the extrapolation that would be expected with a seasonal effect.

Nest synchronisation can be expressed as the percentage of eggs laid in a given four day period. The correlation between this, and the subsequent hatching success of these eggs was highly significant ($p < 0.001$, Fig.28). It would seem, therefore, that irrespective of the time

Figure 28

The relationship between nest synchronisation and percentage hatching success.

Egg laying in the control areas occurs from late April to early June. The synchronisation of nesting is given as the number of nests in which a-eggs are laid in successive four day periods from 28 April to 1 June 1968. The numbers of nests in each period are shown on the graph, but are expressed on the abscissa as a percentage of the total number of nests, and plotted against the subsequent hatching success of eggs laid in each four day period.


80
72
64
56
% hatching success
r = 0·92
185
149
134
132
87
40
46
101
29
4
8
12
16
20
% pairs nesting over a four-day period

in the season, it is the eggs that are laid when most laying occurs that are the most likely to hatch. Late breeding does not appear to be a disadvantage providing that the delay applies to the group as a whole. However, there was selection against any deviation from the main peak of laying, which would tend to maintain a synchronisation of nest timing. Whether this also applies to fledging success will be discussed in the following Section 8.

Table 50. Percentage of addled eggs in the control and delayed areas

	1967			1968		
	No.laid	No. added	per cent	No.laid	No. addled	per cent
Controls	807	67	8.3%	2470	247	10.0%
Delayed	428	66	15.4%	772	112	14.5%
X^2 and P		15.0 $P < 0.001$			12.0 $P < 0.001$	

Addled eggs

The percentage of addled eggs was significantly greater in the delayed areas than in the controls, both in 1967 and 1968 ($p < 0.001$, Table 50). This may be due to poorer incubation, or to a breakdown in pair behaviour later in the season. The success of repeat clutches is not only dependent on the ability of the female to produce the eggs, but also on the male to fertilise these eggs. Both male and female must also retain the drive to successfully incubate the eggs through to hatching, even though this may not occur until middle or late July.

7.4 Nest distribution and breeding success

Although nests were shown to be distributed uniformly within the colony, there was considerable variation in nesting density. Neither Patterson (1965) nor Vermeer (1963) found any correlation between nesting density and breeding success in the Black-headed Gull and Glaucous-winged Gull respectively, though pairs breeding at the most common density were expected to be the most successful. This hypothesis was examined with the Herring Gull data, by grouping individual nests according to the number of neighbouring nests within a radius of 15 feet. Admittedly, this represents the final nesting density, and was based on a two dimensional plan of the colony. Late laying birds have been shown to nest around the perimeter of the colony, in typically less dense areas, and were also less successful breeders. To avoid any bias due to date and therefore density of laying, the analysis was restricted to birds laying within the short period of 14-20 June (Table 51).

There was a trend, though not significant, for clutch size to increase with density, and the hatching success was highest at the most common density (i.e. 4 to 5 nests within 15ft radius)(Fig.29). If the 0 and 1, and 2 and 3 densities are combined, the difference in hatching success between them and the 4 and 5 density becomes significant ($p<0.01$). Similarly, the fledging success, and in particular the number of chicks per nest, shows that the very high and low densities are the least successful (Fig.29).

Table 51. The relationship between nesting density and breeding success. Density calculated as the number of nests within a 15ft radius of individual nests. Breeding success shown ± one standard error

	Density No. nests within 15ft radius				
	0 and 1	2 and 3	4 and 5	6 and 7	more than 8
Frequency	10	42	72	54	33
No.eggs	27	116	201	152	95
Clutch size	2.70 ± 0.14	2.76 ± 0.08	2.79 ± 0.05	2.81 ± 0.06	2.88 ± 0.06
No.chicks hatched	14	73	151	114	63
% Hatching success chicks per egg	51.9%	62.9%	75.1%	75.0%	66.3%
chicks per nest	1.40 ± 0.40	1.74 ± 0.19	2.10 ± 0.12	2.11 ± 0.14	1.91 ± 0.19
No.chicks fledged	4	34	63	45	26
Per cent fledging	28.6%	46.6%	41.7%	29.6%	27.4%
chicks per nest	0.40 ± 0.21	0.81 ± 0.14	0.88 ± 0.11	0.83 ± 0.11	0.79 ± 0.16

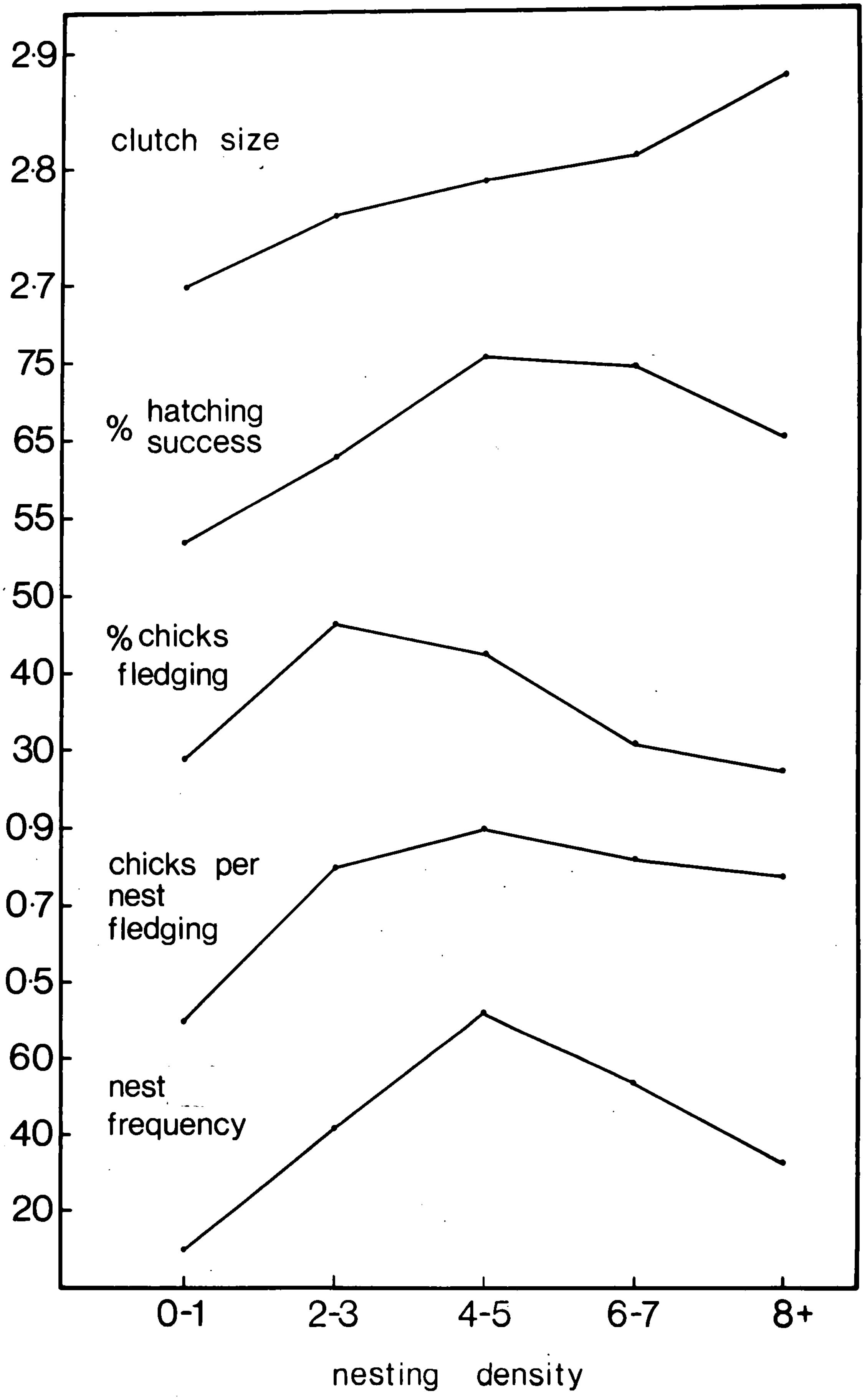
Figure 29

The relationship between nesting success and nesting density.

Variations in :

(i) Clutch size
(ii) percentage hatching success
(iii) percentage chicks fledging
(iv) chicks per nest fledging
(v) nest frequency for variations in nesting density

Density plotted as the number of neighbouring nests within a 15ft radius of individual nests


2·9
2·8
2·7
75
65
55
50
40
30
0·9
0·7
0·5
60
40
20
clutch size
% hatching success
% chicks fledging
chicks per nest fledging
nest frequency
0-1
2-3
4-5
6-7
8+
nesting density

Predation is an important cause of chick and egg loss (see Section 8), and several authors have discussed the probable anti-predator function of colonial nesting and synchronised laying in sea-birds (Kruuk 1964, Patterson 1965). It was suggested that colonial nesting encourages and enhances the use of behavioural defence mechanisms, such as mass attack on predators. The main predator of both eggs and chicks on the Isle of May is the Herring Gull itself, and fortunately it was possible to trace the nests from which chicks were cannibalised (see Section 8). It seemed worthwhile investigating whether cannibals selected nests that were perhaps more isolated or in less dense areas than others. The number of nests within various radii of each of the cannibalised nests was calculated, and this was compared with similar data from a random sample of nests. Nest site numbers for the latter were obtained from a table of random numbers.

The results are shown in Table 52, and illustrate that the cannibals do prey on nests that are situated in significantly less dense areas. This substantiates the poorer fledging success noted in areas of low nesting density. The same lack of success in dense areas is probably the result of increased mortality due to territorial aggression, as opposed to cannibalism by adults. Coulson (1968) with the Kittiwake, and Patterson (1965) with the Black-headed Gull, demonstrated a difference in the breeding success of birds nesting in the centre and on the edge of a colony. The better reproductive rate in the centre of the Kittiwake colony was attributed to the quality of the male birds.

Table 52. Comparing the mean density of nests (N=71) from which chicks were cannibalised with that of a random sample of nests (N=80) selected from a table of random numbers (Fisher & Yates (1963). Density is expressed as the number of nests within a particular radius of the individual nest

	Mean density ± 1 standard error		
	radius of circle - feet		
	7.5	10.0	15.0
"Cannibalised" nests	0.84 ± 0.09	2.07 ± 0.15	4.80 ± 0.21
Random nest sample	1.12 ± 0.09	2.74 ± 0.14	5.39 ± 0.20
Probability	< 0.05	< 0.002	< 0.05

Table 53. Comparing the breeding success of Herring Gulls nesting at the same time in the centre and on the edge of the colony - North Ness 1968

	Edge	Centre	P.
Density (nests within radius 15ft)	4.50 ± 0.25	5.80 ± 0.36	$p < 0.01$
No.nests	161	102	
No.eggs	428	285	
Clutch size	2.66 ± 0.045	2.79 ± 0.045	$p < 0.01$
Hatching success	71.3%	70.5%	
Chicks per egg	1.89 ± 0.87	1.97 ± 0.107	NS
Young fledged/ pair	0.76 ± 0.069	0.80 ± 0.089	NS

Differences in the breeding success of Herring Gulls nesting in the centre and on the edge of North Ness might merely reflect the age structure of the population, since late laying occurs most frequently around the perimeter. However, by comparing birds that laid within the same period, it was hoped to find out whether differences are present irrespective of the age or time of breeding of the adults. The degree of cover around the nest is an important factor contributing to the success of breeding (Brown 1967), but the two areas under comparison were of the same physical structure, and therefore cover was not expected to bias the result.

The results (Table 53) show an expected difference in the nesting density of the two areas. Furthermore, there are significantly fewer eggs laid per pair on the edge of the colony, even though eggs were laid at the same time in both areas. This would indicate a difference in the quality of the birds, although the breeding success does not substantiate this conclusion.

SECTION EIGHT

FLEDGING SUCCESS AND ASPECTS OF CHICK MORTALITY

8.1 Introduction

General

The season has been shown to be important in influencing the numbers and size of eggs laid by the Herring Gull, but is relatively insignificant in determining the numbers of eggs that hatch. To understand the success of this species, it was necessary to evaluate the fledging success, and the factors that contribute to the numbers of chicks failing to fledge. In particular, the study was to determine whether the hatching date was important in aiding the survival of chicks whilst on the island, and during their first winter months. To achieve these aims, a large scale ringing programme was carried out. Chicks were ringed on hatching to assess their immediate survival during the pre-fledging period, and were also colour ringed at all ages on the island to follow the remaining pre-fledging mortality and the survival during the post-fledging period. The latter was monitored by ringing recoveries and sightings of colour ringed gulls.

Methods

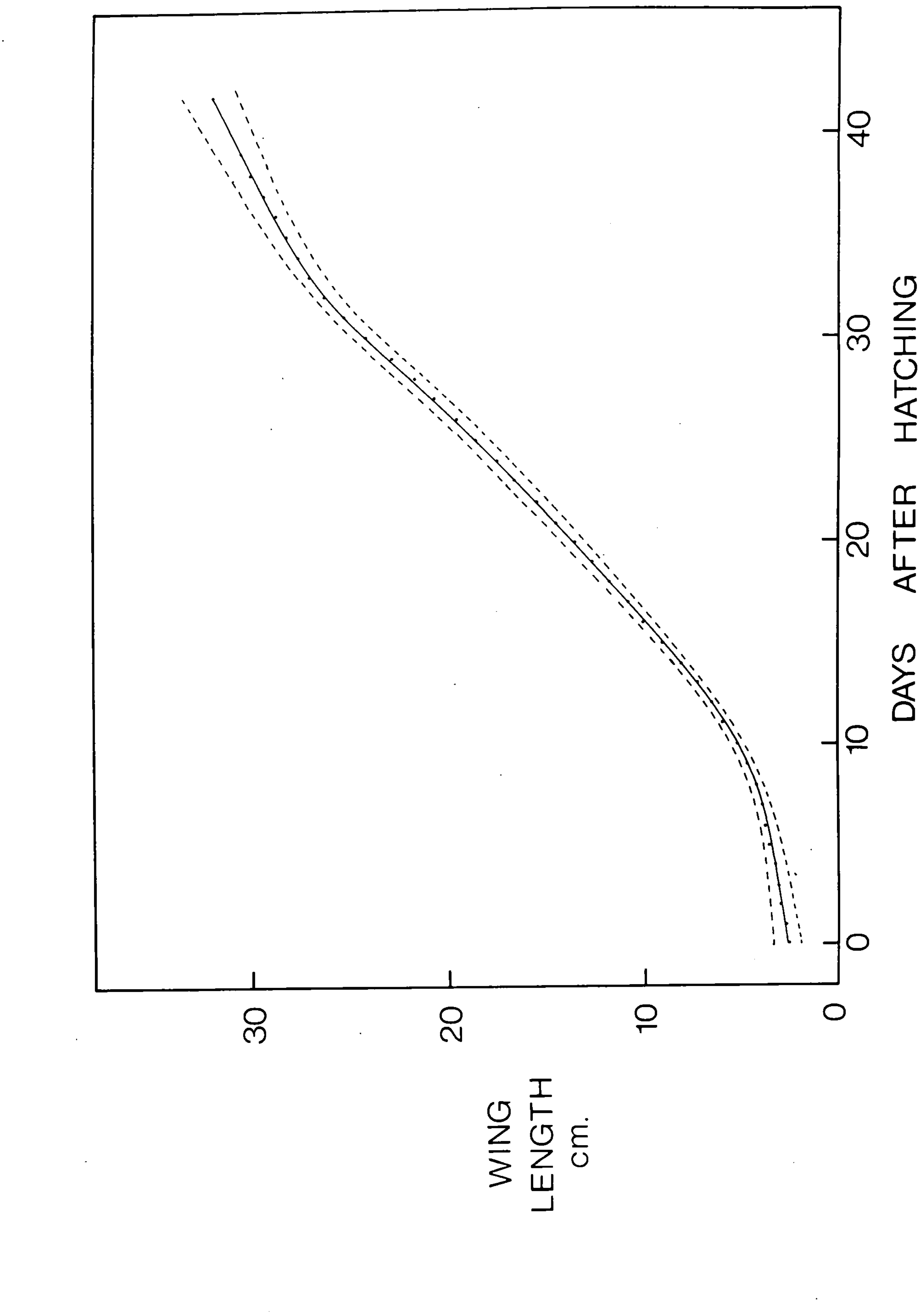
Unless chicks could all be ringed on hatching, some growth factor would have to be measured to ascertain the approximate hatching date of each chick. Wing length measurement is a much easier task, and involves far less disturbance to the chick than weighing. It is also more related to age than weight which fluctuates markedly in young chicks with the presence of food in the gizzard. For example, using 18 chicks of the same known age, the standard deviation was 12 per cent of the mean weight, but only 5 per cent of the average wing length. Frequently a young but well fed chick was found to weigh more than an older and poorly fed chick of longer wing length. For these reasons wing lengths were used as an age parameter.

From wing lengths of chicks of known age, a growth curve was plotted (Fig.30). The rate of growth is a maximum from 16 to 28 days from hatching (wing length 10-22cm), and it is during this time that the age of the individual can be most accurately assessed. Using this graph, the hatching dates of all chicks ringed were estimated.

In the control and experimental areas, most of the chicks were ringed on hatching with the rings of insulating tubing. For example, of the 1722 chicks hatching on North Ness in 1968, 1415 were ringed in this manner with the appropriate nest number written on the ring. In another area, 786 chicks were ringed with the same tubing, but different colours were used according to the date of hatching. Later, all these rings were replaced by the usual monel and darvic rings. However, for general ringing the extrapolation from the wing length graph was the only method of knowing the hatching date of the chicks.

Figure 30

Growth curve of Herring Gull chick wing length. Mean wing length (± 2 standard errors - dotted lines) according to the number of days after hatching


WING LENGTH cm.
0
10
20
30
0
10
20
30
40
DAYS AFTER HATCHING

During the period 1966-68, a total of 14,367 Herring Gull pulli were ringed with the B.T.O. monel rings (Table 54). The pre-fledging recovery of these rings gave estimates of chick mortality during the breeding season. To compare the post-fledging survival of chicks from different hatching dates, chicks were also colour ringed according to their estimated date of hatching (Appendix X). In 1966, only two combinations of monel and red rings were used, to differentiate between normal (3736 chicks) and late (604) chicks hatching chicks. The following year, using yellow rings, various ring combinations denoted the different areas from which the chicks hatched. So, for example, all the chicks from Burrian (3) had the same colour combination and represented a delayed mean hatching date of 2 July.

In 1968, each chick was aged on capture, and colour ringed according to its estimated date of hatching. Four colour combinations were used to divide the hatching period into four groups : up to 9 June, 9-16 June, 16-23 June, after 23 June (Fig.31).

The control and experimental areas were visited regularly, and the deaths or disappearance of chicks noted. After fledging, a thorough search of the whole island was made for rings and dead chicks. In the study areas, it was assumed that all chicks were ringed. This was not necessarily correct, but the best estimatesof pre-fledging mortality were obtained by noting the numbers of chicks monel-ringed, and the number subsequently found dead. Some chicks inevitably avoided capture, resulting in an

Figure 31

The four colour-ring combinations of Herring Gull pulli ringed in 1968, showing the relationship with date of hatching. The percentage ringed of each of the four groups is given according to the date of hatching

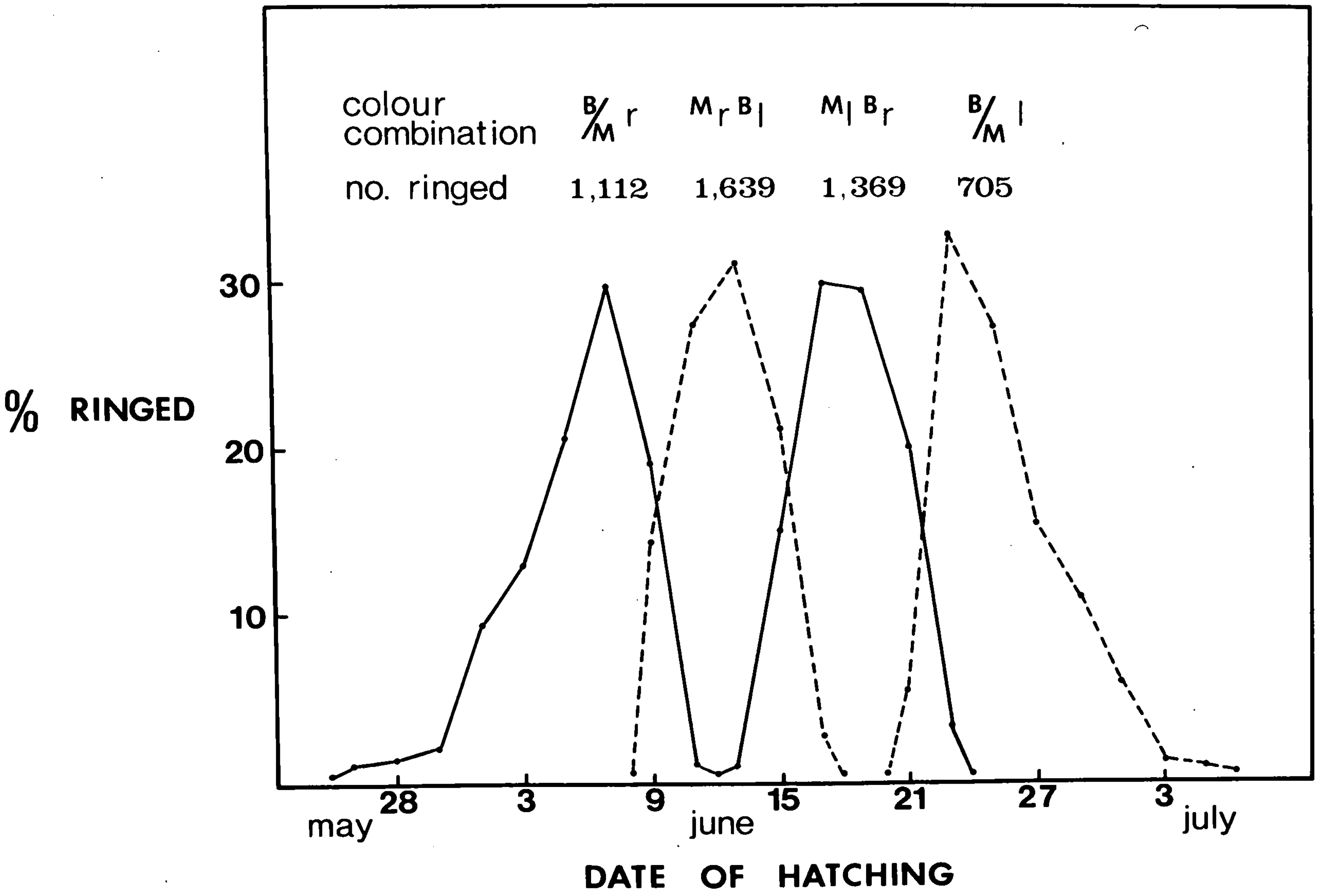

colour combination
B/M r
M r B l
M l B r
B/M l
no. ringed
1,112
1,639
1,369
705
% RINGED
30
20
10
28
3
9
15
21
27
3
may
june
july
DATE OF HATCHING

Table 54. Monel ringing of Herring and Lesser Black-backed Gulls on the Isle of May during 1966-68 breeding seasons

	Number of gulls				
	Herring Gulls		Lesser Black-backed Gulls		
	pulli	adults	pulli	adults	Total
1966	4,325	15	150	10	4,500
1967	5,230	97	614	9	5,950
1968	4,812	64	14	1	4,891
Total	14,367	176	778	20	15,341

underestimate of breeding success. Conversely, there will be dead ringed chicks which will not be found, thereby causing an overestimation of survival. Various studies have based their pre-fledging survival figures on the regular re-capture of ringed chicks. Although this was attempted on the Isle of May, the disturbance caused by the continuous re-capture of chicks seemed too severe to be worthwhile. Instead, only un-ringed chicks or chicks that held the insulating tube rings were captured and monel ringed.

8.2 Age and Mortality

During the hatching period, the adults must change behaviour from incubation to protection and feeding of the young. This transition is not always successful, and therefore a major part of pre-fledging mortality occurs in the post-hatching days (Table 55). A total of 31.2 per cent of the chicks that hatched on North Ness (1968) died

Table 55. Pre-fledging mortality - age of chicks at death (or disappearance) North Ness 1968

	Age of chicks							
	days							
	0 - 4	6 - 10	12 - 16	18 - 22	24 - 28	30 - 34	36 - 40	40 - 46
No. chicks at risk	1722	1190	928	828	764	696	653	630
No.died	532	262	100	64	68	43	23	21
Percentage mortality over 5 day period	31.2%	22.0%	10.8%	7.7%	8.9%	6.2%	3.5%	3.3%
Total percentage of chicks surviving	69.1%	53.9%	48.1%	43.4%	40.4%	37.9%	36.6%	35.4%
Sample of chicks that died of exposure in July 1968	6	16	26	5	3	1	0	0
Percentage of total chicks that died of exposure	10%	28%	45%	10%	5%	2%	0%	0%

within the first four days, and of the 1,113 chicks that died before fledging, 794 or 71 per cent did so before they were ten days old. After this period, the mortality is fairly constant. Paynter (1949), Paludan (1951), Brown (1967), and Kadlec et al (1968, 1969) all agree that most of the mortality occurs in the first week of life, but Harris (1964) suggested a constant mortality rate which is not substantiated by these results. Harris's results were based on the ages of chicks that were found after death. In 1967 and 1968, the wing lengths of all dead chicks were recorded, and a similar table of age at death produced. The results gave an abnormally low mortality in the first ten days of life (20 per cent compared with 46 per cent), because it is this age group that is the most difficult to find, and, more important, the most commonly eaten by predators.

8.3 Brood size and fledging success

Although hatching success was shown to vary significantly with clutch size, no relationship was evident between fledging success and brood size (Table 56). This was in agreement with Paynter's (1949) findings, but Brown (1967) concluded that "a chick in a brood of three has a better chance of survival to ten days than has one in a smaller brood, though there is no such difference for Lesser Black-backed Gulls." Unlike clutch size, brood size has little or no effect on survival, although birds hatching larger broods ultimately rear more offspring (Table 56).

Table 56. Brood size and pre-fledging success

No.chicks hatching per nest	Total no. chicks hatching	No. fledging	% fledging	Chicks per pair
3	1,080	381	35.3%	1.06
2	520	177	34.0%	0.68
1	124	51	41.1%	0.41

8.4 Seasonal variation in fledging success

Brown (1967) and Kadlec et al (1968) found that the most successful chicks were those hatched during the peak of the breeding season, rather than early or late hatched chicks. However, Harris (1969) showed an increase in fledging success as the season progressed. This study on the Isle of May approached the problem in two ways. Firstly, by a detailed analysis of the progress of chicks from hatching onwards and a comparison with delayed areas. Secondly, by general ringing of chicks of all ages, which involved large numbersof chicks and less frequent visits. The results will therefore be presented separately.

In 1968, the fledging success from the North Ness control area showed a significant variation with the season. Chicks from eggs laid early in the season suffered a higher mortality ($p < 0.01$) than those laid in the middle of the season (Table 57 and Fig.32a), and later hatching chicks were even more likely to die before fledging ($p < 0.001$). The numbers of chicks fledged per pair exaggerates this effect, as it also includes the similar seasonal variation

Table 57. Pre-fledging chick survival on North Ness (control) 1968

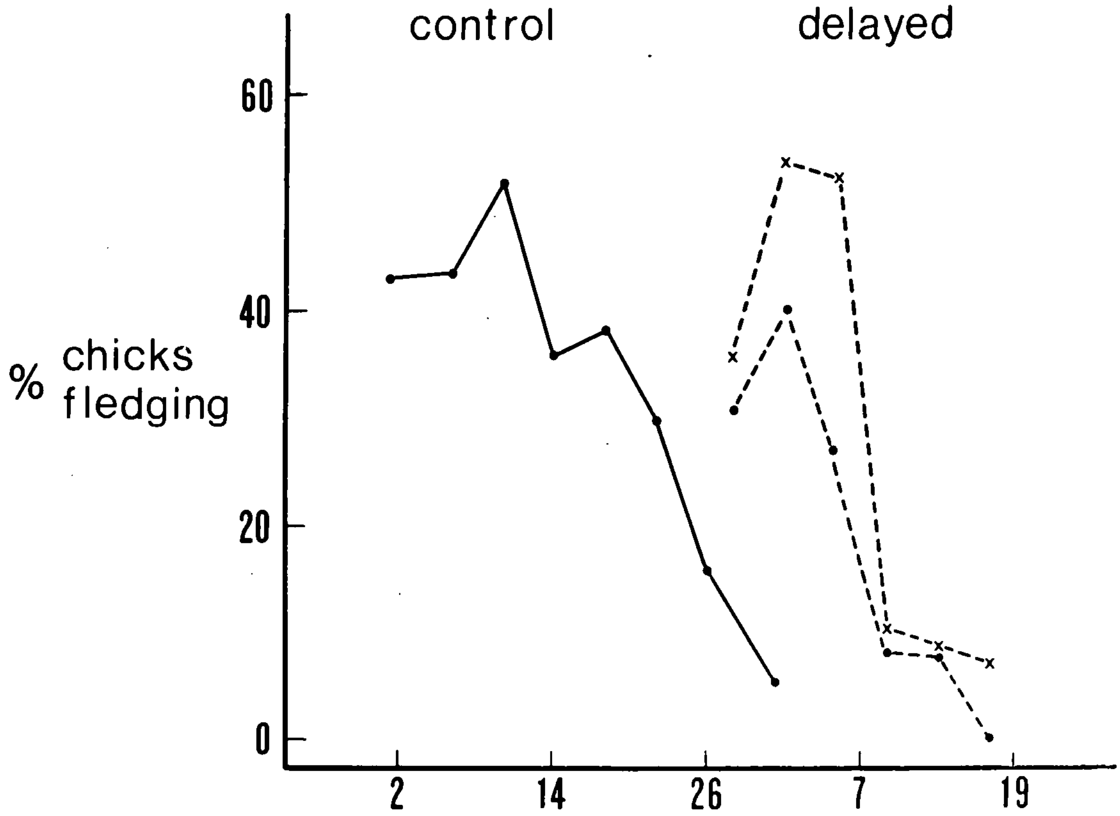
	laying date May							
	up to 4	6 - 8	10 - 12	14 - 16	18 - 20	22 - 24	26 - 28	30 onwards
No.nests	46	87	132	134	185	149	101	69
No.chicks hatching	84	165	259	246	409	302	162	95
Percentage surviving from 0 to 10 days	67.1%	67.9%	65.5%	53.3%	50.9%	32.8%	19.1%	8.4%
No.fledging	36	71	134	88	157	90	26	5
Percentage fledging	42.9%	43.0%	51.7%	35.8%	38.4%	29.8%	16.0%	5.3%
Difference in fledging success over one week	←	p<0.01 →	NS ←	p<0.001 →	NS ←	p<0.001 →	p<0.001 →	-
Chicks per pair ± one st. error	0.78 ± 0.13	0.82 ± 0.10	1.02 ± 0.08	0.66 ± 0.07	0.85 ± 0.06	0.60 ± 0.06	0.26 ± 0.06	0.07 ± 0.03

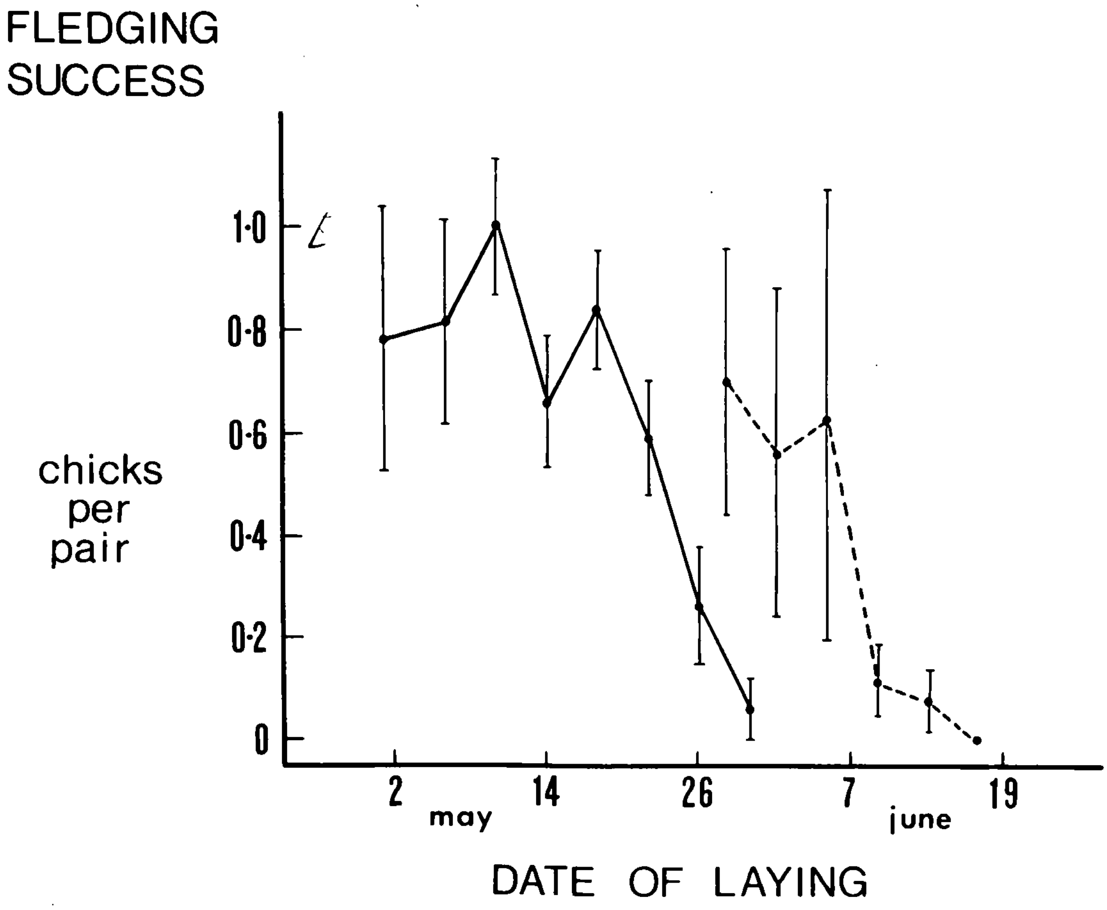
Figure 32

Variation in fledging success of chicks in the control (continuous line) and delayed (dotted line) areas in 1968 according to date of laying :

(a) Percentage of chicks fledging (upper graph); with delayed area results expressed as total pre-fledging success (lower dotted line) and also pre-fledging success excluding mortality due to exposure in July rains (upper dotted line).

(b) chicks per pair ± 2 standard errors (lower graph)


control
delayed
% chicks fledging
60
40
20
0
2
14
26
7
19


FLEDGING SUCCESS
chicks per pair
1·0
0·8
0·6
0·4
0·2
0
2
may
14
26
7
june
19
DATE OF LAYING

in hatching success and clutch size (Fig.32b). However, the peak of fledging success didnot coincide with the peak of the laying period, but was six days earlier in the season.

The fledging success in the delayed areas did not accentuate this seasonal decline. Instead, it again appeared like a control area but displaced in the season (Table 58 and Fig.32), showing the same pattern that was demonstrated with hatching success. Therefore, when comparing the same time groups (eggs laid between 26 May and 2 June), the late hatching chicks from North Ness suffered a significantly higher mortality than the early hatching Tarbet chicks ($X^2 = 71.3$, $p < 0.001$). In other words, the synchronisation of nesting was the most important factor in determining the pre-fledging success. Nevertheless, the season did exert an effect in this year.

From 1 to 4 July, there were torrential rains and gale force winds, which were repeated later in the month from 17 to 19 July. Large numbers of late hatching chicks died of exposure in these conditions throughout the island. Chicks from 6 to 22 days of age suffered the most, since very young chicks were protected by their parents, and those over three weeks of age seemed old enough to survive (Table 55). This is probably due to the development of a more protective feathering at that age. If the losses that were incurred during these rainstorms are discounted in the analysis, then the pre-fledging success resembles more closely that of the control areas (Table 58 and Fig.32). The high mortality of chicks

Table 58. Pre-fledging chick survival on E. Tarbet (delayed) 1968

	laying date					
				June		
	up to 29	31-2	4-6	8-10	12-14	16 onwards
No.nests	47	25	8	117	143	19
No.chicks hatching	107	35	19	180	167	14
No.fledging	33	14	5	14	12	0
% fledging	30.8%	40.0%	26.3%	7.8%	7.2%	0%
Difference in fledging success over one week (P)	-	← NS →	← → <0.001	← <0.01 →	-	-
Chicks per pair ± one standard error	.70 ±0.13	.56 ± 0.17	.63 ± 0.35	.12 ±0.03	.08 ±0.03	0
% fledging, excluding mortality due to exposure during the storms in July	35.5%	54.3%	52.6%	10.0%	7.8%	7.1%

hatching late in both the control and delayed areas generally occured within the first week of hatching. Usually the chicks hatched, then quickly disappeared, and it can only be assumed that most of them were eaten. Whether they died through lack of parental care and were subsequently eaten, or whether they were actually cannibalised is not fully known and will be discussed later.

It will be remembered that in 1968, apart from the detailed study in the delayed area (Tarbet), various parts of the island were generally delayed by the removal of several thousands of eggs. When the normal and repeat clutches hatched, a total of 3,922 chicks were ringed, their hatching date calculated and their fledging success recorded. Taking these chicks as a whole, there was again a significant variation in fledging success according to date of hatching ($p < 0.01$). Chicks hatching around 11 May were the most successful, and before and after this date the pre-fledging mortality increased (Fig.33).

The earlier a chick is ringed, the more chance there is of recovering the ring before fledging. This can be demonstrated by calculating the post-ringing mortality of chicks ringed at different ages (Table 59). Chicks hatching at the same time in the season were used in the analysis, to avoid any bias due to hatching data. It is conceivable that the late hatching chicks were ringed at a younger age than those hatching earlier in the season, and would therefore be expected to suffer a higher post-ringing mortality. In fact this was avoided

Figure 33

Variation in percentage pre-fledging mortality according to date of hatching for all pulli ringed during 1968. Regression lines plotted of mortality of chicks hatching before and after 11 June; open circles refer to the mean mortality over four-day hatching periods, and numbers of chicks ringed also presented on the graph.

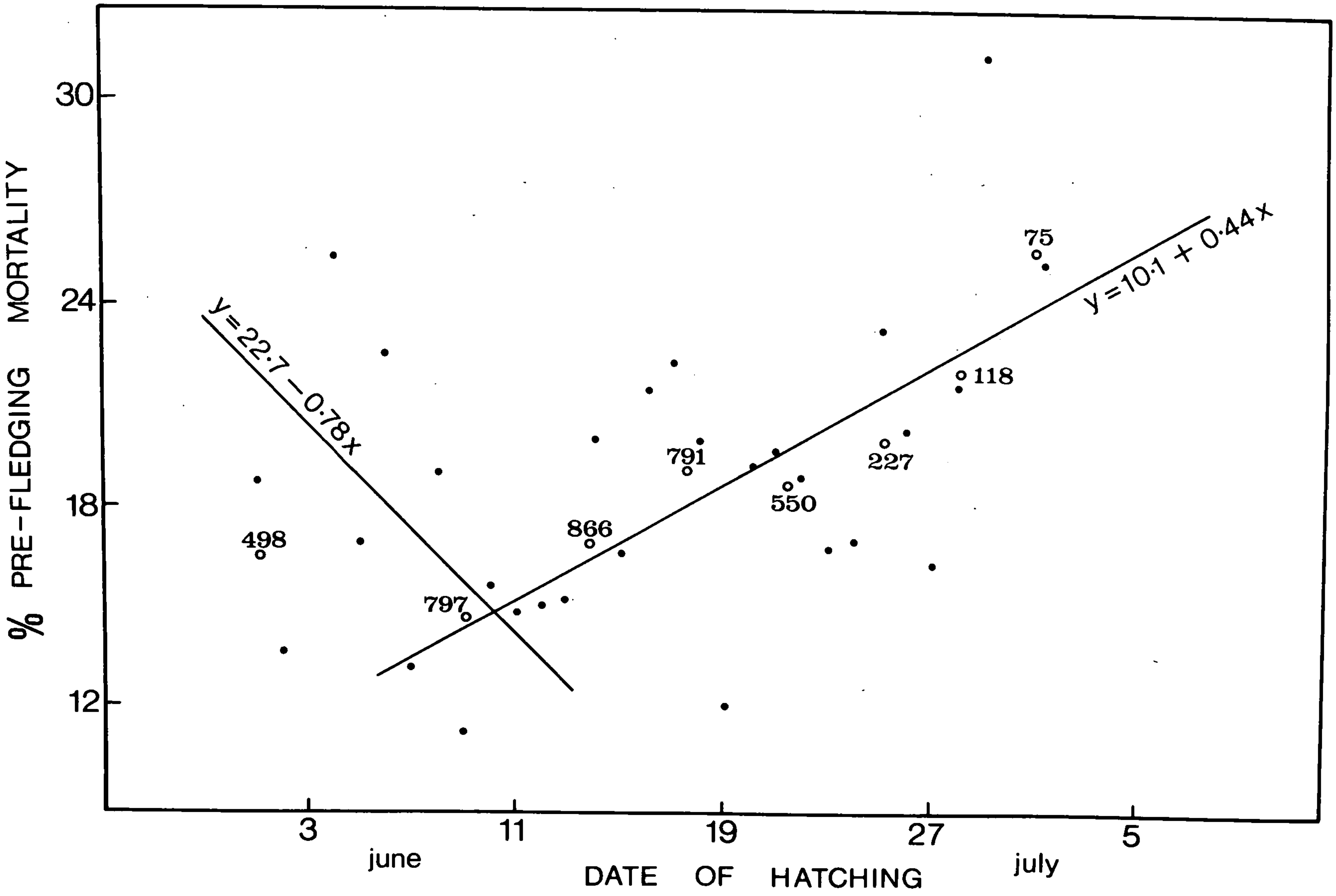

30
24
18
12
% PRE-FLEDGING MORTALITY
3
11
19
27
5
june
july
DATE OF HATCHING
y=22·7 – 0·78x
y=10·1 + 0·44x
75
118
227
550
791
866
498
797

Table 59. Variation in post-ringing mortality with age of chick at ringing (chicks hatching between 8 and 14 June)

	age of chick when ringed - days					
	0-10	11-17	18-24	25-31	32-38	39 onwards
No.ringed	132	116	227	503	579	215
No.died	35	25	46	94	75	17
% mortality after ringing	26.5%	21.6%	20.3%	18.7%	13.0%	7.9%

by attempting to ring chicks from each hatching group at about the same age. Nevertheless, unless all chicks were the same age when ringed, some correction to the analysis must be made to allow for this difference.

The ringing and mortality data were re-assessed by grouping chicks according to their age at ringing, and as usual according to their estimated hatching date. The results are given in Table 60 and show the same variations of pre-fledging with hatching date. However, the differences in mortality are more obvious in those chicks that were ringed when quite young (up to 12 days old).

Similar results were obtained for the 1967 season, when the control areas were compared with delayed colonies (Fig.34 and Appendix XI). The mean hatching date of the control areas was 17 June and on this occasion the peak of fledging success coincided with the peak of hatching. The Tarbet and Burrian (1) delayed nests are combined in the analysis, having a mean hatching date of 23 June,

Table 60. Pre-fledging mortality. General 1968. Seasonal variation according to age of chicks on ringing

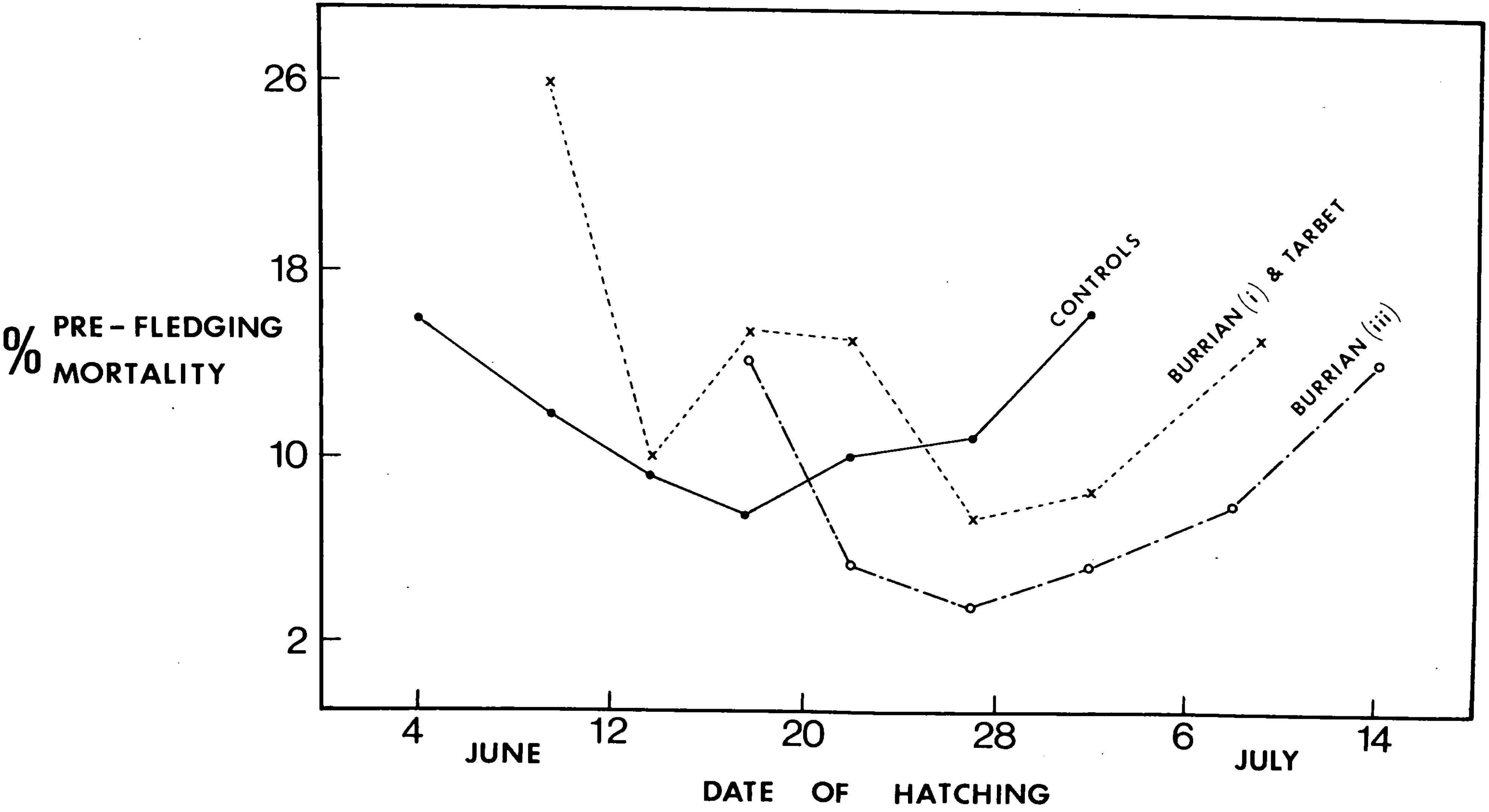
Percentage mortality (number of chicks ringed in brackets)

Hatching date - June

Age of chicks when ringed Days	up to 6	7-11	12-15	16-19	20-23	24 onwards
Up to 12	36.8 (95)	28.0 (100)	19.2 (52)	35.7 (28)	23.1 (13)	28.6 (14)
13-22	11.3 (71)	18.6 (86)	21.9 (73)	20.5 (83)	25.0 (96)	21.7 (69)
23-27	12.8 (47)	8.3 (24)	17.5 (160)	27.4 (189)	19.6 (97)	25.6 (138)
28-34	7.5 (40)	15.3 (300)	18.5 (352)	17.4 (344)	16.8 (267)	19.1 (178)
over 35	12.7 (245)	8.0 (287)	11.8 (229)	10.9 (147)	15.6 (77)	14.3 (21)
Total	16.5 (498)	14.6 (797	16.9 (866)	19.1 (791)	18.7 (550)	21.4 (420)

Figure 34

Variation in percentage pre-fledging mortality of control and experimental areas 1967 according to date of hatching


% PRE-FLEDGING MORTALITY
26
18
10
2
4
JUNE
12
20
28
6
JULY
14
DATE OF HATCHING
CONTROLS
BURRIAN (i) & TARBET
BURRIAN (iii)

and compared with a third group (Burrian 3) which was further delayed to hatch on average around 2 July. The conclusion is the same for all three groups, whether it be the control situation, or either of the delayed colonies. Chicks hatching early or late relative to the rest of the group or sub-colony, are more likely to die before fledging than those that hatch during the peak.

8.5 Causes of chick mortality

Cannibalism and predation

Introduction

The Herring Gull is a notorious killer during the breeding season, and its activities have been well recorded. Young chicks are repeatedly struck on the head, often gripped by the neck, and worried until dead (Dutcher & Baily 1903, Ward 1906, Strong 1914). Chicks may be eaten (Paynter 1949), not only by strangers, but also by their own parents (Moreau 1923, Goethe 1956). Later in the breeding season large chicks may augment this mortality by committing fratricide (Strong 1914).

Usually, most chick predation and egg loss is attributed to these forms of prolicide and cannibalism (Paynter 1949, Paludan 1951, Brown 1967, Harris 1964), although other predators are also known to cause considerable mortality. The most frequent offender is the Greater Black-backed Gull, which collects chicks in the down stage for food (Darling 1938, Gross 1945, Paynter 1949, Harris 1964). However, Kadlec et al (1968) concluded that this species has little overall effect on the reproductive success of the Herring Gulls. Other predators have been implicated, for example, the Heron (Darling 1938) and the Great Skua (Fisher & Lockley 1954), but on the Isle of May only the Herring Gulls and the Lesser Black-backed Gulls were prominent in this respect. The four pairs of Greater Black-backs were singularly unsuccessful at breeding, all but one pair having usually deserted their nest sites before the main hatching period. No other predatory birds or mammals lived on the island, except a pair of Carrion Crows that were occasionally noted breaking eggs.

As there are distinct differences between prolicide and cannibalism, the explanations for their causes or motivation must be treated separately. Prolicide is usually the result of the territorial aggression of neighbouring gulls against trespassing chicks (Herrick 1909, Deusing 1939). However, cannibalism is less easy to interpret. Kirkman (1937) believed that many deaths of the Black-headed Gull are due to "unmated" rogue gulls which have acquired the habit. Similarly, Tinbergen (1953) suggested that three- and four-year-old sub-adult Herring Gulls hanging around the colony are active predators. In this study it will be shown that the most prolific chick eaters were gulls rearing quite normal broods of their own, and that it was indeed a recurring habit.

The cause and role of cannibalism have recently received some attention in the wider context of population regulation. It has generally been argued that the availability of food limits the numbers of most birds, but that this is achieved either directly (Lack 1954, Southern 1959) or indirectly through behaviour mechanisms (Wynne-Edwards 1962). So, for example, Paludan (1951) suggested that "an increasing population probably gives less favourable feeding possibilities and therefore an increased cannibalism." This would then cause a reduced growth of the population. Under these circumstances, cannibalism merely exploits an additional source of food, and its practice could have evolved by individual selection favouring those adults able to make use of this food supply (after Ashmole 1963). The opposing argument favoured group selection as a mechanism for limiting the population. Cannibalism would then be one of a series of density-dependent brakes applied to the rate of recruitment to a population (Wynne-Edwards 1962).

Brown (1967) noted that cannibalism was the main cause of chick mortality on Walney but, at the same time, there was no evidence of a food shortage. This somewhat conflicting evidence was explained by the general scavenging nature of gulls and the density of available food. As such, cannibalism was regarded as "an extension of the normal hunting of young shore-birds and ducklings." In this general role as a predator a gull would collect chicks quickly from the colony more easily than undertake a long flight to another food source, even though this other source were available. Cannibalism is then attendant on a large, dense population which can be efficiently exploited in this way. Even so, it was considered a built-in behavioural check on the increase of a large gull population.

Few observers who have visited Herring Gull colonies have failed to record instances of cannibalism. Nevertheless, a quantitative study of this habit appears to have been neglected.

it therefore seemed worthwhile investigating such matters as the proportion of true cannibals among adults, the number of chicks eaten, and the distances flown in collecting them. An attempt to consider these matters will be made before discussing the role of cannibalism on the Isle of May.

It is possible to divide prolicide or cannibalism into three main categories. Firstly, there are chicks that trespass into other territories, and are killed. As already mentioned, the motivation in this case is clearly territorial behaviour of the adult. Usually the chick lies dead and untouched except for the original, fatal wounds around the head. However, some of these chicks and others that have died of disease or bad weather may subsequently be eaten by the murderous adult or by other gulls nearby. The motivation here is merely the scavenging nature of gulls and this will be regarded as the second category. It is usually distinct from the third possibility, in that the chicks or their remains are found in the vicinity of their own nest site. Thirdly, there are what I prefer to call the "true cannibals." These birds leave their own nest site specifically in search of live chicks as a food source (Plates 6a-e). In this respect they differ little from the Greater Black-back or Great Skua predators except that they are less likely to be harassed by their own species during their raids.

There is, in fact, one other form of intraspecific chick mortality which will be dealt with separately : namely, when adults eat their own offspring (kronism - after Schuz 1957),

(a)

(b)

PLATE 6 a. and b. Cannibalism. A cannibal collecting a chick and being challenged by the parent.

(c)

(d)

(e)

PLATES 6 c,d,and e. Cannibalism. Cannibal on its nest site, killing and eventually swallowing a chick.

or when chicks eat their own siblings (fratricide). The study of all these forms of cannibalism was made possible by ringing chicks at hatching with rings of insulating tubing. The nest site number, and brood number of the chick, were written on the rings and were usually legible even when regurgitated by the cannibal.

Kronism and fratricide

Of all the forms of cannibalism, the killing of offspring by parents would seem at first sight to be the most unnatural, and yet it is not particularly uncommon. This cause of infantile mortality is typically associated with protracted laying, which establishes a nestling hierarchy. For example, the White Stork hatches out a graded series of young and frequently the smaller nestlings are either thrown out of the nest or killed and eaten by their parents (Schüz 1943, 1957). These casualties are usually associated with young adults and are believed by some to be adaptive, eliminating surplus offspring (Wynne-Edwards 1962).

Fratricide is also practised by those species that start incubating as soon as the first egg is laid and is known to occur among birds of prey and owls. Ingram (1959) has studied this juvenile mortality and concludes that "it is eugenically preferable to rear, let us say, one or two healthy well-nourished progeny rather than six or seven weaklings." As such, fratricide reduces the brood size to the most efficient number of chicks that can be reared under the prevailing conditions, and an adequate supply of food precludes any further juvenile mortality.

We have seen that the Herring Gull does not wait until the third egg is laid before starting to incubate. Instead, both egg laying and hatching are somewhat protracted, and there is evidence to suggest that the graduation in time of hatching and inferior size of the third chick are responsible for its relatively high mortality. Frequently, this chick disappeared at an early age from the nest site. It may be assumed that this disappearance of young chicks was most commonly the result of cannibalism. Lack (1954) pointed out that predators tend to take the weakest members of their prey species and it is possible that the third hatched chick is commonly in that position. Of all the chicks that were eaten, the c-chick suffered the most, so that the incidence of cannibalism on this chick was significantly greater than on its siblings ($p < 0.05$, Table 61).

Table 61. The numbers of chicks of different hatching sequence that were found cannibalised

	No.cannibalised	No.ringed	Per cent eaten
a-chick	30	611	4.9%
b-chick	27	509	5.3%
c-chick	26	295	8.8%

Difference between a- and c-chicks : $X^2 = 5.23$ $p < 0.05$

Similarly, the c-chick succumbed more frequently to kronism than either of the other chicks. When the regurgitated remains of a chick have been found on its nest site it has been assumed that its own parent was the guilty party. This mortality usually occurred when the chicks were quite small and, of course, without direct observational evidence, it is not possible to rule out death through 'natural' causes before the chicks were eaten. However, kronism was noted in 15 nests from a total of 747 nests in which at least one chick hatched (i.e. 2 per cent occurrence). This mortality affected 9 c-chicks, compared with 4 b-chicks and 2 a-chicks.

It is difficult to comment with confidence on the motivation for these deaths, or their evolutionary significance. Several small chicks are found either dead or dying on their nest sites, and their condition is usually emaciated. This could be through lack of food, or possibly disease. It is easy therefore to assume that the victims of their parents' attacks are doomed individuals that would have died anyway. This would suggest that the slightly protracted laying, and also the small third egg, are adaptations to unfavourable conditions. The resulting chick competes unsuccessfully with its siblings, is weakened and either dies or is killed by its parents.

However, food does not appear to be short for this species during the breeding season. If this is the case, then the ultimate factor assumed necessary to initiate kronism is absent, and Wynne-Edwards (1962) hypothesis of a socially induced juvenile mortality becomes an alternative solution. Kronism would then be regarded as a social convention which "is not due to the parent's simple inability to supply food" (loc.cit., p.537). Before continuing this discussion it is necessary to look at the more widespread phenomenon of cannibalism.

Cannibalism

A walk through the colony during the pre-fledging period will reveal the large proportion of chicks that have been attacked or eaten by other gulls. In 1967 and 1968, the percentages of dead chicks that were partially or wholly eaten, or that showed head scars, were 56 per cent (N = 226) and 49 per cent (N = 335) respectively (Plate 7). On some occasions these injuries may have been inflicted after death, and it was not uncommon for fledglings to wander around the island pecking and pulling at dead chicks.

Dead chicks with head scars had most probably trespassed into foreign territories and subsequently suffered for their misadventure. Such deaths are more frequent amongst older chicks which are prone to wander. It is the smaller chicks that are more acceptable as food items for cannibals. For example, of the chicks under 10 days of age on North Ness 1968, 92 per cent of those that were killed (N = 221) were also eaten and the rings and bones later regurgitated. Of those chicks that were killed when older than 10 days, only 53 per cent were then eaten (N = 73), and the remainder merely had head scars.

Apart from the territorial aggression of adults on these chicks, there is another type of attack that can cause the mortality of large chicks without the motivation of cannibalism. When chicks are learning to fly they are often chivvied and chased, and beaten down into the sea. This behaviour has also been recorded by Paynter (1949) and Harris (1964), although no reasons for the attacks are suggested.

PLATE 7a. Wandering chick attacked by an adult - territorial aggression.

PLATE 7b. Head scars on a dead chick, typical of death through wandering into a neighbouring territory.

PLATE 7c. Regurgitated remains of chicks (e.g. bones, rings) on the nest site of a cannibal.

More important, the attacks are usually restricted to the young of earliest breeders. As the season progresses, the adults take less notice of newly flying chicks, almost as if accustomed to the novelty. It is possibly the cumbersome nature of the first flights, and perhaps the similarity of chicks to Great Skuas, that elicits this pugnacious response. Whatever the reasons, this mortality may be an important factor selecting against the young of early breeders (Harris 1964).

The extensive ringing programme made it possible to differentiate between the more 'casual' eating of chicks, and the incidence of regular cannibalism. On North Ness (1968) four cannibals ate 167 chicks, or 11.8 per cent of all the chicks available to them from that area. One of these four predators accounted for 70 chicks. This particular bird will be referred to as the 'Whaup cannibal'. Another eight less voracious cannibals were known on North Ness, but these ate less than 10 chicks each, and together with other casual cannibals they increased the chick mortality from this cause to 23.3% (Table 62).

By plotting the nests from which the four North Ness cannibals plundered chicks, it can be seen that the cannibals are ranging some distance from their own nests (Fig.35), and quite commonly from 50 to 150m. There was no chance that the chicks had wandered by chance to the cannibal territories, especially as the Whaup and Mars cannibals were isolated by sea and steep rocks from the rest of North Ness. In fact, these birds were seen to sweep down on poorly protected nests and seize chicks which were then often swallowed in flight. On other occasions, the chicks would be taken alive to the nest site of the cannibal, and then eaten at leisure (Plates a-e).

Figure 35

Scale diagram of North Ness showing nests from which two cannibals took chicks, and the distance the cannibals travelled from their own nests (1968)

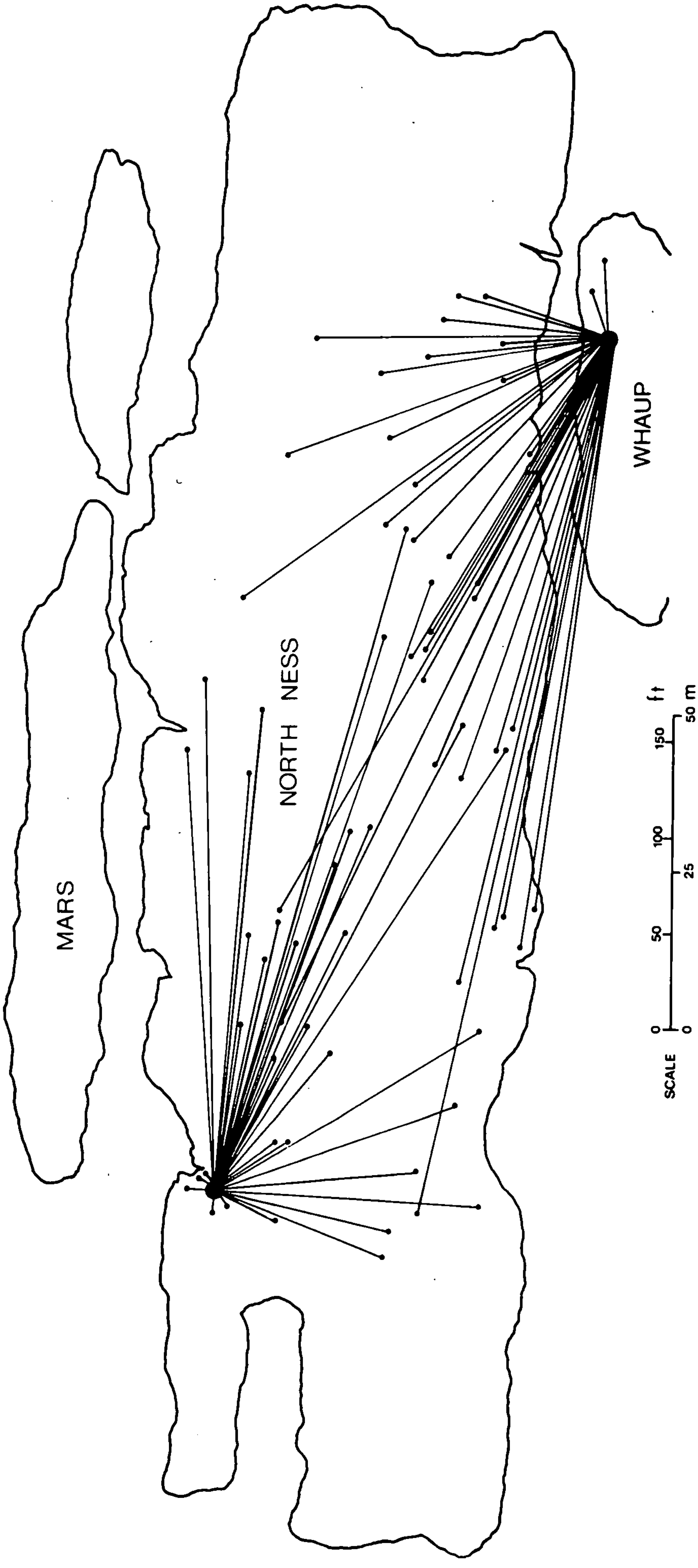

MARS
NORTH NESS
WHAUP
SCALE
0
50
100
150
ft
0
25
50 m

Table 62. Fate of chicks ringed at hatching on North Ness 1968

	No.chicks	Per cent of total
Number of chicks ringed	1,415	
Eaten by four cannibals	167	11.8%
Eaten by other cannibals	162	11.4%
Total chicks eaten	329	23.3%
Died with head scars	47	3.3%
Total chicks believed "killed"	376	26.6%
Found dead - no visible injury	256	18.1%
Known to have fledged	609	43.0%
Unaccounted for	174	12.3%

Cannibals have also been recorded in all other parts of the island. One outside the Low Light flew regularly to the North Plateau, a distance of between 1/4 and ½ Kilometer, to collect chicks. On E.Tarbet in 1967, a cannibal ate 20 ringed chicks, or 4 per cent of the total number ringed. This particular bird was slightly different from the other cannibals. Usually, as mentioned above, the cannibals take young chicks. For example, the number of days between hatching and disappearance were calculated for the chicks on North Ness that were cannibalised, and the mean age was 6.7 days ± 0.34 (N = 55). However, the E. Tarbet cannibal selected much older chicks, often between 10 and 24 days old, and these were taken to the nest site and the viscera removed and eaten.

In 1967, four cannibals were noted and studied, one on Tarbet, one on S.Rona, and two on North Ness. All these birds returned to their nest sites in 1968 and 1969, and all continued their habit of chick eating in these years. It therefore appears that once the habit is formed it remains over the years. Quite what induces cannibalism in the first instance, and at what age it occurs, is not known. There is circumstantial evidence to suggest that it is related to density, for progressively more cannibals were noted between 1967 and 1969, and the numbers of breeding birds has been shown to increase annually by 13 per cent. Again, there is not enough evidence to state whether the habit involves both members of the pair, or whether it is restricted to a particular sex. Observations on two of the cannibals in 1969 indicated that the male gull was the offender, but not enough results are available to rule out the possibility that females also eat chicks.

Presumably, cannibals must distinguish between their own chicks and neighbouring chicks and, moreover, the dissociation must be so distinct as to freely allow predation on its own species. There is evidence to suggest that some cannibals find difficulty in separating the behavioural drive needed on the one hand, to feed and care for their offspring, whilst on the other hand to kill and eat the offspring of other Herring Gulls. The Whaup cannibal was incubating a clutch of three eggs until late June 1968, and during this incubation period, it ate over 40 chicks. It can safely be assumed that food was not short at that time, nor did the adults have the extra demands of feeding chicks. The quite dense breeding population on North Ness must have provided an easy and near-at-hand source of food, a better alternative to flying six or more miles to the mainland.

On 26 June the clutch of this particular cannibal began to hatch. It must be remembered that the nest was isolated on its own rocky outcrop, and that whatever happened next was the act of the cannibal alone. This bird continued to collect chicks, but appeared unable to kill them. By 28 June, there were 9 chicks on the nest site, its own brood of three, and six others. Of these six chicks, four were less than two days old, whereas there were two of 6 to 8 days of age. The cannibal was observed trying to feed this enlarged clutch, with some success. However, two days later, two chicks had been eaten and an additional chick had joined the brood to make eight live chicks.

On 3 July all that remained alive was a brood of three chicks of peculiar composition. One chick was its own, and another was one of the original kidnapped chicks. The third, however, was a new arrival from a nest 80 feet from that of the cannibal, the chick being about 12 days old. The remaining chicks had been eaten and four more also. Unfortunately, the fierce storms and rain in early July interrupted this intriguing situation for, two days later, two of the chicks had died of exposure. The remaining chick was one of the original kidnapped brood and it grew well on subsequent cannibalised chicks until fledging in late July.

These somewhat bizarre records illustrate the conflict between the instinct to care and feed a brood and the instinct to kill to provide that food. This is perhaps why some authors have accused unmated or sub-adult birds, with imperfectly developed instincts, as being the majority of those that turn to cannibalism. However, of the four true cannibals on North Ness, we have seen that one reared a chick, and in the previous two years it had also held a territory and nest site. The other three all laid clutches of three eggs, but only one of them successfully reared young. Two other cannibals studied in different parts of the island were also successful breeders. It therefore appears that cannibalism is not necessarily restricted to any year class or group of reproductive failures.

Cannibalism on North Ness in 1968 was quite obviously an important cause of mortality, accounting for the deaths of over 20 per cent of chicks. It cannot be concluded that these chicks were weak and liable to die. All the kidnapped chicks that were found alive on the Whaup cannibal nest site appeared in good health on the date of capture. This again poses the problem of the factors that cause cannibalism. The density of the population is regarded by some as a primary cause (Paludan 1951, Brown 1967), and cannibalism is likened to the "shock disease" recorded in some overcrowded mammals (Barnet 1964). This "disease" is closely associated with the number of direct conflicts with neighbours. It is interesting that four out of the six true cannibals studied nested in relatively uncrowded parts of the island (e.g. around the perimeter of North Ness). This would indicate that the immediate density, or number of contacts with neighbours, is not particularly important; for, if this were the case, cannibalism would be more prevalent in the most dense areas.

It is possible that the importance of density is related to the number of chicks available in a confined area, rather than to any stimulation that conflict or contact may have between adults. Whether food shortage encourages this behaviour is not known, although it is unlikely that there is any scarcity of food when cannibals begin their predation. In dense populations there are large numbers of chicks and the frequent territorial battles between adults in such populations may leave these chicks exposed or vulnerable to predation. The chicks could then be a more accessible and preferable source of food, and the cannibals acting within the confines of natural or individual selection.

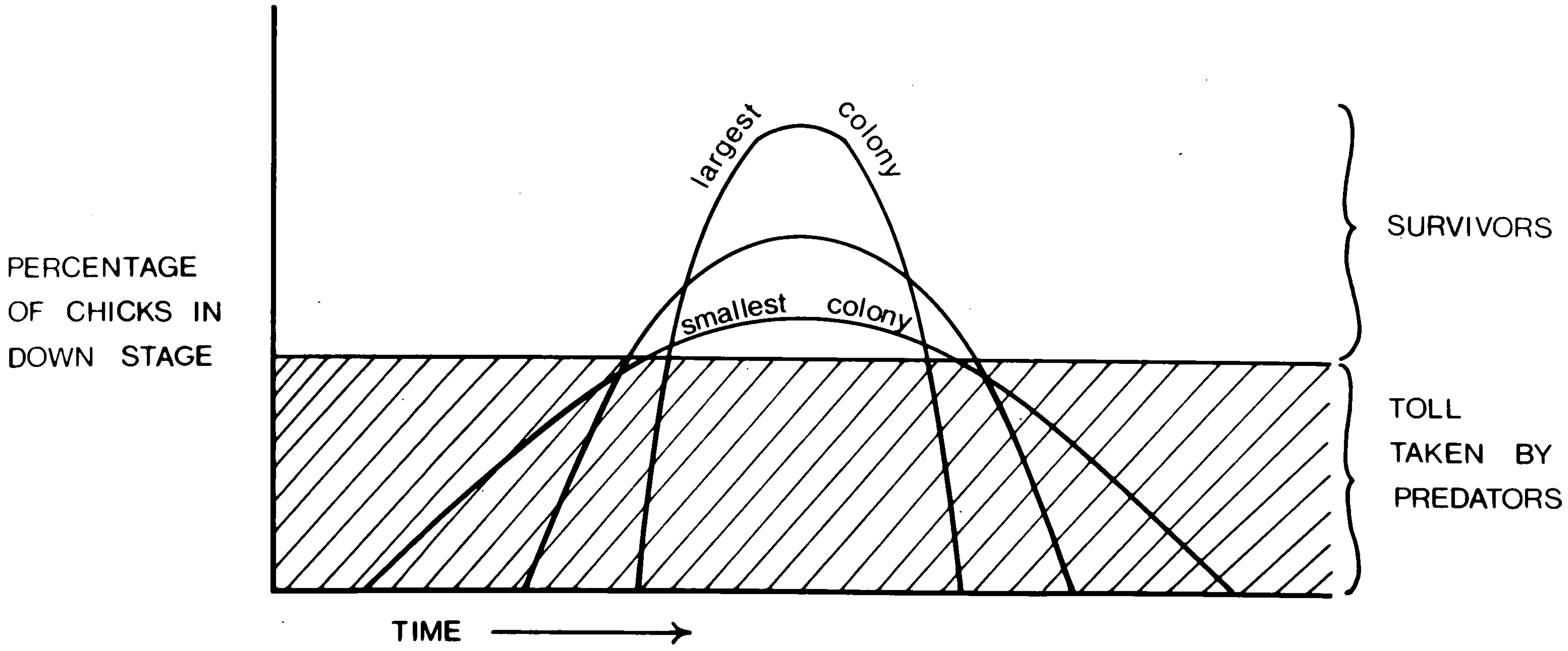
Cannibals as predators

It is now possible to view the cannibal as a predator, irrespective of the intraspecific relationship it has with its prey. Darling (1938) found that the Greater Black-backed Gull and the Heron took a steady toll of chicks while they were in the down stage and theorised that, if this period were short, the percentage mortality due to predation would be comparatively less than in an extended breeding season (Fig.36). Using the data from the four 'true cannibals' on North Ness it was possible to see whether predation creates a selective advantage towards a shortened breeding season.

The hatching dates of chicks killed by the cannibals were recorded and, therefore, the percentage mortality due to cannibalism for various hatching dates could be calculated (Table 63). It can be seen that early and late hatching chicks suffer a significantly higher mortality from these four cannibals than those hatching in the middle of the season ($p < 0.001$). In fact, the cannibals take a steady

Figure 36

Diagram illustrating how the survival rate is influenced by the "spread" of time in which the eggs of a colony of Herring Gulls are laid (from Darling 1938, p.70)


largest
colony
smallest
colony
PERCENTAGE
OF CHICKS IN
DOWN STAGE
SURVIVORS
TOLL
TAKEN BY
PREDATORS
TIME →

number of chicks throughout the season, although the numbers available change considerably, and this must create a selective advantage for breeding in the middle of a well defined breeding season. A similar result was obtained from just one cannibal on another part of the island (S.Rona 1968). It will be remembered that chicks were ringed with colour rings according to their date of hatching. The various colour rings regurgitated by the cannibal gave estimates of the percentage mortality for the four different hatching groups. The seasonal variation in the percentage of chicks killed by this cannibal conformed to the pattern already shown by the North Ness cannibals (Table 64).

However, cannibalism is not the only cause of the seasonal variability in fledging success. If the estimated predation by the four cannibals on North Ness (1968) is discounted from the mortality of young chicks (0 to 10 days old), there is still a decrease in post-hatching survival as the season progresses (Fig.37). Nevertheless, the higher mortality of early hatching chicks is no longer evident in the assumed absence of cannibalism, nor is the mortality of late hatching chicks as marked as in the actual field results. It therefore seems that without explaining all the variation in hatching success, the cannibals play a substantial part in creating the higher pre-fledging mortalities noted for chicks hatching early and late in the season.

Finally, attention must be drawn to a subtle difference between these cannibals and normal predators. Usually there are only a handful of predators attacking a particular colony

Table 63. Season variation in the numbers of chicks eaten by four cannibals on North Ness 1968

	Hatching date of chicks						
	June						
	up to 4	5-9	10-14	15-19	20-24	25-29	30 onwards
No.chicks eaten	22	22	21	34	29	23	7
No.at risk	99	201	289	443	260	84	22
Per cent mortality	22.2	11.0	7.3	7.7	11.2	27.4	31.8

$X^2 = 53.6$ (5 degrees of freedom) $p < 0.001$

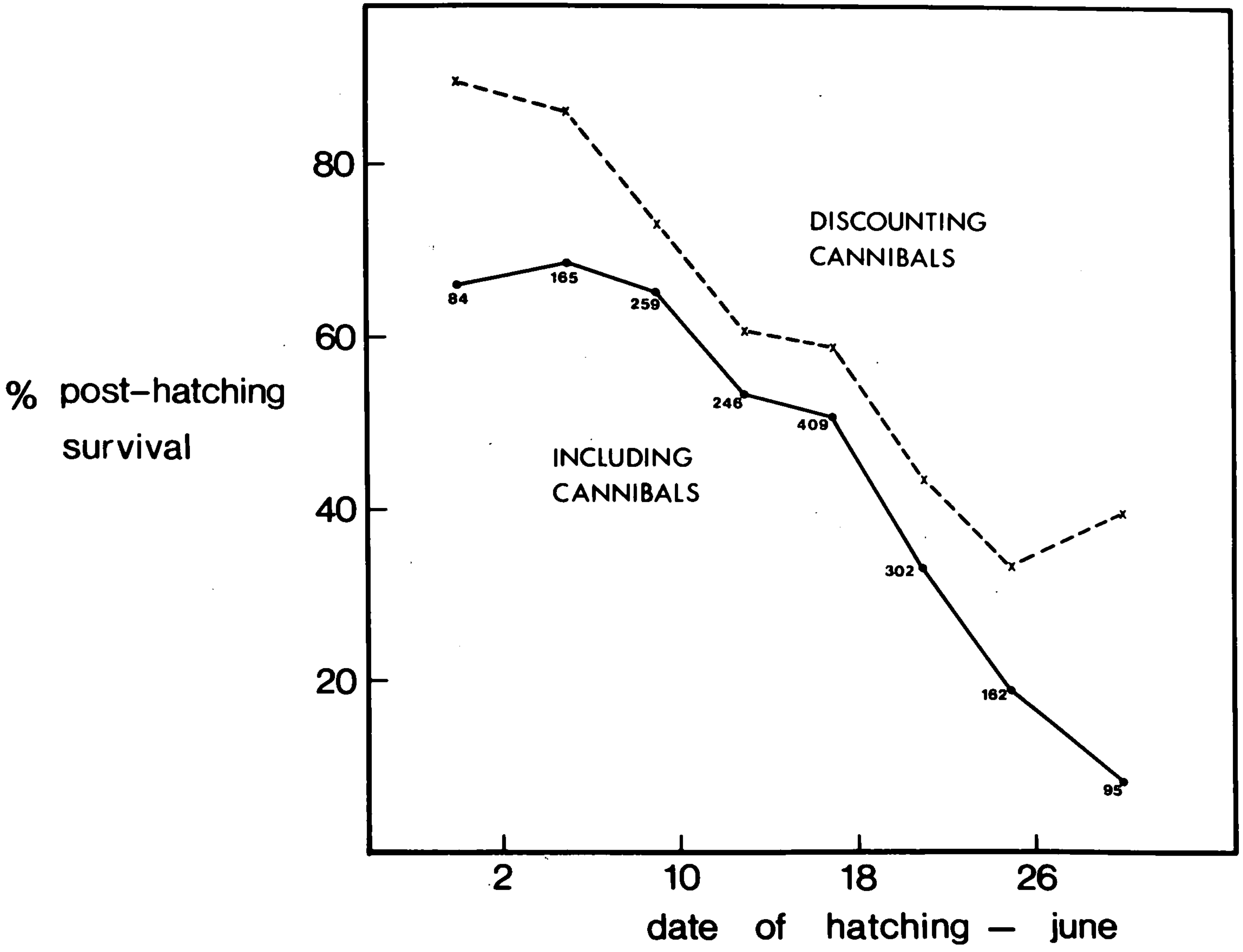
Table 64. Mortality due to one cannibal on S.Rona 1968. Different hatching date groups given by various colours of rings (insulating tubing)

	Blue rings early up to 9 June	Yellow rings middle 9-16 June	Green rings middle 16-22 June	Black rings late 22 June onwards
No.eaten	6	3	9	8
No.ringed	40	104	375	113
% eaten	15.0%	2.9%	2.4%	7.1%

and, for this reason, a fairly constant number of prey are removed in any given period. Admittedly, the Herring Gull cannibals seem to be consistent with this viewpoint, for there were a set number on North Ness, and they ate more or less the same number of chicks each day. However, while there are

Figure 37

Variation in percentage post-hatching survival on North Ness (1968) through the season, both including and excluding the effect of mortality due to four cannibals. Numbers refer to chicks hatching


% post-hatching survival
80
60
40
20
2
10
18
26
date of hatching – june
DISCOUNTING CANNIBALS
INCLUDING CANNIBALS
84
165
259
246
409
302
162
95

potentially many more cannibals in a Herring Gull colony, there was no indication that the number of cannibals altered with the availability of small chicks. If cannibalism merely corresponded with this seasonal source of food it is strange that the cannibals took so many early and late chicks when the supply was short, and did not increase their consumption markedly in the middle of the season; and also strange that more adults did not turn to cannibalism in the middle of the season when many chicks were hatching.

Human disturbance

In view of these savage attacks by gulls on wandering chicks, concern has often been expressed of the disturbance caused by the presence of humans, which could possibly result in additional mortality. Harris (1964) compared the mortality of chicks in areas of differing cover, arguing that any mortality due to human visits would be more obvious in the exposed areas. As the percentages of dead chicks were the same in all five subcolonies it was concluded that the observer's visits had little effect. However, Brown (1967) found a very significant difference in the breeding success between the Lesser Black-backed Gulls nesting in cover and in no cover. It was attributed to predation, though whether this mortality was increased by human disturbance was not discussed.

Kadlec et al (1968) studied the New England population of Herring Gulls and suggested that visits to the islands lowered the reproductive success according to the frequency and duration of visits, the type of weather in which they took place, and the density of the colony. The final conclusion was that "three meticulous visits per week may lower the breeding success by no more than 0.4 young per nest."

On the Isle of May, wing lengths were measured at the time of ringing, and also at the time of death. From the increase in wing length, the time the chicks lived after being disturbed by ringing was calculated. It was argued that if human disturbance was a major cause of mortality, then several chicks would die soon after the initial ringing. In fact, the results (Table 65) did not indicate that any such additional mortality had taken place. Much will depend on the numbers of people visiting a colony, and the extent of their activities, for as Paludan (1951) pointed out, a slow walk through the colony creates very little disturbance. Also for a comparative study between different sub-colonies, providing each area is visited the same number of times, and in the same conditions, then any bias due to human disturbance will be shared equally. The comparative aspect of the study will therefore remain valid.

Weather, food shortage and disease

Weather conditions can have some effect on the breeding success of the Herring Gull. In this study it was shown that heavy rain probably reduced both clutch size and hatching success, and definitely killed chicks between one and three weeks of age. Strong sun and heavy rain are mentioned as mortality agents by Darling (1938), Paynter (1949), Paludan (1951) and Harris (1964).

Much of the Herring Gull's success has been attributed to its food supply which is generally independent of weather and reasonably constant. Harris (1964) stated that the many

Table 65. Number of days dead chicks had lived after ringing

days after ringing

	0-1	2-3	4-5	6-7	8-9	10-11	12-13	14-15	16-17
No.chicks dying	10	12	11	15	13	10	9	11	9
% of total	7.6	9.1	8.3	11.4	9.8	7.6	6.8	8.3	6.8

	18-19	20-21	22-23	24-25	26-27	28-29	30-31	32-33	34-35
No.chicks dying	6	7	6	2	0	4	3	2	2
% of total	4.5	5.3	4.5	1.5	0	3.0	2.3	1.5	1.5

thousand chicks on Skomer showed no sign of starvation, and concluded that the reason was this supply of man's waste and offal. His experiments on gulls fostering additional chicks and chicks of other species (Harris 1964, Harris & Plumb 1965) appeared to verify this conclusion. Nevertheless, on the Isle of May chicks were found that had apparently died of starvation, and it was felt that it was due to a breakdown in parental care, rather than to an actual food shortage (Section 6, Table 45). This starvation occurred in the post-hatching period, during the important behavioural change from incubation to feeding of the young. Once this initial change had been made successfully, there appeared to be no further difficulty in providing food for the fledglings. Therefore, no chicks over a week old were found to be starving whilst in the confines of their own nest site. Later, there were several instances when post-fledglings were found dying apparently of starvation, and this was presumably because they had left, or been driven away from their parents. It seemed that unless post-fledglings moved to the mainland, they quite quickly became emaciated on the island, where little or no food was available.

In 1968, several fledglings died in the late summer on the island, and many appeared to have starved. However, on eight occasions, chicks in poor condition were collected and fed, and yet they still succumbed. Six dead chicks taken generally around the island were sent to Lasswade (Veterinary laboratories), and four of them were found to contain Salmonella typhimurium. The laboratory report did not suggest that this was the cause of death, but that it accelerated death in these already weak chicks. The remaining two chicks were both in poor condition, and lack of food was regarded as being responsible. Any fatal or semi-fatal disease that the chicks may contract will be rapidly transferred by the fledglings' habit of picking at, and often eating, dead chicks.

Various other diseases have been recorded in immature gulls, including Aspergillus sp. (Poulding 1952, Harris 1964), and Paynter (1949) mentions a case of dysentery. However, only these six chicks were analysed from the Isle of May.

8.6 Summary of breeding success

The breeding success of the Herring Gulls on the Isle of May is summarised in Table 66, which compares the control areas with delayed nests in both 1967 and 1968. It will be noticed that the fledging success in 1968 was considerably less than in the previous year. From the general large scale ringing programme in 1966 and 1967, between 8 and 9 per cent of all chicks ringed were recovered before leaving the island. The following year, of 4,825 chicks ringed during the season, 916 or 19 per cent were found dead on the island before autumn (Table 69). The factors contributing most to this difference were the poor weather in July 1968, and the large numbers of apparently diseased chicks that died not long after fledging.

It appears that approximately 30 per cent of eggs give rise to fledged young in the control area, so that

0.7 - 0.9 chicks are fledged per pair. Similar figures are given by Paynter (1949), Drost et al (1961), Harris (1964), and Brown (1967). The New England Herring Gull population were slightly more successful, producing on average 0.8 - 1.4 chicks per pair, whereas a far lower estimate of 0.5 chicks per pair was quoted for Christiano (Paludan 1951, Table 67).

The differences between normal and delayed breeding are shown for both years. Essentially, clutch size is the major factor causing the reduced productivity in delayed nests. In 1967, the hatching and fledging success of repeat clutches was similar to the controls. In fact, repeat layers raised more young than natural layers breeding at the same time in the season, although both categories laid the same number of eggs. The following year, this situation was masked by the high mortality of late hatching chicks caused by very bad weather conditions.

Table 66. Summary of breeding success of Herring Gulls on the Isle of May, comparing control areas with delayed areas for the 1967 and 1968 seasons

	1968		1967		
	Control	Delayed	Control	Delayed	
				(i)	(ii)
No.nests	903	358	1,101	303	197
No.eggs	2,463	772	3,062	771	428
Clutch size	2.73	2.16	2.78	2.54	2.17
No.eggs hatching	1,722	522	1,968	513	220
Hatching success %	69.9%	67.6%	64.3%	66.5%	51.4%
No.chicks/pair	1.91	1.46	1.79	1.69	1.12
No.chicks fledged	609	78	999	256	109
% chicks fledged	35.4%	14.9%	50.8%	49.9%	49.5%
Chicks fledged/egg	0.25	0.10	0.33	0.33	0.25
Chicks fledged/pair	0.67	0.22	0.91	0.84	0.55

The 1967 delayed areas are shown divided into :

(i) mean hatching date 23 June

(ii) mean hatching date 29 June, compared with the controls with mean hatching date 17 June

Table 67. Comparison between Herring Gull population studies

Locality		No.nests	% eggs hatched	% young fledged	% eggs giving fledged young	approx. chicks/pair	Source
Summer Isles, Irish seas	1936	40	85.7	48.6	41.7	0.88	Darling (1938)
	1937	65	95.8	42.0	40.2	1.16	Darling (1938)
Kent Island, Canada		100	71.4	48.5	36.8	0.91	Paynter (1949)
Christianso, Baltic		90	90.0	-	ca15	0.5	Paludan (1951)
Wilhelmshaven, Germany		150	-	-	ca25	0.7	Drost et al (1961)
Skomer Island, Wales		220	63	ca30	ca20	0.56	Harris (1964)
Walney Island, England		139	65.6	35.5	ca30	0.91	Brown (1967)
New England, America		ca13,000	ca80	-	ca40-50	0.8 - 1.4	Kadlec et al (1968, 1969)
Isle of May, Scotland	1967	1,101	64.3	50.8	32.6	0.91	This study
	1968	903	69.9	35.4	24.7	0.67	This study

SECTION NINE

POST-FLEDGING SURVIVAL AND DISPERSION

9.1 General survival estimates

Several attempts have been made to construct life tables and population models of Herring Gulls based on ringing material (Paynter 1949 and 1966, Paludan 1951, Hickey 1952, Drost et al 1961, Kadlec et al 1968). Unfortunately, rings are frequently lost or corroded away and, for this reason, it is often concluded that mortality tables based on ringing recoveries are unreliable (Poulding 1954, Coulson & White 1955 and 1959, Harris 1964, Paynter 1966). Nevertheless, the introduction of the more durable monel rings may reduce this error. The analysis of the Isle of May gull recoveries will be restricted to birds ringed during this study, and with monel rings, and therefore band loss should be absent or negligible.

An analysis of population growth involves estimates of juvenile or first year mortality compared with adult mortality. Lack (1954) noted that young birds may be more easily shot than adults. The inclusion of shot birds may therefore introduce a bias, especially if they are more likely to be reported. However, although as many as 60 per cent of Herring Gull recoveries in Scandinavian studies had been shot (Paludan 1951, Olsson 1958), far fewer (3.3 per cent) are killed in this way in Britain (Table 68). The Lesser Black-backed Gulls are not so fortunate, for of the 42 recoveries of pulli ringed on the Isle of May, 36 per cent had been shot. Nearly all of these deaths had been incurred during their winter migration to the Mediterranean, where shooting of birds is commonplace. This, and the general hazards of a long migration, probably accounts for the difference in the first year mortality between the two species. Only 1.7 per cent of fledged Herring Gulls are recovered between fledging and July of the following year. Significantly more Lesser Black-backed Gulls are recovered during this period (3.6 per cent, $X^2 = 14.1$, $p < 0.001$).

Various causes of death are recorded, and in fact twice as many Herring Gulls were killed by cars as shot by man (Table 68). Obviously, the vast majority of recoveries are not diagnosed, but a few and often bizarre mortality factors have been noted. A post mortem examination was carried out on an Isle of May gull found on Inner Farne Island (Northumberland). The bird had swallowed a hypodermic needle which had then punctured the peritoneum and caused death. Two birds that had died during severe gales had suffered internal haemorrage, and it is possible that inexperienced fliers may have difficulties in such weather. One of these birds had been observed to be dashed against the sea wall by a powerful gust of wind.

9.2 Monthly variation in recovery

It is well known that a large proportion of first year gull recoveries occur in the three or four months after fledging (Gross 1940, Harris 1963, Fordham 1969). If the first year is taken as the interval between fledging and the

Table 68. Isle of May post-fledging recoveries.

Causes of death

Causes	No. recoveries
No diagnosis	282
Injured : broken wings or legs	34
Killed by cars	26
Shot	13
Swallowed fishing hooks, caught in nets	12
Oiled	11
Killed by overhead power cables	11
Killed by trains	5
Killed by dog	1
Killed by fox	1
Drowned in sewage pit	1
	Σ 397

following July (after Paynter 1966), then 58 per cent of the first year recoveries were recorded between fledging and October inclusively (Fig.38). There is no doubt that this is due to inexperience in these post-fledging months when the juveniles must learn to find food and avoid predation or accidents.

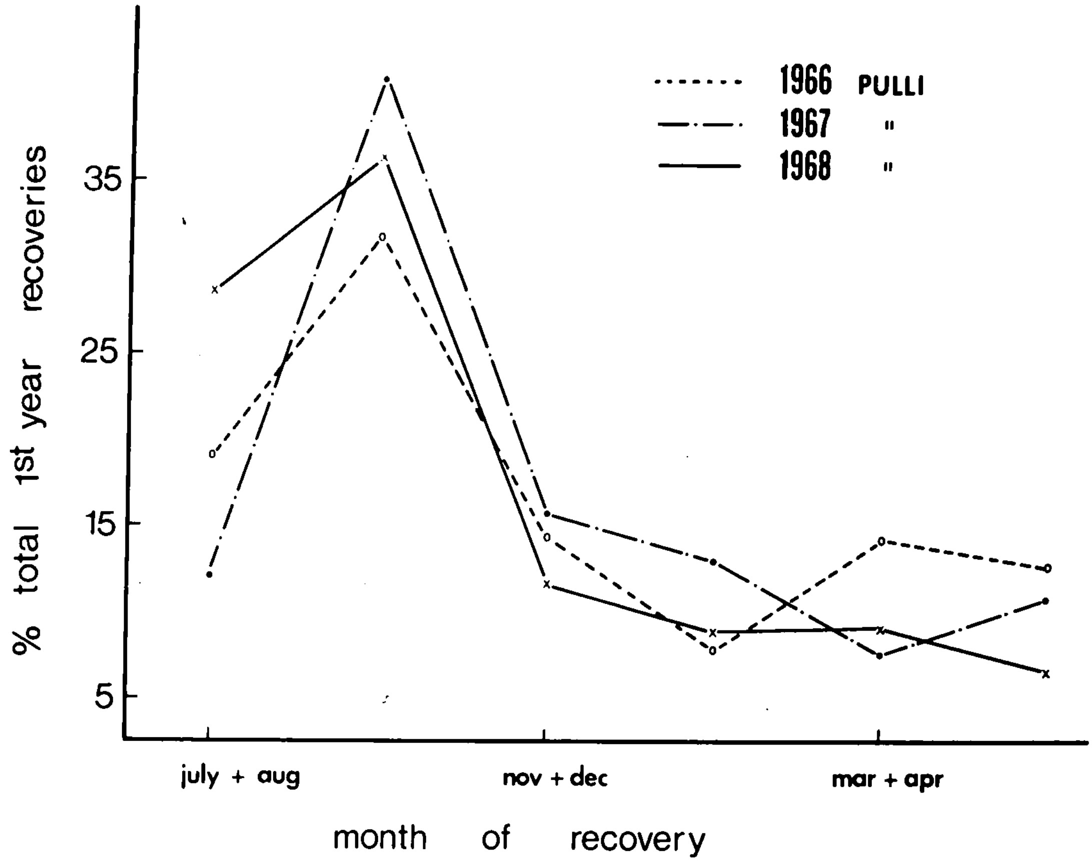
After the first year, the highest mortality apparently occurs in the summer months (Harris 1963); the Isle of May data (Fig.39) and the summary of Kent Island Herring Gull returns given by Gross (1940, p.143) also show an increase in

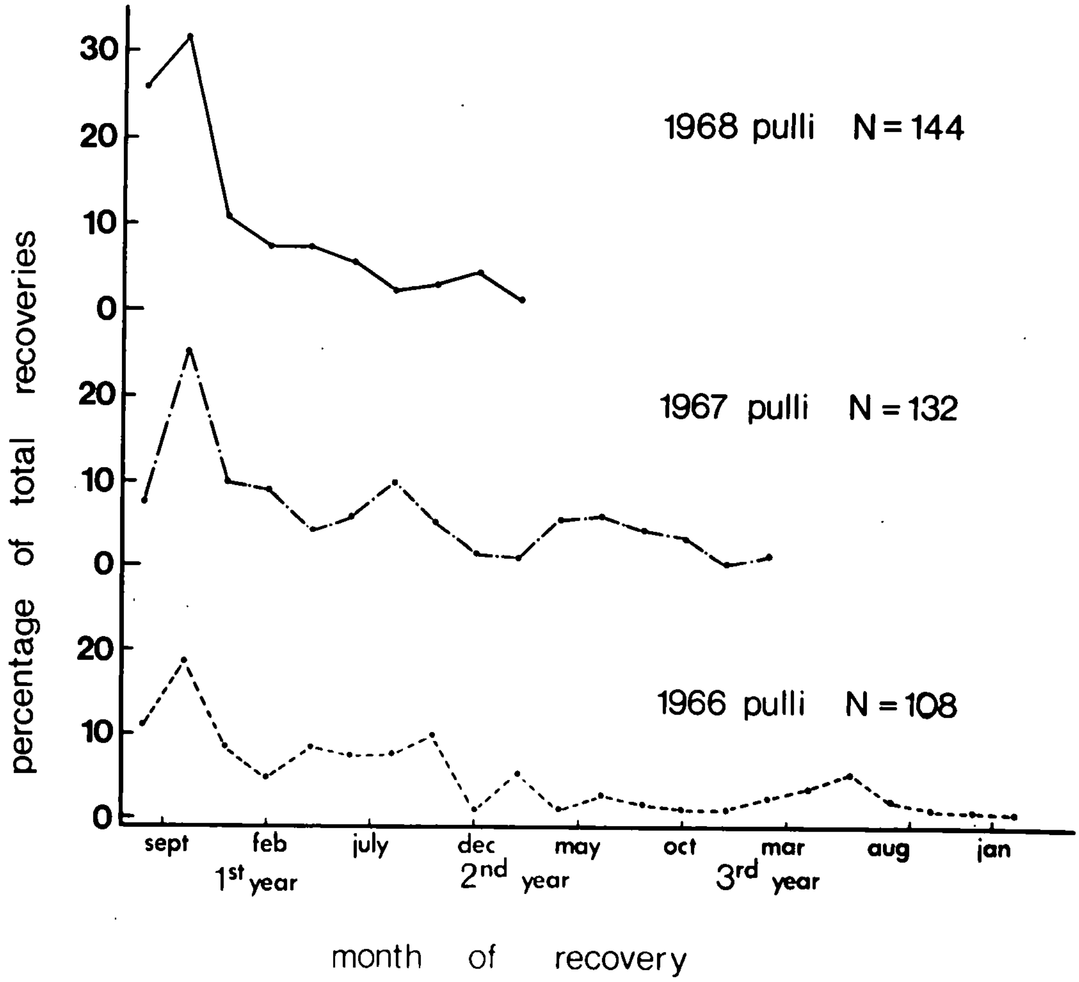
Figure 38

Monthly distribution of first year recoveries of Herring Gull pulli ringed on the Isle of May 1966 - 1968 inclusively. Recoveries every 2 months expressed as a percentage of the total first year recoveries

Figure 39

Monthly distribution of recoveries up to spring 1970 of Herring Gull pulli ringed during this study. Recoveries every 2 months expressed as a percentage of the total recoveries received for each year class up to spring 1970


% total 1st year recoveries
35
25
15
5
1966 PULLI
1967 "
1968 "
july + aug
nov + dec
mar + apr
month of recovery


percentage of total recoveries
30
20
10
0
20
10
0
20
10
0
1968 pulli N = 144
1967 pulli N = 132
1966 pulli N = 108
sept
feb
july
dec
may
oct
mar
aug
jan
1st year
2nd year
3rd year
month of recovery

recoveries during July and August. Harris (1963) suggested that during the winter gulls can disperse to areas of abundant food, whereas in the summer both adults and non-breeding birds are restricted to areas within range of their breeding colonies. However, analysis of recoveries from two colonies near to good food supplies also showed this summer peak of mortality, and it was concluded that other reasons may also apply. In the colonies it is not uncommon to find adults with broken wings and other injuries inflicted in the course of territorial battles. This could create an additional mortality, but it may also be that dead birds are more likely to be found in the summer months.

Table 69. Annual recoveries of Herring Gull ringing material

	Year of ringing pulli		
	1966	1967	1968
Total no. ringed	4,325	5,230	4,812
Recoveries on island	382	419	916
% recovered on island	8.8%	8.0%	19.0%
No. leaving island	3,943	4,811	3,896
No. recovered in 1st year	63	83	129
% 1st year recoveries	1.6%	1.7%	3.3%
No. recovered in 2nd year	28	37	-
% 2nd year recovery	0.71%	0.77%	-
No. recovered in 3rd year	14	-	-
% recovered in 3rd year	0.36%	-	-

not including 4th year

9.3 Hatching date and post-fledging mortality

Pre-fledging mortality has been shown to vary with the hatching date of chicks, but this relationship is more a function of nesting synchrony than an actual abiotic effect of the season. Whether laying dates are important also in determining the extent of post-fledging survival is not generally known in bird species, although no correlation was found in the Oystercatcher (Harris 1969). The first winter recoveries of Herring Gull pulli ringed during this study were therefore grouped according to hatching date, to investigate whether any advantage is conferred on a particular hatching group (Table 70).

A statistical analysis of this nature presupposes that a certain percentage of rings will be recovered. The chances of detecting differences in post-fledging mortality will be increased as the number of recoveries increases. Paludan (1951) recorded a 10 per cent recovery of first year birds outside the colony, and over 3 per cent of juvenile Dominican Gulls were recovered in the same period (Fordham 1970). Unfortunately, there was a smaller recovery rate of Isle of May Herring Gull pulli (Table 69). In 1966 and 1967, the percentages of recoveries in the first year were only 1.6 and 1.7 per cent respectively. However, in 1968 there was a significant increase in these first year returns ($X^2 = 22.8$, $p < 0.001$), with a doubling of the recovery rate to 3.3 per cent.

It is possible that an epidemic contributed to this increased mortality. Many fledglings died on the island that year, as has already been mentioned, and <u>Salmonella typhimurium</u>

Table 70. Variation in percentage post-fledging mortality (up to March of first year) according to date of hatching of Isle of May pulli. 1966-68

	Date of hatching - June						
	up to 4	5-9	10-14	15-19	20-24	25 onwards	
1968 pulli							Σ
No.recoveries	10	25	30	26	13	13	117
No.fledged	236	570	892	999	625	285	
% recovered	4.2%	4.4%	3.4%	2.6%	2.1%	4.6%	
1967 pulli							
No.recoveries	1	2	12	9	14	4	42
No.fledged	24	183	871	921	645	398	
% recovered	4.2%	1.1%	1.4%	1.0%	2.2%	1.0%	
1966 pulli							
No.recoveries	-	10	19	14	14	6	63
No.fledged	-	287	922	716	392	319	
% recovered	-	3.5%	2.1%	2.0%	3.6%	2.0%	
TOTAL							
No.recoveries	11	37	61	49	41	23	222
No.fledged	260	1,040	2,685	2,636	1,662	1,002	
% recovered	4.2%	3.6%	2.3%	1.9%	2.5%	2.3%	

$X^2 = 13.57$ for 5 degrees of freedom

$p < 0.05$

was found in the carcasses examined. The disease may have reduced the growth of the chicks prior to fledging and resulted in a poorer later survival. On the other hand, the mortality may reflect a genuine shortage of food which affected both pre- and post-fledging survival, and which may also have encouraged the incidence of cannibalism.

Combining the recoveries for the three years 1966-1968 showed that there was a significant variation in first winter recoveries according to the date of hatching ($p < 0.05$, Table 70). However, the difference was mainly due to a poorer survival of early hatching chicks. In all three years there was a trend for a higher mortality of this group and in 1968 the chicks hatching before 9 June yielded significantly more recoveries than the remainder ($p < 0.05$). Again, comparing the same hatching intervals (i.e. before and after 9 June) for the total of three years' recoveries, the difference in the percentage recoveries is very significant (3.7% : 2.2% respectively, $p < 0.001$). It is difficult to envisage a reason for this result. Admittedly, the first chicks to fly are repeatedly mobbed by adults, but this behaviour is probably restricted to the vicinity of the island. Nevertheless, it may drive these chicks from the island and force them to be prematurely independent of their parents. It is possible that early hatched juveniles do not disperse very rapidly from the Fife coast but wait until the general dispersion from that area begins. Were this so, they would be competing for food against the dense breeding population of adults who are feeding not only themselves but also the major proportion of fledglings.

However, this seems unlikely as no difference was found between the percentage of early birds dying in the Firth of Forth (i.e. near the island) and the remainder of the juveniles.

In 1968, the latest hatching group also suffered a higher first winter mortality compared with those hatching in the middle of the season ($p < 0.05$). Although the pre-fledging weights of chicks were not recorded, it is possible that chicks reared at the tail-end of the season have received less parental care than most other chicks. Several aspects of the breeding biology of late laying Herring Gulls have indicated a lowering of the reproductive drive, which may result in chicks fledging in a poorer condition than otherwise. Under these circumstances the survival of this group of fledglings through the winter might well compare unfavourably with chicks reared during the peak of the season. The analysis of first winter returns therefore indicates a selective advantage for nesting during the middle of the breeding season in addition to that already determined by the variations in pre-fledging mortality. However, any selection is more against very early breeding than for other time groups.

The sightings of colour-ringed gulls during the winter gave an estimate of survival, but the results did not verify the above conclusions. Instead, in 1968 a higher percentage of early and late hatching chicks were recorded, but the difference was not significant (Table 71). Similarly, in 1967 the sightings of 126 juveniles gave no difference at all between the estimated survival of the various hatching groups.

Table 71. Sightings of colour ringed juveniles (1968 pulli) during the winter of 1968

Colour combination and estimated hatching date

B = blue, M = monel, r = right leg, l = left leg

	B/Mr	Bl Mr	Br Ml	B/Ml
	up to 9 June	9-16 June	16-23 June	23 June onwards
No. seen	72	92	65	47
No. fledged	915	1,323	1,116	567
% sighted (survival)	7.9%	7.0%	5.8%	8.3%

Difference between early and late chicks and the middle groups

$$X^2 = 3.56, \text{ p = not significant}$$

9.4 Survival and productivity

Large gulls are potentially long lived species, with a relatively low annual adult mortality. Various authors have summarised the ringing evidence of longevity (Gross 1940, Harris 1963), and recently a gull ringed in the Netherlands as a pullus was recovered 30 years later. Even older birds have been recorded, including a Herring Gull of 49 years, but they were all reared in complete or semi-captivity.

Estimates of the average annual mortality of adult Herring Gulls vary from 8 per cent (Kadlec & Drury 1968) and 10 per cent (Drost et al 1961, Brown 1967), to 15 per cent

(Paludan 1951, Paynter 1966). Similar values are given for other gulls. For example, this mortality is 12 per cent in the Kittiwake (Coulson & White 1959), 10 per cent in the Glaucous winged Gull (Vermeer 1963). Naturally the figures will depend on the specific environmental factors influencing each population.

A total of 98 adult Herring Gulls were known to return to the Isle of May from 111 ringed the previous year, which gives a maximum annual adult mortality of 11.7 per cent. However, a few of the adults were originally ringed in roosting groups rather than on nest sites, and therefore their attachment to the island is somewhat questionable. This is emphasised by the report of one of the 'presumed dead' adults breeding the following year on Coquet Island, Northumberland (Dunn pers.comm.). The adult mortality may therefore be considerably lower than this figure.

In many bird species the mortality in the second year (m_2) approaches annual adult mortality (Lack 1954), and population studies have usually assumed this to be the case. The first year mortality may then be calculated according to the expression used by Coulson & White (1959) for the Kittiwake :

$$\frac{m_1}{m_2} = \frac{\text{No.recoveries of 1st year birds}}{\text{No.recoveries of 2nd year birds}} \times (1-m_1)$$

where m_1 is the first year mortality

m_2 is the second year mortality and assumed equal to adult mortality.

By combining the recoveries from both the 1966 and 1967 ringed pulli, an estimation of the first year mortality is obtained by assuming the annual subsequent mortality (m_2) :

If m_2 = 10 per cent

$$\frac{m_1}{0.1} = \frac{146 \times (1 - m_1)}{65}$$

therefore $m_1 = 0.18$ or 18 per cent.

It is now possible to examine the potential population change and compare it with the known increase for the Isle of May Herring Gulls. Capildeo & Haldane (1954) published tables which interrelated fecundity, the average age at which females start to breed, and population change :

$$\text{Fecundity } (f) = \frac{c.k}{2.s}$$

where c = mean number of eggs laid per year

k = fraction of eggs from which chicks survive for one year, assuming an equal sex ratio (c.k is therefore the number of young alive after one year produced by each female).

s = annual adult survival

Combining the control data for the 1967 and 1968 seasons, a total of 1,313 chicks were alive after one year, and were produced by 2,004 females nesting on the Isle of May (based on the estimated m_1 of 18 per cent). Thus, if s = 0.9 and c.k = 0.655, then f = 0.364. From Table I (Capildeo & Haldane 1954, p.218), for a species taking four years to mature, when f = 0.364, x = 1.2064 where x is a variable such that (s.x) is an estimation of the population change.

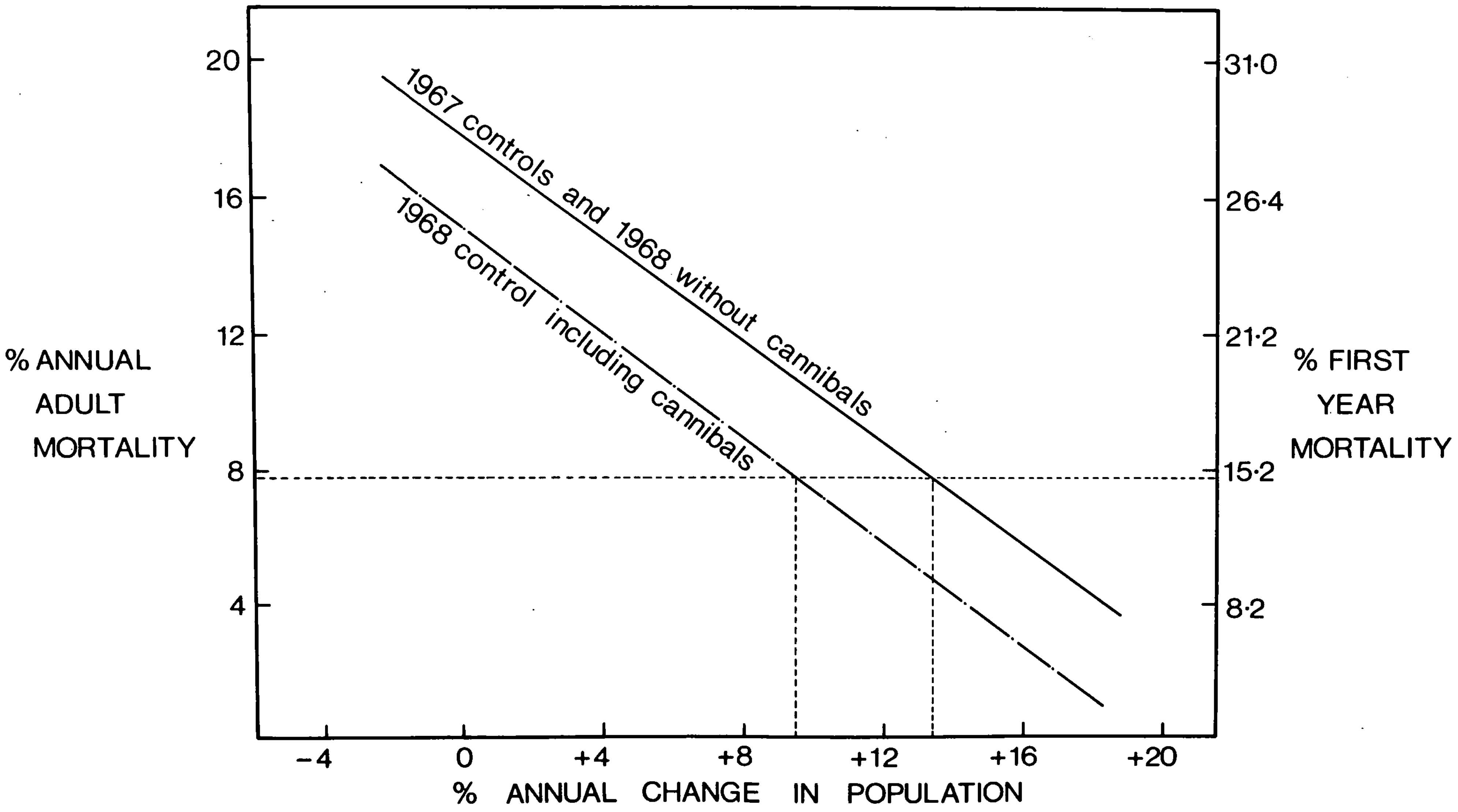
$$s.x = 1.086$$

therefore the percentage increase in the population each year is 8.6 per cent.

This figure is not consistent with the known facts, i.e. 13.3 per cent increase (see Section 3). The most likely error in these calculations is the estimate of annual adult mortality, since clutch size, fledging success and first and second year recoveries have been studied in detail. Using the same formulae for fecundity and mortality estimates, the first year mortality and population change were calculated for various estimates of annual adult mortality from 4 to 20 per cent (Fig.40). In this analysis the 1967 and 1968 data were treated separately, as there was considerable difference between the fledging success in the two years. Most of this can be attributed to the four cannibals on the North Ness control area in 1968. Only two of these were active the previous year, and the control areas in 1967 included parts of the island where cannibalism was less evident than on North Ness. In fact, if the 11.8 per cent pre-fledging mortality caused by these four cannibals in 1968 is discounted, the modified fecundity is similar to the previous year (i.e. 0.90 chicks fledged per pair compared with 0.91 in 1967); the regression lines for the estimated population change is also the same (Fig.40).

Figure 40

The relationship between the estimated annual change in the Herring Gull population for various values of annual adult mortality under known conditions of fecundity. The two lines refer to the estimated fecundity with and without the four cannibals on North Ness 1968, the latter being similar to the 1967 estimates of fecundity. The equivalent values of first year mortality for various estimates of annual adult mortality are based on the relationship between first and second year recoveries



20
16
12
8
4
% ANNUAL
ADULT
MORTALITY
31·0
26·4
21·2
15·2
8·2
% FIRST
YEAR
MORTALITY
1967 controls and 1968 without cannibals
1968 control including cannibals
−4
0
+4
+8
+12
+16
+20
% ANNUAL CHANGE IN POPULATION

These results indicate that the known population increase could only be achieved by an annual adult mortality as low as 7.5 per cent and a first year mortality of only 14.5 per cent. These estimates are low compared with other studies, for although figures of 10 per cent and less are given for m_2 (see earlier), the first year mortality is usually much higher (e.g. 62% - Paludan 1951, 60% - Hickey 1952, 57% - Olsson 1958, 45% - Paynter 1966, 30% - Brown 1967, 25% - Kadlec & Drury 1968). The reason for the difference does not lie with variations in breeding success (see Table 67), but with the relatively low proportion of first year recoveries compared with subsequent recoveries. For example, if the first year recoveries are expressed as a percentage of all the recoveries from both the first and second years, the figures are 69.2 per cent (1966 pulli N = 91) and 69.1 per cent (1967 pulli N = 120). This compares with 88.4 per cent in Denmark (Paludan 1951 N = 704) and 82.8 per cent at Walney (Brown 1967 N = 99). That the percentages were consistent from one year to the next suggest that the result is valid, and indeed that this low first year mortality is the reason for the Isle of May Herring Gulls showing the fastest increase of non-immigratory populations recorded (see Section 3).

One final point may be gathered from this analysis. If the incidence of cannibalism on North Ness was representative of the situation elsewhere on the island, then the population increase would be reduced from 13.3 per cent to 9.2 per cent by this agent alone (i.e. only 4 cannibals from 903 pairs - Fig.40). This assumes a constant adult and first year mortality, a period of years under this altered regime, and the premise that the 1967 breeding success is similar to those earlier years that produced the present population dynamics. Of course the 1967 season with its cannibalism may also have been less successful than earlier years, and it is therefore possible that cannibalism has already altered the fecundity and rate of increase of the population. Any long term increase in the relative numbers of cannibals will affect the fledging success and ultimately the rate of population change.

It is possible to calculate the average expectancy of further life, using the relationship given by Lack (1954) :

$$e = \frac{2 - m}{2.m}$$

where e = average expectancy of further adult life

m = proportional annual adult mortality.

Assuming a 7.5 per cent annual adult mortality, the average expectancy of further life for adults breeding for the first time becomes 12.8 years. The four years of immaturity then give a total age of 16.8 years, which will be similar to estimates by Kadlec & Drury (1968), but older than figures given in studies where higher adult mortality rates were recorded. For example, a 10 per cent annual adult mortality would result in an average age of 13.5 years (Drost et al 1961).

These calculations emphasise the longevity of the Herring Gull, and above all illustrate the need for long term control methods if populations are to be successfully checked or reduced.

9.5 Dispersion

After fledging the young Herring Gulls disperse quite rapidly to both sides of the Firth of Forth. By September the recoveries illustrate the southerly movement of the gulls down the east coast of England, and also across land to the south west coast of Scotland. Very few ringed gulls were recovered or seen north of Dundee (Fig.41), whereas reports from the south of England and even Holland were not uncommon.

After their first winter there is a noticeable return of young gulls to the Firth of Forth. This is shown statistically by expressing dispersion as the mean distance of recoveries from the Isle of May measured in log.miles (Fig.42). First winter recoveries (December to February) were 1.83 ± 0.07 log. miles from the island, which is reduced significantly to 1.63 ± 0.06 log.miles in the spring and summer - i.e. May to August ($p < 0.05$). However, although Gross (1940) suggested that the first year birds fly further than second year and older birds, the Isle of May recoveries indicate an equally distant second winter dispersion (Fig.42). This is followed by a more convincing return to the Firth of Forth in the summer. These second year birds are often seen roosting on the outlying rocks of the island during the breeding season.

It is in the third winter that the southerly dispersion becomes less extensive, and many three year old birds are seen on the island in the following spring and summer. Indeed, some of this year class take up territories and a few laid eggs and reared chicks. Two pairs of Lesser Black-backed

Figure 42

Recoveries in Northern England and Scotland of Herring Gulls ringed as pulli during this study (i.e. 1966 - 1969); excluding 22 recoveries in southern England, 3 in Holland, and one in each of Belgium, France and Germany

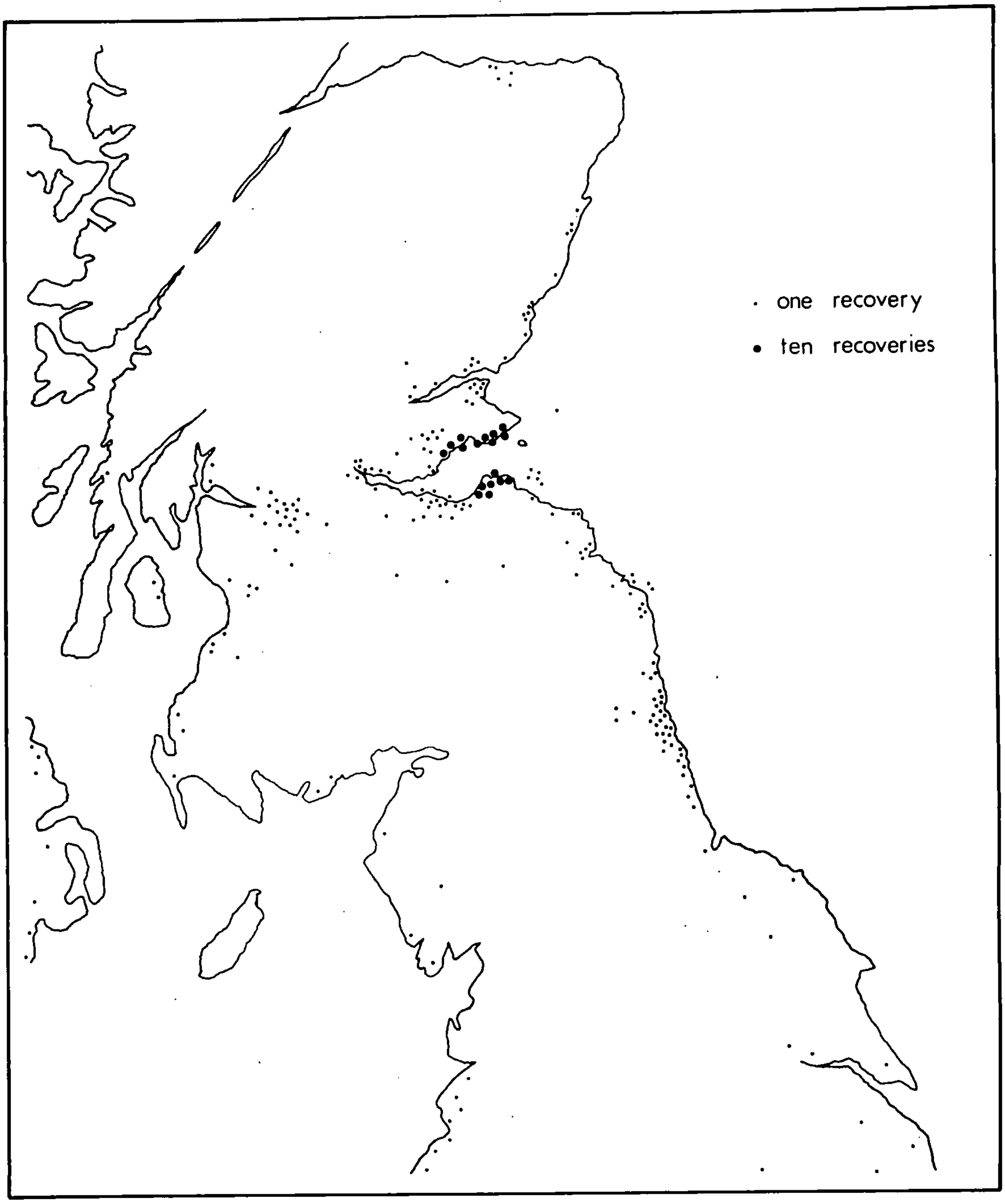
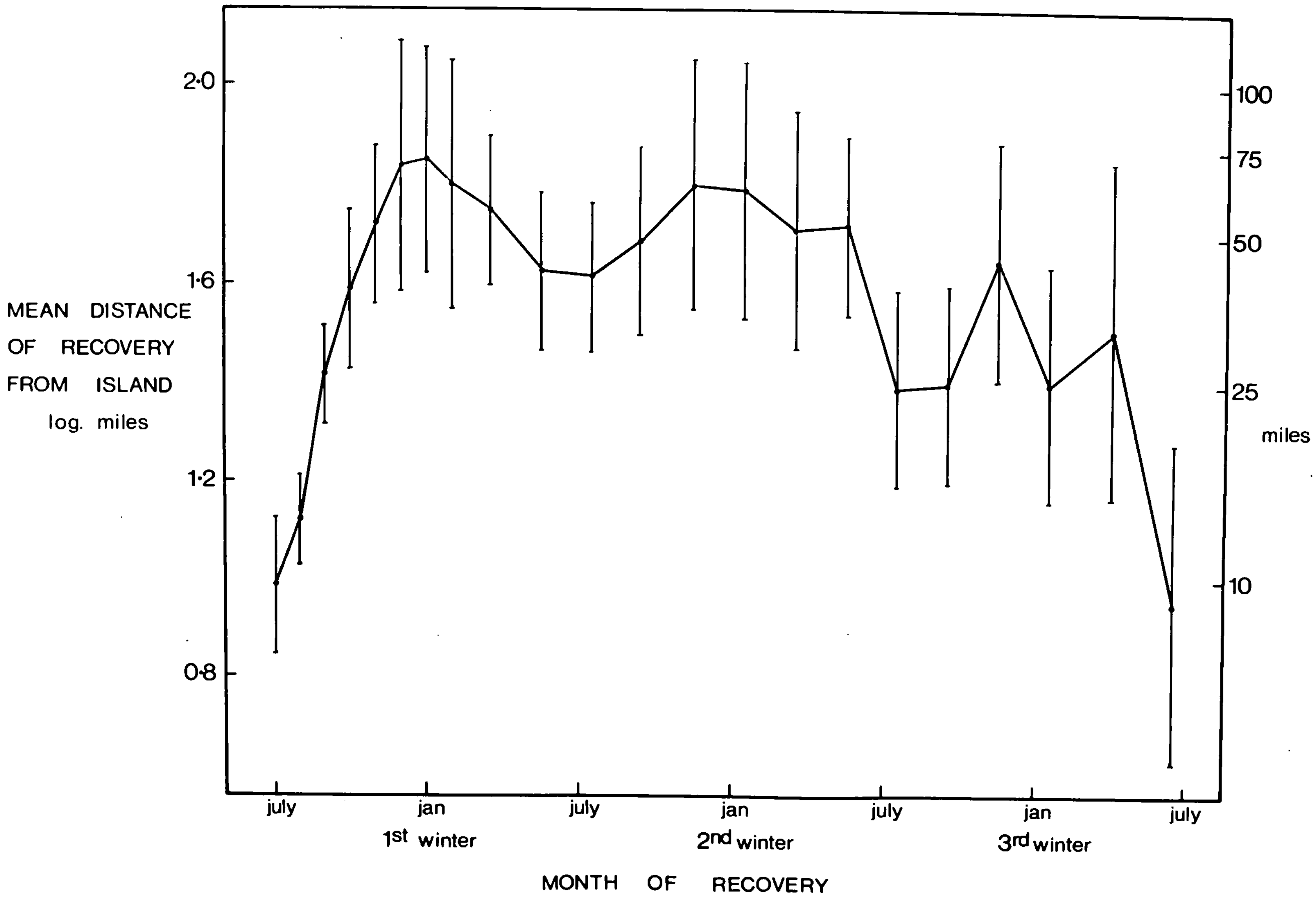

· one recovery
● ten recoveries

Figure 41

Mean distance of recoveries from the Isle of May (log.miles ± 2 standard errors) according to the month and year of fledging


MEAN DISTANCE
OF RECOVERY
FROM ISLAND
log. miles
2·0
1·6
1·2
0·8
100
75
50
25
10
miles
july
jan
1st winter
july
jan
2nd winter
july
jan
3rd winter
july
MONTH OF RECOVERY

Gulls also reached maturity at that age. Although it was a subjective impression, it appeared that those gulls which defended territories and attempted to breed as three year old birds had a more advanced adult plumage than the non-breeders of the same age. This onset of maturity and return to the vicinity of the Isle of May is clearly reflected by the recoveries (Fig.42).

SECTION TEN

DISCUSSION

10.1 Seasonal variations in breeding success

The timing of breeding seasons in temperate regions is ultimately regulated by the availability of food, and many factors in the breeding biology of birds are regarded as adaptations to a seasonal supply of food (Lack 1954). The time of laying, clutch-size and subsequent success of fledglings are directly or indirectly affected by the amount of food the individual parents can collect (Perrins 1970). However, some species of sea-birds, notably the gulls (Vermeer 1963, Harris & Plumb 1965), may be capable of rearing more chicks than their clutch-size allows, and Lack (1966) regards this as a result of an unusually favourable local food supply.

An increase in food availability, particularly fish offal, human waste and agricultural material are probably responsible for the increase in Herring Gull populations noted in many colonies. Naturally, a change in the feeding behaviour of gulls was necessary before these relatively recent food sources could be fully exploited, and the Herring Gulls breeding on the Isle of May appear to have achieved this change. This population has been increasing annually at a rate of 13.3 per cent since the beginning of this century. Normal, and an experimentally delayed, breeding seasons were therefore studied to examine whether the time of breeding limits subsequent nesting success.

Perrins (1970) presented evidence that bird species may delay egg laying until the female can find enough food to form eggs; also, Lack (1967) showed that clutch-size and the relative size of eggs in waterfowl are inversely related, and suggested that "the female has limited food reserves which can be used to form either a few large eggs or more small ones". Both egg-size and clutch-size of the Herring Gull were largest at the beginning of the season, which indicates that early breeders had ample food supplies for egg production. Indeed, the timing of the breeding season was so similar over four years that it must be independent of a variable, even if favourable, food supply.

The termination of laying is likewise independent of food supplies. It occurs at a time when there is enough food for young as well as adults, and yet the size and numbers of eggs laid by each female decreases progressively and significantly through the season. Even in the control areas, 79 per cent of the females lay less than the usual c/3 after 22 May, although egg removal shows that 60 per cent could lay at least four eggs each. Other species, for example, the Kittiwake (Coulson & White 1958a) and Great Tit (Kluijver 1951), also have a reduced clutch-size later in the season, and Perrins (1970) suggests that it is an adaptation to a poorer chance of raising late hatching young.

Egg size, and particularly the food reserve of the yolk, are important in assisting the survival and activity of chicks in their first post-hatching days. Indeed, the correlations between egg-size and both hatching success and especially post-hatching survival indicate a selective advantage for laying large eggs. There is evidence from protracted and repeat layings that follicles and eggs must reach a certain size before ovulation occurs, and it is therefore suggested that this is an adaptation to prevent the laying of small eggs with little chance of producing fledged young. Nevertheless, despite this minimal size limit there is considerable variation between the extremes of egg volume, for example from 66-90cc for a and b-eggs (i.e. means ±2standard deviations). This range in egg-size, and also in clutch size, illustrates differences in the capability of individuals to lay eggs and, furthermore, it appears to be a behavioural response to the intensity of the reproductive drive, rather than to the food availability.

To summarise, egg laying in the Herring Gull is determined by proximate factors that are related to the timing of the season rather than to the local food supply. Individual variations in the numbers and size of eggs laid reflect the fitness of the parents which may, in part, be due to the age of the female. However, irrespective of age, some gulls lay small clutches and small eggs and these stand less chance of hatching than larger eggs and eggs in the usual c/3; it is these differences that seem to reflect the intensity of the reproductive drive.

A decreasing survival of young with an increasing lateness of season found in some species was regarded by Perrins (1970) as evidence for a worsening food supply, and he added that "theoretically it is possible that some other form of counter-selection acts against early breeding, but none seems to be known. The one most likely to affect the date of laying is that of increased mortality among early breeders .... there is no evidence that this occurs". Since early breeding in the Herring Gull is not delayed by food availability, the question arises as to why the species does not breed even earlier than at present.

The hatching success in both control and delayed breeding was correlated with nesting synchronisation rather than the time of laying, so that eggs laid during the peak laying period in any area were the most successful. It is probable that egg predation by Herring Gulls themselves is responsible for this relationship. Similarly, early and late hatched chicks suffered a higher pre-fledging mortality than those hatching in the middle of the season. This again applied to both control and delayed areas, so that the synchronisation of nesting was once more the most important factor in determining the pre-fledging success. The studies on cannibalism showed that much of the lower survival of early and late hatched young was also due to predation, although very late hatching chicks in 1968 also succumbed to adverse weather conditions.

There was no evidence throughout the study for a direct shortage of food, and so the synchronisation of nesting appears to have an anti-predator function. The Herring Gull itself caused a selection against any deviation from the main peak of laying, and therefore that selection will tend to maintain the timing of the breeding season irrespective of food availability. Furthermore, late breeding did not appear to be a disadvantage, providing that the delay applied to the group as a whole.

The analysis of first winter recoveries also showed a selective advantage for nesting in the middle of a well defined breeding season, and in particular a selection against early breeding. The reasons for a significantly greater first winter mortality of early hatched chicks is somewhat obscure, but it was further evidence for the disadvantages of breeding too early in the season.

10.2 Aspects of chick mortality

The Herring Gull starts to incubate eggs before its clutch is complete, and this results in the asynchronous hatching of chicks. This hatching sequence, and the smaller size of the c-egg, both contribute to the higher post-hatching mortality the c-chick suffers compared with its siblings. In some species this phenomenon is regarded as an adaptation to an unpredictable food supply, so that the weaker, later hatching chicks die rather than the entire brood suffer (Lack 1954). However, there appears to be ample food available to the adult Herring Gulls during the hatching period, and yet these chicks are dying of exposure and starvation. The changes involved between incubation and parenthood are obviously important to the survival of the chicks. It is suggested that this differential mortality is an indication of a breakdown in the behaviour of the adults, rather than a response to a food shortage.

An extreme case of the inability of the adult to adjust to a complete brood is the incidence of kronism. This form of juvenile mortality is believed in some species to indicate shortage in the prevailing food supplies (Ingram 1959). Perhaps the chicks eaten by their parents, or even by their siblings, are already weak and doomed individuals. However the physical state may not be the result of a general food shortage and indeed in the Herring Gull this seems unlikely. Instead, it may again be an example of a lowered reproductive drive and a breakdown in the behaviour required to successfully rear chicks and inhibit predation near the nest site. It is not possible to judge whether this inability to cope with chicks is related to density or population size, nor whether kronism is a form of socially induced mortality reducing recruitment in a colony approaching the limits of its food supply in the manner suggested by Wynne-Edwards (1962).

Similar difficulties are encountered over the interpretation of the reasons for cannibalism. It may be that in a dense breeding colony, chicks are a more accessible and preferred source of food. As such, cannibalism need not indicate a food shortage, nor need it be an adaptation evolved by group selection to curb recruitment. Nevertheless, only four cannibals in an area of over 900 nests are able to reduce the annual fecundity of the sub-colony, and could, potentially, reduce the annual rate of increase in breeding pairs from 13 per cent to 9 per cent under existing conditions.

10.3 Control of the Herring Gull population

The Herring Gull population on the Isle of May has been doubling its numbers every six years, resulting in saturation and the displacement of other breeding sea-birds, especially terns. Its effect on wildlife alone justifies a control programme aimed not only at curbing the increase but also at reducing the present numbers of breeding pairs.

The removal of adult gulls is the most effective way of achieving these aims quickly, but the use of drugs to kill or sterilise and the possible public outcry to any slaughter may make this method unacceptable.

With or without control of adult gulls, a continuous and effective reduction in breeding efficiency is necessary. With limited funds and labour available, this should be done by the cheapest and least laborious method. In small colonies painting or pricking of eggs may be effective if done thoroughly. However, when dealing with as many as 30,000 - 40,000 eggs this method, requiring a person to bend down and administer to each egg, becomes both tiring and laborious. The alternative is to break eggs but not in a haphazard and inefficient manner.

The Herring Gull takes four weeks to incubate eggs and two weeks to re-lay. As the laying season starts in late April, all accessible eggs should be broken in mid-May and subsequently every three weeks to allow for late layers and repeat clutches. Clutches can be broken merely by stabbing then with a stick and only three or, at the most, four breaking sessions are necessary. It is felt that this would be the most effective method of control for easily accessible colonies, though a more permanent sterilisation such as painting once a season might be preferred in colonies that are difficult to visit.

The effectiveness of this method must be considered in the context of a species with a low annual adult survival rate and, therefore, one which requires only a low annual recruitment rate. Successful breeding in a few isolated or inaccessible areas could undo a considerable amount of egg destruction. Further, problems of immigration into the area and the length of time egg destruction has to continue to produce a given reduction mitigates against this method. The choice of method is largely determined by public relations and the speed at which a decrease is desired.

SUMMARY

1. Various aspects of the breeding biology of the Herring Gull were studied on the Isle of May, Scotland, from 1966-1969 inclusive. Research was primarily concerned with the relationship between nesting success and the timing of the breeding season.
2. The breeding seasons were extended by an egg removal programme to exaggerate any effects due to the time of laying in the season.
3. The Isle of May Herring Gull population has been increasing since 1907 at a rate of 13.3 per cent per year. It is suggested that this increase is due to a favourable food supply provided mainly by man, which has led to a low first year and annual adult mortality.
4. The numbers of Herring Gulls in many parts of the world have led to concern over their propagation of diseases, collisions with aircraft, and their effect on other species of wildlife.
5. In all, 95 per cent of ringed adults returned to their previous territories in subsequent years, and Herring Gulls breeding for the first time returned to that part of the island from which they fledged.
6. The first eggs were laid between 26-28 April (1967-69) and 50 per cent of the total laying in the control areas took place between 16-18 May.

7. Nests were distributed uniformly within the colony, as a consequence of territorial behaviour. However, the onset of laying was synchronised with various aggregations within the colony laying at the same time. It is suggested that this is a result of social stimulation. Late laid clutches were commonly situated on the edge of the colony.

8. The interval between the laying of eggs is 48.9 hours, and Herring Gulls take on average 13.2 days to re-lay after a lost clutch. The ability to re-lay decreases progressively through the season.

9. The usual number of eggs in a clutch is three, but 60 per cent of Herring Gulls are able to lay a fourth egg if the first egg is removed within 12 hours of laying. When eggs were repeatedly taken from 102 nests, each within 12 hours of laying, protracted layings of up to twelve eggs occurred in 11 nests. Also, in 60 nests, six or more eggs were laid. The Herring Gull is therefore not a determinate layer, but only a few individuals are capable of the protracted laying associated with indeterminate layers.

10. The numbers and size of eggs illustrated the varying fitness of females to lay eggs. Protracted layers produce larger and more eggs than those females who require a resting interval during an extended laying period. Similarly, in control conditions the eggs laid in c/2 were significantly smaller than those laid in c/3.

11. The clutch-size can be reduced and laying even suppressed by the addition of eggs during the pre-laying period, but not after the first egg (a-egg) has been laid.

12. The mean incubation period from laying to hatching is 29.96 days for the a-egg and 27.00 days for the c-egg. Incubation begins during the laying period so that the a-egg embryo is 12 hours in advance of the b-egg embryo, and 44 hours in advance of the c-egg embryo during the initial stages of incubation.

13. The c-egg is significantly smaller than the a-egg by 11 per cent. The onset of incubation during the laying period appears to be responsible for this difference, but the depressive effect on the size of the c-egg is restricted to the albumen and not to the yolk.

14. Comparisons of yolk sizes of eggs indicates that a follicle must attain a certain size before it will undergo ovulation. Instead of laying progressively smaller eggs, this minimum size limits the number of eggs a particular individual can lay.

15. There is a progressive and significant decrease in the mean egg volumes through the season, which is least in the a-egg and most in the c-egg.

16. Re-laying causes a small but additional loss in total egg volume above that expected by the progress of the season. It is mainly due to a smaller a-egg in re-laid clutches. There is a minimal size for the c-egg, below which it is re-absorbed and not laid, resulting in a clutch of two eggs. The seasonal decline in egg volume is therefore coincident with a decrease in clutch size.

17. Gulls nesting at the same time in the season laid fewer and smaller eggs on the edge of the colony compared with the centre. This indicates a difference in the quality of the birds, although no difference in the breeding success was detected.
18. The yolk is the least variable component of the egg, but eggs laid in the middle of the laying period contained relatively more yolk than earlier or later laid eggs. The hexane soluble lipid weight of yolk is positively correlated with egg size and so the latter is an appropriate guide to the energy available to the embryo and chick.
19. The incubation period is longer for large eggs compared with small eggs, and shorter for eggs laid later in the season.
20. Hatching success was positively correlated with egg size, except for very large eggs, and the hatching success of re-laid clutches was not significantly different from normal clutches.
21. Egg volume and chick hatching weight are positively correlated.
22. The chick hatching from the c-egg suffered a significantly higher post-hatching mortality than its siblings (55 per cent compared with 20 per cent within seven days of hatching). It also weighed less than either of the other two chicks. To evaluate whether the chick weight or the sequence of hatching was important in determining this differential mortality, an egg transfer experiment was carried out. The results showed that both factors were influencing the mortality of the c-chick.

23. Egg size and chick survival were closely correlated, but the survival of the c-chick was 10 per cent lower for eggs of the same size, presumably due to the sequence of hatching.

24. Egg volume and the soluble lipid content of hatching chicks were positively correlated. It is suggested that the parent-chick relationship takes some time to develop, and that the food reserve (i.e. lipid content) is of considerable importance in assisting the survival and activity of the chick in its first post-hatching days. It also appears that the Herring Gull has difficulty in forming a further parent-chick bond when there are already two earlier hatched chicks in the nest.

25. The mean clutch size in the control areas was 2.73 eggs per nest. Clutch size decreased significantly after late May, and the decrease was maintained with repeat clutches in the delayed areas. Therefore the time of laying seems to be of prime importance in determining the number of eggs laid.

26. The hatching success was 69.9 per cent in the control areas, and throughout the season clutches of one and two eggs hatched fewer chicks per egg than three egg clutches. This may be an illustration of a lower reproductive drive in those birds laying fewer than the normal clutch of three eggs.

27. Eggs laid during the peak laying period were the most successful and both early and late laid eggs had a significantly lower hatching success. A similar situation occurs with re-laid eggs in the delayed areas, and therefore hatching success and nest synchronisation were correlated irrespective of the time in the season. This creates a selection against any deviation from the main peak of laying.

28. Hatching success was highest at the most common nesting density, and the fledging success was least at the very high and low densities. It is suggested that predation contributes to the poorer fledging success noted in areas of low nesting density. This was verified by the Herring Gull cannibals since they preyed on chicks reared in the significantly less dense areas. The higher mortalities in the dense areas were attributed to the increased territorial aggression associated with high densities.

29. The majority of the pre-fledging mortality (71.3% of the total) occurs within ten days of hatching.

30. There was no difference between the fledging success of broods of varying sizes.

31. In the control areas the fledging success decreased progressively through the season, but very early hatching chicks also suffered a higher mortality. However, the peak of fledging success did not coincide with the peak of laying but was six days earlier in the season.

32. The delayed areas did not accentuate this seasonal decline in fledging success but showed a peak similar to the control areas but delayed in the season. Thus the late hatching chicks in the control areas suffered a significantly higher mortality than chicks hatching at the same time in the delayed areas, and nesting synchronisation was again important in determining the number of chicks fledging. Nevertheless, in 1968 the weather also contributed to the mortality later in the season.

33. The c-chick succumbed more frequently to cannibalism and also to kronism than either of its siblings. Kronism was noted in 2 per cent of all the control nests. This form of mortality is normally associated with protracted laying and a period of unfavourable food supply. Although asynchronous hatching has been demonstrated in the Herring Gull, the food supply does not appear unfavourable. Kronism may therefore be another example of a lower reproductive drive.

34. Four cannibals in 1968 ate 11.8 per cent of all the chicks available to them on North Ness (control area). Eight more less specific cannibals ate another 11.4 per cent. These cannibals were flying distances of 50-150m to collect chicks, and preferred small chicks of 6.7 days mean age.

35. Cannibals continued their habit from one year to the next, but an example was given of the conflict between the instinct to care and feed its own chicks, and the behaviour

necessary to kill chicks of the same species to provide this food. It is possible that cannibals were exploiting an accessible source of food found in a relatively dense breeding colony, but there was no evidence that cannibalism and density were related.

36. Cannibals took a higher percentage of early and late hatched chicks than chicks hatching in the peak of the season, and must therefore create a selective advantage for breeding in the middle of a well defined breeding season.

37. Approximately 30 per cent of eggs in the control areas gave rise to fledged young, so that 0.7 - 0.9 chicks were fledged per pair. Reduced recruitment in the delayed areas (0.2 - 0.55 chicks per pair) was caused mainly by the lower clutch size, although the very bad weather in 1968 created a high pre-fledging mortality of late hatching chicks.

38. 58 per cent of the first year recoveries were recorded between fledging and October inclusively, but after the first year the highest mortality apparently occurs in the summer months.

39. Only 1.6 - 3.3 per cent of fledged pulli were recovered during the first year. There was a higher recovery of early and late hatched chicks, particularly the former, but the survival estimates from sightings of colour-ringed gulls did not verify this result.

40. The known population increase could only be achieved by an annual adult mortality of 7.5 per cent and a first year mortality of 14.5 per cent under the calculated fecundity. The four cannibals on North Ness could potentially reduce the population increase from 13.3 per cent per year to 9.2 per cent under constant conditions of first year and adult mortalities.

41. The average life expectancy for the Herring Gull under these conditions of adult survival is 16.8 years.

APPENDIX I. Details of laying in North Ness control area 1968-69. Number of nests in which a-egg laid (excluding repeat clutches) through the season, with percentage of total and accumulative percentage. (In 1969 a smaller part of North Ness was studied).

	1968			1969		
Date of laying a-egg	No.nests	% total	acc. %	No.nests	% total	acc. %
up to 2 May	20	2.2	2.2	8	2.0	2.0
4	26	2.9	5.1	15	3.8	5.8
6	24	2.7	7.8	25	6.3	12.0
8	63	7.0	14.7	34	8.5	20.5
10	68	7.5	22.2	36	9.0	29.5
12	64	7.1	29.3	41	10.3	39.8
14	52	5.8	35.1	23	5.8	45.5
16	82	9.1	44.2	25	6.3	51.8
18	94	10.4	54.6	35	8.8	60.5
20	91	10.1	64.7	42	10.5	71.0
22	70	7.8	72.4	33	8.3	79.3
24	79	8.7	81.2	26	6.5	85.8
26	50	5.5	86.7	14	3.5	89.3
28	51	5.6	92.4	12	3.0	92.3
30	40	4.4	96.8	15	3.8	96.0
1 June	15	1.7	98.4	7	1.8	97.8
after 3 June	14	1.6	100	9	2.3	100

APPENDIX II. The difference in egg size of clutches laid during the continuous egg removal experiment, and production of d-egg experiment. ± one standard error.

	N		laying sequence	
		a-egg	b-egg	c-egg
			(egg wt. g.)	
Continuous removal				
(i) c/3 - interval	29	86.69 ± 1.12	84.37 ± 1.24	82.07 ± 1.22
(ii) c/4 - interval	39	89.09 ± 0.77	87.26 ± 0.97	84.67 ± 1.02
(iii) c/5 - interval	11	90.86 ± 1.68	90.56 ± 1.44	89.02 ± 2.26
			(egg vol.cc)	
d-egg experiment				
(i) c/3 No d-egg laid	31	78.94 ± 0.88	76.06 ± 1.01	73.26 ± 0.89
(ii) c/4 d-egg laid	38	79.03 ± 0.98	77.58 ± 1.01	74.95 ± 0.96

APPENDIX III. Mean egg volume (cc) and yolk weights (g) of 11 series of protracted layings, showing percentage decrease in volume from the a-egg onwards

Sequence of laying	Egg volume cc	± 1 st.error	Yolk weight g	± 1 st.error	% decrease in volume from a-egg
a-egg	80.86	1.45	22.10	0.49	-
b-egg	80.90	1.57	23.37	0.36	0
c-egg	76.65	1.45	22.18	0.47	5.2
d-egg	76.82	2.02	22.08	0.49	5.0
e-egg	75.66	1.98	21.16	0.42	6.4
f-egg	75.65	1.84	20.50	0.51	6.4
g-egg	76.70	2.14	20.35	0.75	5.1
h-egg	74.23	1.56	20.52	0.55	8.2
i-egg	74.92	2.10	20.60	0.50	7.4

APPENDIX IV. Egg volumes (± one standard error) through the 1968 season on North Ness, not including repeat clutches

Date May 1968	N	Egg volume cc a-egg	b-egg	c-egg
3	28	80.25 ± 0.98	78.58 ± 1.07	71.74 ± 1.11
8	50	78.80 ± 1.02	78.14 ± 0.96	70.59 ± 1.04
11	38	78.56 ± 0.98	75.56 ± 0.99	70.80 ± 1.06
13	38	77.22 ± 1.04	76.69 ± 1.04	70.46 ± 0.99
15	30	78.18 ± 1.19	75.67 ± 1.28	68.89 ± 1.24
17	45	77.92 ± 0.98	75.56 ± 0.88	68.62 ± 0.87
19	37	77.47 ± 1.06	77.73 ± 0.91	69.99 ± 0.93
21	39	77.69 ± 0.95	75.60 ± 0.93	68.35 ± 1.03
23	34	77.94 ± 0.86	76.16 ± 0.84	69.58 ± 1.00
25	41	77.68 ± 1.01	76.29 ± 1.10	69.44 ± 1.04
27	27	75.09 ± 1.14	73.53 ± 1.09	67.27 ± 1.25
29	22	78.04 ± 1.37	74.47 ± 1.09	66.87 ± 0.87
31	24	77.65 ± 1.22	73.34 ± 1.15	66.38 ± 1.07

APPENDIX V. Regressions of yolk weight on egg weight for early (up to 9 May), middle (9-17 May), and late (after 17 May) laid clutches, and for re-laid eggs. Slopes given with ± one standard error, and number in sample given in brackets

Slopes of yolk wt. on egg wt. (all positive)

	early	middle	late	total	re-lay
a-egg	$0.137_{(59)}$	$0.171_{(42)}$	$0.123_{(20)}$	$0.146 \pm 0.018_{(121)}$	$0.141 \pm 0.026_{(71)}$
b-egg	$0.133_{(56)}$	$0.199_{(42)}$	$0.187_{(20)}$	$0.168 \pm 0.019_{(118)}$	$0.162 \pm 0.030_{(71)}$
c-egg	$0.095_{(47)}$	$0.198_{(42)}$	$0.163_{(20)}$	$0.162 \pm 0.020_{(109)}$	$0.174 \pm 0.028_{(71)}$
all eggs	$0.115 \pm 0.017_{(162)}$	$0.187 \pm 0.016_{(126)}$	$0.145 \pm 0.017_{(60)}$		

APPENDIX VI. Laying sequence and post-hatching mortality in broods of three chicks

(mortality within 7 days of hatching)

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

Significant difference between a-chick and other chicks

in the hatching sequence :

* $p < 0.05$ *** $p < 0.001$

APPENDIX VII. Laying sequence and post-hatching mortality when only two chicks hatch

(mortality within 7 days of hatching)

No. chicks dying in brood	No. nests	a-chick	b-chick	No. nests	b-chick	c-chick	No. nests	a-chick	c-chick
Nil (all survived	43	43	43	23	23	23	15	15	15
One chick	20	8	12	3	0	3	5	0	5
Both chicks	7	7	7	8	8	8	4	4	4
Total no.hatched		70	70		34	34		24	24
Total no.died		15	19		8	11		4	9
% mortality		21.4%	27.1%		23.5%	32.4%		16.7%	37.5%
Significance			NS			NS			NS

APPENDIX VIII. Comparing the laying period of Whaup and N. Ness in 1969 to detect any differences due to the continuous egg removal on Whaup in 1967 and 1968

	Laying period - May (date of laying a-egg)									
	30-2	4-6	8-10	12-14	16-18	20-22	24-26	28-30	1-3	Total nests
Whaup										
No.nests	2	21	36	33	30	55	18	12	5	202
% acc.f.	1.0	11.4	29.2	45.5	60.4	82.7	91.6	97.5	100	
North Ness										
No.nests	6	19	33	32	30	37	20	18	8	203
% acc.f.	3.0	12.3	28.6	44.3	59.1	77.3	87.2	96.1	100	

APPENDIX IX. Hatching success through the season in control and delayed areas, 1968

				May			Laying date				June	
		up to 4	5-8	9-12	13-16	17-20	21-24	25-28	29-4	6-10	11-13	14 onwards
	No.eggs	133	245	374	370	525	402	254	160	-	-	-
CONTROL (North Ness)	No.chicks	84	165	259	246	409	302	162	95	-	-	-
	% hatching	63.2	67.4	69.3	66.5	77.9	75.1	63.8	59.4	-	-	-
	No.eggs	-	-	-	-	-	-	109	90	275	224	86
DELAYED (E. Tarbet)	No.chicks	-	-	-	-	-	-	80	68	185	140	46
	% hatching	-	-	-	-	-	-	73.4	75.6	67.3	62.5	53.5

APPENDIX X. Colour-ringing scheme for Isle of May Herring Gull pulli 1966-69

Rings : M = Monel R = Red Y = Yellow B = Blue

r = Right leg l = left leg

Year	Date or area of hatching	No.ringed	Ring combination
1966	normal	3,736	Mr Rl
	late	604	Ml Rr
1967	controls (N.Ness, S.Rona, Burrian(2))	2,282	Mr Yl
	General	1,832	Ml Yr
	Tarbet	508	Y/Mr Yl
	Burrian (1)	260	Y/Mr
	Burrian (3)	242	Y/Ml
	N.Rona	106	Y/Ml Yr
1968	up to 9 June	1,112	B/Mr
	9 - 16 June	1,639	Mr Bl
	16 - 23 June	1,369	Ml Br
	after 23 June	705	B/Ml

APPENDIX XI. **Comparing pre-fledging mortality in 1966 and 1967 with hatching dates**

Percentage mortality
(No.chicks ringed in brackets)

	June						July		
	4-7	8-11	12-15	16-19	20-24	25-29	30-6	7-11	12-16
1966 general	9.1% (121)	5.0% (519)	5.1% (846)	6.2% (553)	5.3% (414)	5.1% (336)	16.8% (101)	-	-
1967 control	15.9% (88)	11.9% (286)	9.3% (821)	7.5% (562)	10.0% (529)	10.4% (280)	16.3% (49)	-	-
1967 delayed i) Tarbet and Burrian (1)	-	25.9% (27)	10.0% (121)	15.4% (182)	15.2% (184)	7.4% (121)	8.5% (94)	15.2% (33)	-
ii) Burrian (3)	-	-	-	14.3% (7)	5.3% (19)	3.5% (20)	5.4% (92)	7.9% (66)	14.3% (7)

APPENDIX XII. Scientific names of species referred to in the text.

Albatross, Laysan	*Diomedea immutabilis*
Capercaillie	*Tetrao urogallus*
Domestic hen	*Gallus domesticus*
Eider duck	*Somateria mollissima*
Flicker	*Colaptes auratus*
Fulmar	*Fulmarus glacialis*
Gannet	*Sula bassana*
Gull, Black-headed	*Larus ridibundus*
Common	*canus*
Dominican	*dominicanus*
Glaucous-winged	*glaucescens*
Great Black-backed	*marinus*
Herring	*argentatus*
Laughing	*atricilla*
Lesser Black-backed	*fuscus*
Heron	*Ardea cinerea*
Kittiwake	*Rissa tridactyla*
Mallard	*Anas platyrhynchros*
Oystercatcher	*Haematopus ostralegus*
Pigeon, wood	*Columba palumbus*
Quail, Bobwhite	*Colinus virginianus*
Shag	*Phalacrocorax aristotelis*
Skua, Great	*Stercorarius skua*
Stork, White	*Ciconia ciconia*
Tern, Common	*Sterna hirundo*
Sandwich	*sandvicensis*
Tit, Great	*Parus major*
Wren, House	*Troglodytes aedon*

REFERENCES

ANDERSEN, F.S. 1957. Egg size and the age composition of bird populations. Vidensk. Medd. Dansk naturh. Foren. 119 : 1-24.

ASHMOLE, N.P. 1963. The regulation of numbers of tropical oceanic birds. Ibis. 103b : 458-473.

BAKER, J.R. 1938. The evolution of breeding seasons. In "Evolution; essays presented to E.S. Goodrich". Oxford University Press.

BARTH, E.K. 1967. Egg dimensions and laying dates of *Larus marinus*, *L. argentatus*, *L. fuscus* and *L. canus*. Nytt. Mag. Zool. 15 : 5-34.

BAXTER, E.V. & RINTOUL, L.J.. Fluctuations in breeding birds on the Isle of May. Scot. Nat. 175.

BEER, C.G. 1961. Incubation and nest-building behaviour of Black-headed Gulls. I. Incubation behaviour in the incubation period. Behaviour 18 : 62-106.

BELOPOL'SKII, L.O. 1957. (The ecology of the colonial sea-birds of the Barent Sea) Moscow. Translated and published by Israel Program for Scientific Translations.

BOSWALL, J. 1960. Observations on the use by sea-birds of human fishing activities. Brit. Birds 23 : 212-15.

BROUGH, T. 1969. Damage by Gulls. Ibis 111 : 445-46.

BROWN, R.G.B. 1967. Breeding success and population growth in a colony of Herring and Lesser Black-backed Gulls, *Larus argentatus* and *L. fuscus*. Ibis 109 : 502-15.

CAPILDEO, R. & HALDANE, J.B.S. 1954. The mathematics of bird population growth and decline. J. Anim. Ecol. 23 : 215-23.

COLLINGE, W.E. 1924-27. The food of some British Wild Birds. York.

COULSON, J.C. 1963. Improved coloured-rings. Bird Study 10 : 109-11.

" 1963. Egg size and shape in the Kittiwake (Rissa tridactyla) and their use in estimating age composition of populations. Proc. Zool. Soc. Lond. 140 : 211-27.

" 1966. The influence of the pair-bond and age on the breeding biology of the Kittiwake Gull. Rissa tridactyla. J. Anim.Ecol. 35 : 269-79.

" 1968. Differences in the quality of birds nesting in the centre and on the edges of a colony. Nature 217 : 478-79.

COULSON, J.C. & WHITE, E. 1955. Abrasion and loss of rings among sea-birds. Bird Study 2 : 41-44.

" " 1956. A study of colonies of the Kittiwake (Rissa tridactyla L.) Ibis 98 : 63-79.

" " 1958a. Observations on the breeding of the Kittiwake. Bird Study 5 : 74-83.

" " 1958b. The effect of age on the breeding biology of the Kittiwake Rissa tridactyla Ibis 100 : 40-51.

" " 1959. The post-fledging mortality of the Kittiwake. Bird Study 6 : 97-102.

" " 1961. An analysis of the factors influencing the clutch size of the Kittiwake. Proc. Zool. Soc. Lond. 136 : 207-17.

COULSON, J.C., POTTS, G.R. & HOROBIN, J. 1969. Variation in the eggs of the Shag (Phalacrocorax aristotelis) Auk. 86 : 232-45.

DARLING, F.F. 1938. Bird flocks and the breeding cycle. Cambridge Univ. Press.

DAVIS, D.E. 1942. Number of eggs laid by Herring Gulls. Auk 59 : 549-54.

DAVIS, T.A.W. 1956. Gulls feeding on grain. Brit. Birds 49 : 400-404.

DEUSING, M. 1939. The Herring Gulls of Hat Island, Wisconsin Wilson Bull. 51 : 170-75.

DRENT, R.H. 1967. Functional aspects of incubation in the Herring Gull (Larus argentatus Pont.) Leiden.

DROST, R., FOCKE, E. & FREYTAG, G. 1961. Entwicklung und Aufbau einer Population der Silbermowe. J. Orn. 102 : 404-29.

DUTCHER, W. & BAILY, W. 1903. A contribution to the life history of the Herring Gull (Larus argentatus) in the United States. Auk 20 : 417-31.

EGGELING, W.J. 1960. The Isle of May. London.

FISHER, J. & LOCKLEY, R.M. 1954. Sea-birds. London. Collins.

FISHER, R.A. & YATES, F. 1963. Statistical tables. 6th edit. London and Edinburgh.

FLORENCE, L. 1912-15. The food of birds. Trans. High. Agric. Soc. Scotland. 1912 : 180p219, 1911 : 1-74, 1913 : 1-53.

FOCKE, E. 1959. Zur Ernahrungder Silbermowe (Larus argentatus) Vogelwarte 20 : 86-88.

FORDHAM, R.A. 1967. History and status of the Dominican Gull in Wellington. Notornis 14 : 144-53.

" 1970. Mortality and population change in Dominican Gulls in Wellington, New Zealand. J. Anim. Ecol. 39 : 13-27.

GEMPERLE, M.E. & PRESTON, F.W. 1955. Variation in shape in the eggs of the Common Tern in the clutch sequence. Auk 72 : 184-98.

GODFREY, G.F., WILLIAMS, C. & MARSHALL, C.E. 1953. The relative influence of egg-size, age at sexual maturity, and mature body weight on growth to twelve weeks of age. Poult. Sci. 32 : 496-500.

GOETHE, F. 1956. Die Silbermowe. Wittenberg Lutherstadt.

GROSS, A.O. 1940. The Migration of Kent Island Herring Gulls. Bird Banding 11 : 129-55.

" 1945. The present status of the Great Black-backed Gull on the coast of Maine. Auk,62 : 241-56.

HALBERSLEBEN, D.L. & MUSSEHL, F.E. 1922. The relation of egg weight to chick weight at hatching. Poult. Sci. 1 : 143-44.

HARRIS, M.P. 1962. The _Larus_ gulls breeding on Skomer, Skokholm and Grassholm Islands. Native in Wales 8 : 56-58.

" 1963. Recoveries of ringed Herring Gulls. Bird Study 11 : 183-91.

" 1964. Aspects of the breeding biology of the Gulls _Larus_ _argentatus_, _L_. _fuscus_ and _L_. _marinus_. Ibis 106 : 432-56.

" 1965. The food of some _Larus_ gulls. Ibis 107 : 43-53.

HARRIS, M.P. 1967. The biology of Oystercatchers Haemotopus ostralegus on Skokholm Island, S. Wales. Ibis 109 : 180-93.

" 1969. Effect of laying date on chick production in Oystercatchers and Herring Gulls. Br. Birds 62 : 70-75.

HARRIS & PLUMB, W.J. 1965. Experiments on the ability of Herring Gulls Larus argentatus and Lesser Black-backed Gulls L. fuscus to raise larger than normal broods. Ibis 107 : 256-57.

HERRICK, F. 1909. Organisation of the gull community Proc. 7th Internat. Zool. Cong. Boston 1907.

HICKEY, J.J. 1952. Survival studies of banded birds. Spec. Sci. Report : Wildlife No.15 U.S. Fish & Wildl. Service. Washington 177pp.

HICKLING, R.A.O. 1967. The inland wintering of gulls in England 1963. Bird Study 14 : 104-113.

INGRAM, C. 1959. The importance of juvenile cannibalism in the breeding biology of certain birds of prey. Auk 76 : 218-226.

KADLEC, J.A. & DRURY, W.H. 1968. Structure of the New England Herring Gull Population. Ecology 49 : 644-76.

KADLEC, J.A., DRURY, W.H. & ONION, D.K. 1969. Growth and mortality of Herring Gull chicks. Bird Banding 40 : 222-33.

KEAR, J. 1965. The internal food reserves of hatching Mallard ducklings. J. Wildlife Mgmt. 29 : 523-28.

KENDEIGH, S.C., KRAMER, T.C. & HAMERSTROM, F. 1956. Variations in egg characteristics of the house wren. Auk 73 : 42-65.

KIRKMAN, F. 1937. Bird Behaviour. London.

KLUIJVER, H.N. 1951. The population ecology of the Great Tit Parus m. major L. Ardea 391 : 1-135.

KRUUK, H. 1964. Predators and anti-predator behaviour of the Black-headed Gull (Larus ridibundus L.) Behaviour suppl. 11 : 1-130.

LACK, D. 1954. The Natural Regulation of animal numbers. Oxford. Clarendon Press.

" 1966. Population Studies of birds. Oxford.

" 1967. The significance of clutch-size in waterfowl Wildfowl Trust 18th Annual Report 125-28.

LLOYD, D. 1969. The use of inland habitats by Gulls, Larus sp., in the Ythan Valley, Aberdeenshire. M.Sc. thesis Aberdeen Univ.

MARCSTRÖM, V. 1960. Studies on the physiological and ecological background to the reproduction of the Capercaillie (Tetrao urogallus L.) Viltrevy 2 : 1-69.

" 1966. Mallard ducklings (Anas platyrhynchos L.) during the first days after hatching. Viltrevy 4 : 343-70.

MARSHALL, A.J. 1959. Internal and environmental control of breeding Ibis 101 : 456-77.

MENDALL, H.L. 1939. Food habits of the Herring Gull in relation to the freshwater game fishes in Maine. Wilson Bull. 51 : 223-26.

MOREAU, R.E. 1923. Herring Gull eating its own chick. Brit. Birds 16 : 221-22.

MORRIS, R.H., HESSELS, D.F. & BISHOP, R.J. 1968. The relationship between hatching weight and subsequent performance of broiler chickens. Brit. Poult. Sci. 9 : 305-15.

NELSON, J.B. 1964. Factors influencing clutch-size and chick growth in the North Atlantic Gannet, Sula bassana. Ibis 106 : 63-77.

NELSON, J.B. 1966. The breeding biology of the Gannet, Sula bassana, on the Bass Rock, Scotland. Ibis 108 : 584-626.

OLSSON, V. 1958. Dispersal migration, longevity and death causes of Strix aluco, Buteo buteo, ardea cinerea and Larus argentatus. A study based on recoveries of birds ringed in Fenno-Scandia. Acta Vert. 1 : 91-189.

O'NEIL, J.B. 1950. Relationship of chick size to egg weight and its effect upon growth and mortality. Poult. Sci. 29 : 774.

OTTERLIND, G. 1948. Til gratrutens (Larus a. argentatus Pont) naringsoch spridningsekolgi. K. Fysiogr. Sallsk. Lund. Fork. 18 : 36-46.

PALUDAN, K. 1951. Contributions to the breeding biology of Larus argentatus and L. fuscus. Vidensk. Medd. Dansk. Naturh. Foren. 114 : 1-128.

PATTERSON, I.J. 1965. Timing and spacing of broods in the Black-headed Gull. Larus ridibundus. Ibis 107 : 433-59.

PAYNTER, R.A. 1949. Clutch-size and the egg and chick mortality of Kent Island Herring Gulls. Ecology 30 : 146-66.

" 1966. A new attempt to construct life tables for Kent Island Herring Gulls. Bull. Mus. Comp. Zool. Harvard Univ. 133 : 489-528.

PERRINS, C.M. 1970. The timing of bird's breeding seasons. Ibis 112 : 242-55.

PHILLIPS, C.L. 1887. Egg-laying extraordinary in Colaptes auratus Auk. 4 : 346.

POTTS, G.R. 1969. The influence of eruptive movements, age, population size and other factors on the survival of the Shag (Phalacrocorax aristotelis L.) J. Anim. Ecol. 38 : 53-102.

POULDING, R.H. 1952. Five cases of aspergillosis in immature gulls. Ibis 94 : 364-66.

" 1954. Loss of rings by marked Herring Gulls. Bird Study 1 : 37-40.

PRESTON, F.W. & PRESTON, E.J. 1953. Variation in the shapes of birds' eggs within a clutch. Ann. Carnegie Mus. 33 : 129-39.

RICE, D.W. & KENYON, K.W. 1962. Breeding cycles and behaviour of Laysan and Black-headed Albatrosses. Auk 79 : 517-67.

ROMANOFF, A.L. & ROMANOFF, A.J. 1949. The Avian Egg. New York and London.

ROWAN, W. 1926. On Photoperiodism, reproductive periodicity, and the annual migrations of birds and certain fishes. Proc. Boston Soc. Nat. Hist. 38 : 147-89.

" 1938. Light and seasonal reproduction in animals. Biol. Rev. 13 : 374-402.

SALOMONSEN, F. 1939. OOlogical studies in gulls. 1. Egg-producing powers of Larus argentatus Pont. Dansk. Orn. Foren. Tidsskr. 33 : 113-33.

SCHÜZ, E. 1943. Uber die Jungenaufzucht des Weissen Storches. Z. Morph. Okol. Tiere. 40 : 181-237.

" 1957. Das Verschlingen eigener Junger ("Kronismus") bei Vogeln und seine Bedentung. Vogelwarte 19 : 1-15.

SKOGLUND, W.C., SEEGAR, K.C. & RINGROSE, A.T. 1952. Growth of broiler chicks hatched from various sized eggs when reared in competition with each other. Poult. Sci. 31 : 796-99.

SKOGLUND, W.C., & TOMHAVE, A.E. 1949. Relationship between egg weight, initial chick weight, and subsequent broiler growth. Bull. 278. Univ. Delaware Agric. Expt. Station.

SNOW, D.W. 1958. The breeding of the Blackbird, Turdus Merula, at Oxford. Ibis 100 : 1-30.

SOUTHERN, H.N. 1959. Mortality and population control. Ibis 101 : 429-36.

SPARCK, R. 1951. The food of North European Gulls. Proc. 10th Orn. Congr. 1950 : 588-91.

STRONG, R.M. 1914. On the habits and behaviour of the Herring Gull Auk 31 : 22-49, 178-99.

STURKIE, P.D. 1954. Avian Physiology. Bailliere, Tindell and Cassell.

SYKES, A.H. 1959. Egg formation in the Hen. New Biol. 30 : 7-25.

TINBERGEN, N. 1953. The Herring Gull's World. London : Collins.

" 1956. On the functions of territory in Gulls, Ibis 98 : 401-11.

" 1957. The functions of territory. Bird Study 4 : 14-27.

TINDELL, D. & MORRIS, D.R. 1964. The effects of egg weight on subsequent broiler performance. Poult. Sci. 43 : 534-39.

VERMEER, K. 1963. The breeding ecology of the Glaucous-winged Gull (Larus glaucescens) on Mandrate Island, B.C. Occ. Pap. Br. Columb. prov. mus. 13 : 1-104.

VINCE, M.A. 1964. Social facilitation of hatching in the Bob-white Quail. Anim. Behav. 12 : 531-34.

WALKER, F. 1936. The Geology of the Isle of May. Trans. Geol. Soc. Edin. 13 : 275.

WARD, F. 1914. Report of sub-committee appointed to make arrangements for and to investigate the feeding habits of gulls during 1913. Sussex & Essex Fisheries Board. 1914 : 1-15.

WARD, H.L. 1906. Why do Herring Gulls kill their young? Science. 24 : 593-4.

WEIDMANN, U. 1956. Observations and experiments on egg-laying in the Black-headed Gull (*Larus ridibundus* L) Brit. J. Anim. Behav. 4 : 150-61.

WILEY, W.H. 1950. The influence of egg weight in the pre-hatching and post-hatching growth rate in the fowl. 2. Egg-weight - chick-weight ratios. Poult. Sci. 29 : 595-604.

WILSON, J.E. & MACDONALD, J.W. 1967. Salmonella infection in wild birds. Brit. Vet. J. 123 : 212-19.

WYNNE-EDWARDS, V.C. 1962. Animal Dispersion in Relation to Social Behaviour. Edinburgh.