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CERTAIN ASPECTS OF THE BREEDING BIOLOGY OF THE KITTIWAKE (*RISSA TRIDACTYLA*)

Callum S. Thomas B.Sc. (London)

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being a thesis presented in candidature for
the degree of Doctor of Philosophy in the
University of Durham, 1980

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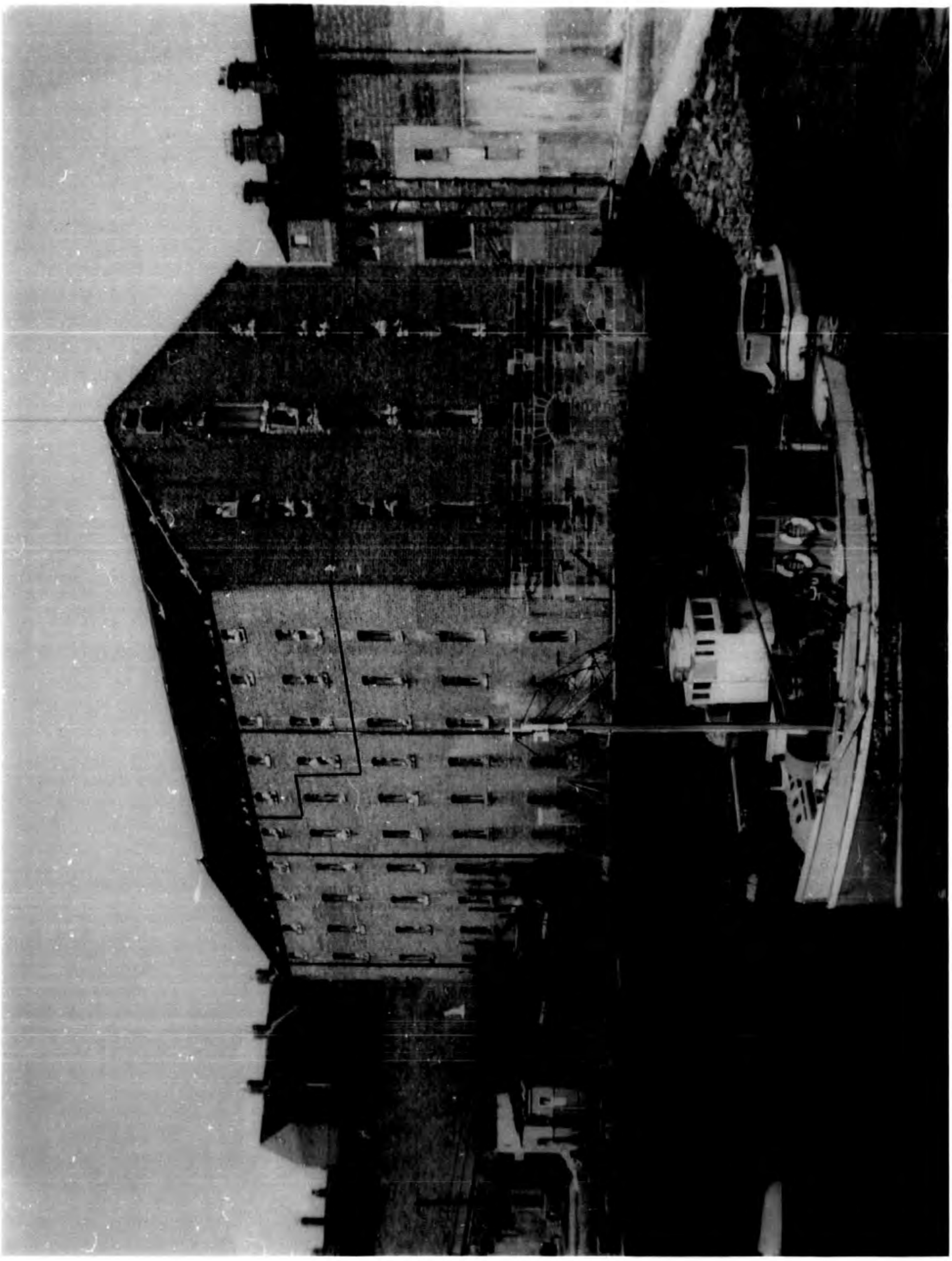
Frontispiece : The South and West Faces of the Study Colony - a riverside warehouse at North Shields, Tyne and Wear

The 'centre' of this part of the colony (see text) comprises that area lying above and enclosed by the black line marked on the frontispiece



ABSTRACT

Data on aspects of the breeding biology of a colony of Kittiwakes in North East England, in which all breeding adults are individually colour-marked, have been collected annually since 1954. The inter-relationships between different factors have been investigated and year-to-year changes in the breeding biology of the colony, related to changes in population structure.

Date of return to the colony is shown to be primarily determined by age. Synchrony of return between the members of a breeding pair is associated with the maintenance of the pair bond.

Other factors influencing the duration of the pair bond are investigated, including the prior association between the members of the pair, breeding success in the previous year and mortality rates in different years. As birds get older, the main cause of the break-up of the pair bond changes from 'divorce' to bereavement.

Time of breeding is related to the location of the nest site (centre or edge of the colony) and the breeding experience of the two members of the pair. There is a tendency for breeding to become more synchronised amongst older age groups, with females laying progressively closer to the mean date of laying for the colony as a whole. The possible interactions between environmental cues, stimulus from the mate and stimulus from the rest of the colony are discussed.

Clutch size is shown to be independently influenced by breeding experience, date of laying, location of the nest site and the status of the pair (retention of the same mate as in the previous year, or change).

Variations in the size and shape of eggs laid by different females are investigated with respect to many of the above factors.

The breeding success of pairs is primarily determined by clutch size although the experience of adults and egg size are also involved. To separate the effects of the last two variables, a number of clutches were exchanged between different nests in the colony. Causes of, and times of egg and chick loss, are compared with those reported in other colonies of Kittiwakes.

Throughout this work, data have revealed a marked consistency in the breeding characteristics of individual females in different years.

Similarities between some of the relationships found here and in other avian species are compared with those investigated in other groups of animals. The need for more comprehensive long-term studies to be carried out is stressed.

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CHAPTER 1 : INTRODUCTION

1.1 Background and Aims

Seabirds occupy a position high up in the marine food chain. For populations breeding in Shetland, it has been estimated that they consume between 20 and 35% of the annual food-fish production from within a 45km radius of each colony (Furness 1978). As a result, the breeding success and survival of the birds in particular years may reflect changes in fish stocks and any build-up in levels of marine pollution. Recently, poor breeding of Kittiwakes in North Norway was attributed to local food shortages (Barrett 1978) and Belopol'skii (1961) found that in years of poor feeding conditions, breeding was later and clutch size reduced.

The recent decline in the population of Cormorants and Double-crested Cormorants breeding in the Gulf of St Lawrence and the decline and reduced breeding success of Gannets on Bonaventure during the late 1960s and early 1970s is thought to be linked to the increased use of organochlorines and in particular, in the case of the Gannet, to the increase in the use of DDT (Peakall *et al.* 1978). So far, only low levels of DDT, PCBs and heavy metals have been found in the eggs and chicks of Kittiwakes (Fimreite *et al.* 1974, 1977, Robinson *et al.* 1967) and it is thought that larids in general are rather insensitive to organochlorines (Peakall *et al.* 1978).

Ecological studies of birds can have an important applied, as well as pure aspect, since they can act as monitors of the marine environment. A full understanding of the factors associated with breeding and survival is necessary however, in order that 'normal' year to year variations can be differentiated from those attributable to changes in environmental factors such as pollution levels.

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Fraser Darling (1938) published the first major work which showed that the breeding biology of single species of birds varied from one colony to another. These differences he attributed to the degree of social stimulation within each colony, which in turn was related to the population size. Coulson and White (1956) suggested that many of these differences could be explained in terms of the age structure of the populations and, more recently, Coulson (1966, 1972) has shown that breeding experience, as well as the association between two individuals from one year to the next, can have a marked effect upon the breeding biology of the pair and, hence, the colony as a whole. The breeding biology of single colonies has been shown to vary from year to year, e.g. the Fulmar (Dunnet *et al.* 1979), as has the annual survival rate of adults from single populations, e.g. the Kittiwake (Coulson and Wooller 1976). Most studies of particular species, at best, make comparisons with other work on the same bird, without adequate attention being paid to the possible differences which could arise from any of the above variables. Seabirds are long-lived, exhibit delayed maturity and, in general, produce only one, two or three offspring in any year. As a result, small changes in the environment which affect either breeding success or survival can have prolonged effects upon the breeding biology of the birds.

Despite these facts, very few long-term studies have been made on any avian species, notable exceptions being the work on the Fulmar (Dunnet *et al.* 1979); the Red-billed Gull (Mills 1979); the Gannet (Nelson 1966); the Yellow-eyed Penguin (Richdale 1957) and amongst non-seabirds, the Wood-pigeon (Murton 1965); the Great Tit (Perrins 1965) and the White Stork (Tantzen 1962). Even amongst these, the nature and size of the study populations have been such that in many cases it has only been possible to mark a small proportion of the birds involved.

A study of a discrete population in which all the breeding birds are individually colour-marked is unique to the work which has been carried out on a colony of Kittiwakes nesting on a warehouse in North Shields, Tyne and Wear, England. Data have been gathered on the breeding biology of all birds at the colony in each year since 1954. Coulson and other workers have made detailed analysis of various aspects of the breeding biology of the Kittiwake as outlined below. In several of the papers however, it was necessary to contrast North Shields with other colonies in order to compare different breeding seasons and any effect of colony size. A large body of data has now been built up which permits long-term changes in the breeding biology of the birds to be investigated in relation to changes within the colony itself. In addition, computer-based statistical tools have become more readily available to biologists, which enable large amounts of data to be handled, so that the inter-relationships between different variables can be evaluated and hence the major factors affecting each aspect of the breeding biology discovered.

1.2 The Species

The Black-legged Kittiwake, *Rissa tridactyla*, is a small gull which is distinguished in its adult plumage by black legs, an unmarked yellow bill and black wing tips which have no 'wing mirrors'. The bird has a pure white body with grey mantle and wings. The first-year bird differs from the adult in having a black band across the upper side of the closed wing which has a characteristic "M" appearance when the bird is in flight. In addition, the beak is black, as is the tip of the tail, whilst the legs are slate grey. At the end of the first year, the black band across the wings and mantle is gradually replaced by grey feathers and the black tip of the tail is lost. The bill changes to a grey-yellow colour and the webs become dark brown with yellow patches in some individuals.

The Black-legged Kittiwake breeds extensively throughout the North Atlantic and along the Arctic-facing coasts of North America and Russia. Studies have been made on colonies in Alaska (Swartz 1966); in Britain (Coulson, Coulson and White, Coulson and Wooller (various papers), Cullen 1957); in Denmark (Paludan 1955); in Newfoundland (Maunder and Threlfall 1972); in North Norway (Barrett 1978, Johansen 1977) and in the U.S.S.R. (Belopol'skii 1961, Uspenski 1956). In the winter months, the birds enter a pelagic phase and disperse from their breeding colonies. Ringing recoveries show that birds from North Shields move across the Atlantic to Newfoundland and Nova Scotia, north to Scandinavia and Greenland, across the North Sea and south as far as the coast of Spain.

The number of Kittiwakes breeding in England and Wales has been increasing progressively since 1900. Until the 1930s this consisted of an enlargement of existing colonies; however, this was followed by the formation of new colonies which grew rapidly in size. This has been accompanied by a change in nesting habits. Once only found on precipitous cliffs, usually over 200 feet high, new colonies have been formed on cliffs as low as 30 feet. In addition, at least two were started unsuccessfully on flat sand on the Norfolk coast, although in the Danish colony on the island of Hirsholme, Kittiwakes started to nest on the top of boulders and later moved onto flat sand-dunes nearby (Coulson 1963b). A further change has been the move onto waterside buildings in various parts of Britain and abroad. The colony at North Shields is on one such building.

1.3 The North Shields Colony

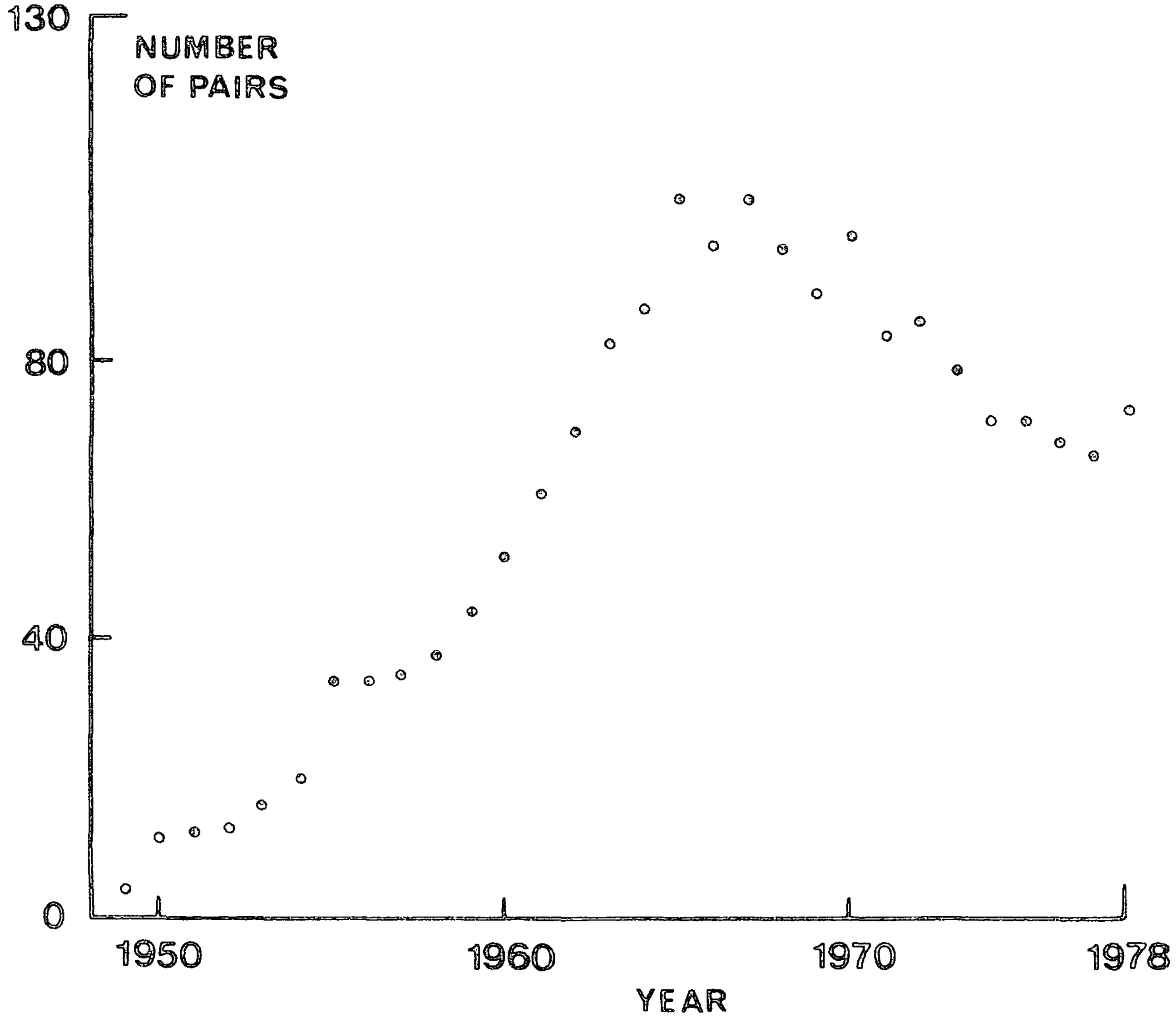
The warehouse at North Shields (see Frontispiece), which is the subject of this study, was first colonised in 1949 by four pairs of Kittiwakes which started nesting on the south side of the building.

Since then the population has increased, recently spreading onto the other three sides and onto the window-ledges and guttering of neighbouring buildings. Only the birds breeding on the main warehouse are included in this study and there is good reason to consider it a separate colony (or sub-colony) from the other buildings, since few colour-marked breeding birds have ever moved from one building to another.

The growth of the colony is shown in Figure 1.1. The number of breeding pairs increased to a maximum in 1967, since when there has been a gradual decline to 73 pairs in 1978. During the growth phase (1954-67), birds utilised ledges on all four sides of the building, occupying progressively lower levels. In general, two nests were built on each window-ledge, although on some, usually on the lower levels of the north and west faces, no more than one nest was ever constructed. On the south side of the building, the ledge below the large doors (denoted 'S1B') has been occupied by four pairs of breeding birds in several years. Wooller (1973) found a significant positive correlation between the percentage of window-ledges occupied by two breeding pairs and the total number of pairs in the colony as a whole ($r = 0.98$, $N = 21$, $P < 0.001$). This indicated that colony size may be used as a gross measure of the density of breeding birds in this study.

Coulson (1968) suggested that the breeding colony at North Shields could be split into two parts. The 'Centre' he defined as that area which was occupied when the colony was half its maximum size. He found that once birds bred in one part of the colony they very rarely moved to the other. The two areas, then, could be considered as being almost discrete. The central part of the colony may be broadly described as that occupying the top three levels of window-ledges across the south face of the building, with part of the top two levels of the west face and one window on each of the north and east faces. (The centre of the west and south sides of the

Figure 1.1 : The number of pairs of Kittiwakes breeding in the colony at North Shields in each year since the colony's formation in 1949

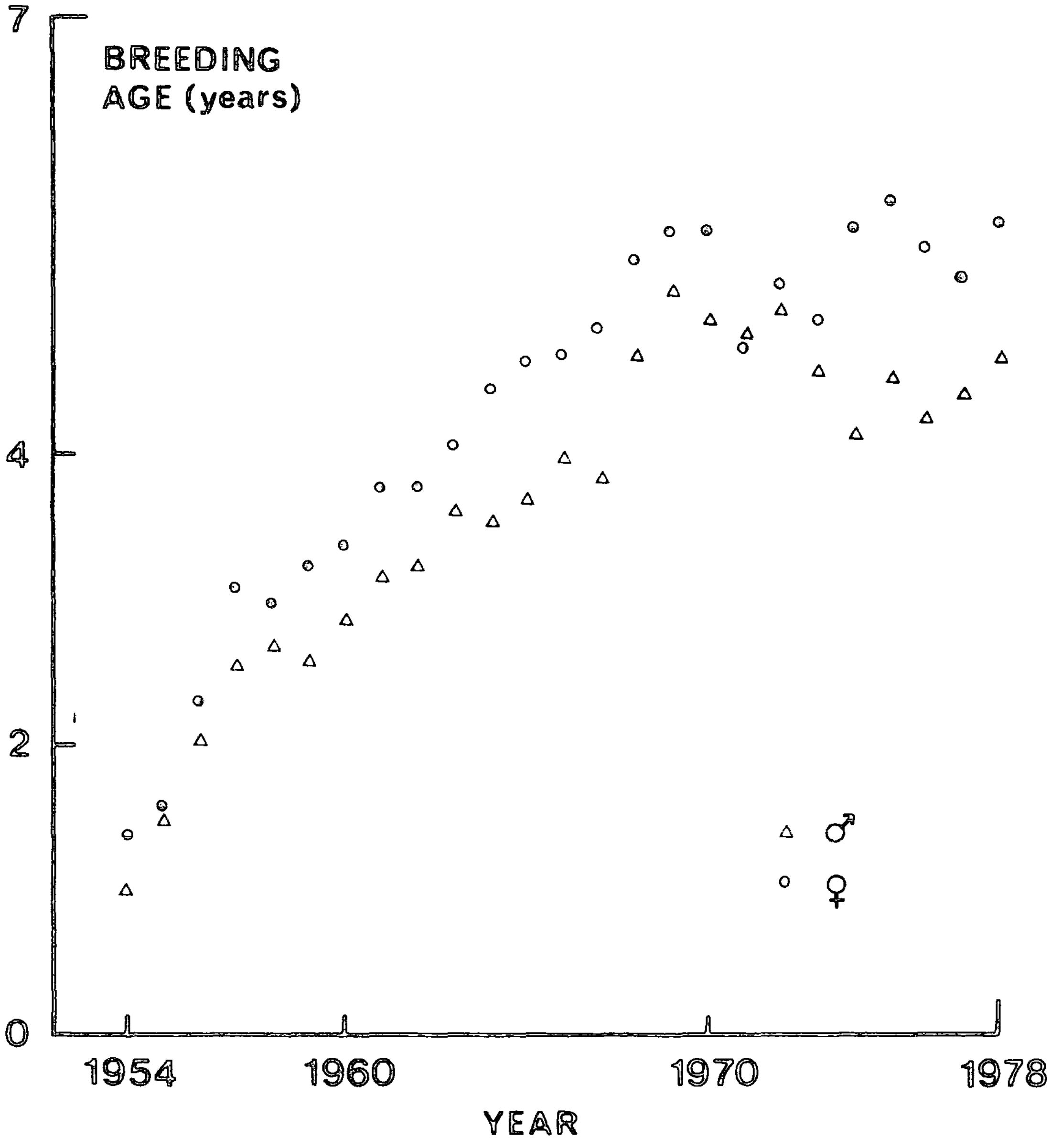


building is that area lying above, and enclosed by, the black line marked on the Frontispiece.) Birds nesting in each part of the colony were found to have significantly different breeding characteristics; 'edge' nesting males having a higher mortality rate, changing mate more often, their mates laying later, smaller clutches and showing lower breeding success than those in the 'centre'. The differences were attributed to the quality of birds found in each part and the intensity of competition for breeding sites.

Studies began at North Shields in 1952 and since 1954 all breeding birds have been individually colour-ringed. Kittiwakes breed for the first time at ages from 3 to 8 years, although most are aged either at 4 or 5 years (Wooller and Coulson 1977). On average, males return to the colony earlier and breed for the first time when one year younger than females. Searches of other colonies along the North East coast of England and part of the South East coast of Scotland have revealed that once a bird breeds at North Shields it rarely, if ever, moves to another colony (Coulson and Wooller 1976). As a result, it was reasonable to assume that all non-ringed birds nesting in the colony were breeding for the first time. By operating a system of ringing all first breeders, it was subsequently possible to identify the number of breeding attempts each individual had made. This is known as the breeding experience, or breeding age of the bird. (A first breeder has a breeding age of one. A bird with a breeding age of four has attempted to breed in three years previously.)

The mean breeding age in each year of males and females in the colony is shown in Figure 1.2. Between 1954 and 1970 there was a gradual increase in the mean breeding age of both sexes. However, since then, whilst there has been little change amongst females, the mean age of males has declined slightly. In each year except 1971, the mean age of females in the colony was greater than that of males, reflecting the higher mortality

Figure 1.2 : The mean breeding ages of male and female Kittiwakes nesting in the colony at North Shields in each year since 1954

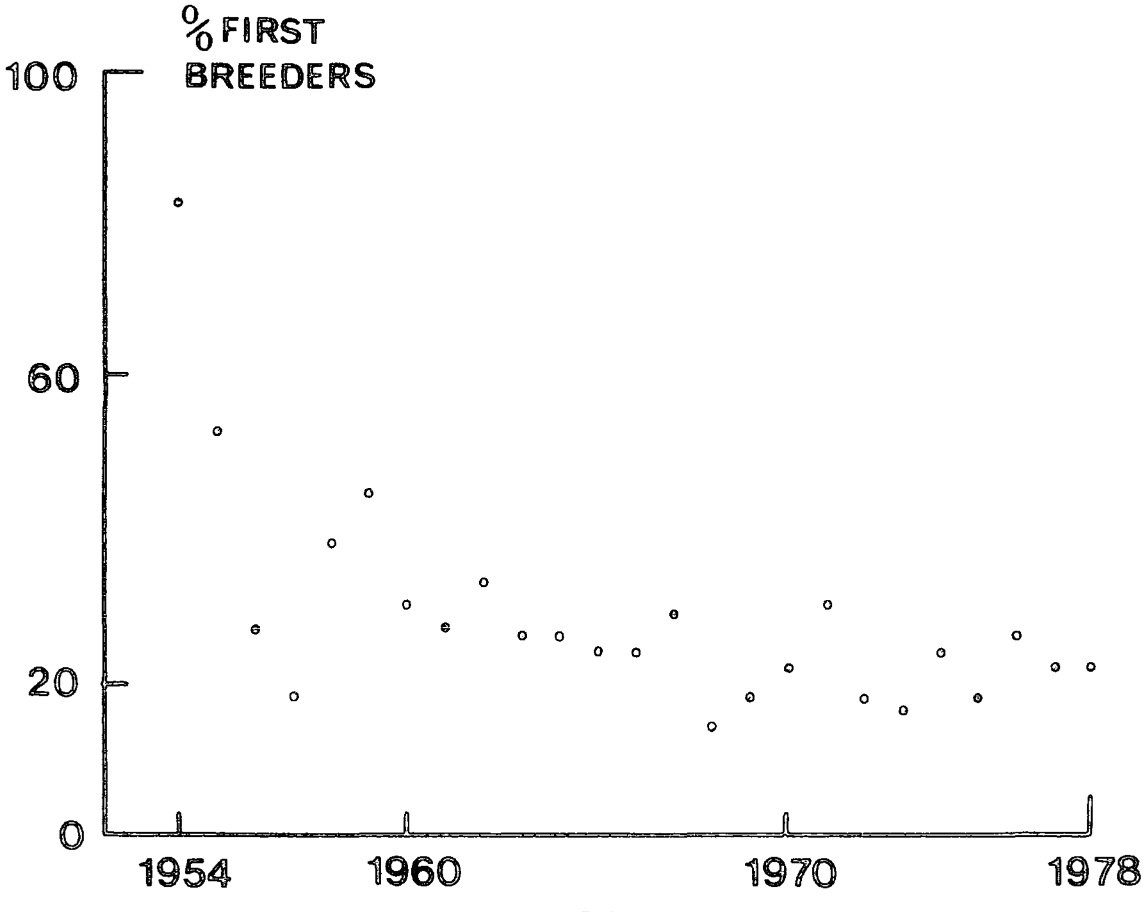


rate found in males (Coulson and Wooller 1976). Year-to-year variations outside the overall trend will reflect differences in the annual mortality rate and hence the number of first breeders entering the colony. The proportion of first breeders in the colony declined during the 1950s, since when it has remained consistent, between 13% and 33% (Figure 1.3). During the early part of the growth phase, first breeders were mainly involved with the colonisation of new nest sites, although gradually the proportion which replaced dead mates in already existing pairs increased.

Kittiwakes are long-lived birds; one female has bred in the colony for 19 years, whilst the oldest male has bred for 18 years. On average, females breed for between 3-4 years and males slightly less. Many birds remain with the same breeding partner from one year to the next, although in any year, an average of 43% of pairs split up. When this occurs, females especially,will move to a new site, although normally a pair will remain on the same nest site from one year to the next. Change of mate, which occurs either as a result of the death of a partner, or through 'divorce' (i.e. both members of the pair return to the colony to breed, but take new mates), has been shown to have a significant effect upon the breeding of the birds in the following year, causing a delay in laying and a reduction in breeding success (Coulson 1966, 1972).

Much of the early work by Coulson (various papers) and Coulson and White (various papers) involved studies on the effect of breeding age, nest site location and the status of the pair bond upon date of laying, clutch size and breeding success in the Kittiwake. More recent work by Wooller (1973) and Hodges (1974) has investigated some of the behavioural aspects of the breeding of the birds. A comprehensive picture has now been built up which shows some aspects of the complexity of the breeding system at this colony.

Figure 1.3 : **Annual variations in the proportion of birds breeding for the first time in the colony**



1.4 Methods

Visits were made to North Shields on two days in each week from the time when the birds first returned to the colony (usually in the first week of January) until the onset of laying in April. Thereafter, the colony was visited on alternate days, until the last chicks had fledged at the end of August.

Throughout the season, on each visit, records were kept of the occupants of each nest site, individual adults being recognised from a unique combination of three darvic colour-rings and a single B.T.O. monel ring. Early in the season these 'counts' were made between 10.00 and 12.00 hrs to avoid the effect of any diurnal variations in attendance. In this way, information was gathered on the date of return to the colony of each bird and the formation of pairs.

Laying dates were recorded as the day on which the first egg of the clutch was found. Upon discovery, each egg was marked, using a felt pen in such a way that the number could be read from within the building without the egg being moved. In addition, the maximum length and breadth of each egg was measured to the nearest 0.1mm using a pair of vernier callipers. Occasionally, when two eggs were laid between visits, the second egg could be distinguished by its colour and, in some cases, its size. (Normally, the second egg is smaller; the first is often darker and dirtier after an extra two days in the nest.) In all these cases the data were excluded from the analysis where the order of laying was important.

Date of hatching was recorded as the date on which the chick was first seen. Upon discovery, newly hatched chicks were marked with a felt pen to distinguish order of hatching and, when about a week old, each was fitted with a B.T.O. monel ring and a single laminated darvic colour-ring. A new colour was used for each season and each ring was engraved with a unique combination of one letter and one number. The engraving, which was carried out at two points around the ring, would allow the chick to be identified on a cliff face using a telescope.

Dates on which eggs were lost or damaged were recorded and later, any eggs which did not produce chicks were removed from the nest 4-5 days after they were expected to have hatched. Eggs collected in this manner were opened and the stage at which development had ceased was recorded, using the photographs of embryo growth in Maunder and Threlfall (1972) as a reference. Dates on which chicks died or were lost from the nest were recorded and, where possible, corpses were sent to M.A.F.F. at Lasswade for post-mortem examination.

Towards the end of the laying season first breeders without rings, which had already produced eggs, were caught from inside the building using a small wire hook looped around the leg of the bird, above the tarsus. The bird was then weighed, using a Mettler Balance (accurate to the nearest gram), its wing length measured, as outlined in the B.T.O. Ringers Manual (Spencer 1972) and colour-marked, as explained above. The age of the bird was determined from its plumage, as outlined in Coulson (1959) and sexed from a combination of its size (males are larger than females - Table 1.1, the sex of the partner, if known, or its behaviour earlier in the season (males exhibit courtship feeding towards females and males can be seen mounting females during copulation). Non-breeders were also caught after the last eggs had been laid and processed in the same manner. At the end of the season the fledging dates of chicks and the departure date of the breeding adults were recorded.

Data gathered in this manner were combined with that collected in every year since 1953 in which the same methods were used. These were then analysed using the Northumbrian Universities Multiple Access Computer (an IBM 360/67 and an IBM 370/168) at Durham. In particular, use was made of

Table 1.1 Wing Length and Body Weight of Male and Female Kittiwakes**
caught in the Colony as First Breeders

		FEMALES	MALES
Wing Length (mm)	Mean	301.1	309.5
	S.D.	6.3	6.7
	N	212	252
Body Weight (gms)	Mean	347.1	383.8
	S.D.	31.3	26.5
	N	205	231

** Sexed either from behaviour (see text) or if sex of partner known.

programmes provided in the Statistical Package for the Social Sciences (S.P.S.S.), details of which are found in Appendix 1.2. Data incorporated into the file included at least some information on over 99% of all breeding attempts made in the colony between 1954 and 1978. Clutches which were robbed were counted as missing data and excluded from the analysis of breeding success and none of the few cases of re-laying were included.

Experiments were carried out to separate the effects of egg size and breeding age of adults upon success. These included the exchange of clutches between selected breeding pairs. Details of the methods employed are given in the relevant chapter below.

Throughout the analysis, means are given ± 1 S.E. and differences were accepted as being significant at the 5% level, unless stated otherwise.

CHAPTER 2 : DATE OF RETURN TO THE BREEDING COLONY

2.1 Introduction

At the end of the breeding season adult Kittiwakes enter a pelagic phase and move out to sea for the winter months. Early in the new year they start to return to the cliffs and re-occupy the breeding colonies. The date on which the first birds arrive back at North Shields has advanced steadily since data were first collected in 1956, However, there has been no corresponding change at nearby, older colonies (Wooller 1973). Darling (1938) would have explained this change in terms of the increase in size of the colony over the same period, whilst Coulson and White (1956) would look to changes in the age structure of the population. A study of the factors which influence the date of return of individual birds should give an indication of those factors which will affect the date of return of the colony as a whole. It is then possible, using data which have been collected over the years, to investigate changes in date of return of the colony, in relation to changes in the size and structure of the breeding population in each year.

Throughout this chapter the value given for date of return represents the date on which the bird was first seen in the colony, unless otherwise stated. All dates are measured as the number of days after 31 December in a particular year. Thus 1 January equals 1, 1 February is given the value 32 and 1 March the value 60, except in leap years where an extra day is added.

2.2 Date of Return of Individual Birds

2.2.1 Date of Return and Breeding Age

The fact that older birds tend to return to the colony first has been known for a long time and has been shown to occur in various species including Arctic Tern (Coulson and Horobin 1976); Common Tern (Austin 1949); Gannet (Nelson 1978); Kittiwake (Coulson and White 1956); Royal Penguin (Carrick and Ingham 1970) and Shag (Coulson 1971). The equations describing the relationship between date of return and breeding age, based on all data gathered at North Shields between 1956 and 1978, are given in Table 2.1. The progressive advancement with breeding age is a logarithmic relationship which is similar for both males and females and does not show the tailing off amongst older birds found in the Arctic Tern (Coulson and Horobin 1976). On average, first breeders return to the colony approximately 43 days later than birds with a breeding age of ten.

2.2.2 Date of Return and Sex

There is no significant difference between the slopes of the equations describing the relationships between date of return and breeding age given in Table 2.1 for males and females, although the intercepts of the two lines at the value 0.664 (the log of the mean breeding age of all females) are significantly different ($t = 2.55$, d.f. = 2100, $P < 0.02$). This indicates that amongst birds of the same age, males tend to return to the colony before females. Data confirming this are given in Table 2.2. On average, males return 3.7 days earlier than females of the same age, although within each age group differences between the sexes are not significant.

If the effect of age is ignored, there is no significant difference between the date of return of males (55.5) and females (56.1) and this arises from the difference in age structure between the two sexes, caused by the higher mortality rate amongst males (Coulson and Wooller 1976).

Wooller (1973) observed that although there was no pronounced trend for one sex to return to North Shields before the other, males represented a higher proportion of birds returning early in January during the three

Table 2.1 : Regression Equations describing the Relationship between Breeding Age (x) and Date of Return to the Colony (y)

Females

$y = -43.7\log_{10}x + 83.7$

$r = -0.40$, $N = 1058$, $P < 0.001$

S.E. Slope = 3.1

Intercept (at x value 0.664)* = 54.7 ± 0.97

Males

$y = -41.4\log_{10}x + 78.7$

$r = -0.39$, $N = 1044$, $P < 0.001$

S.E. Slope = 3.0

Intercept (at x value 0.664)* = 51.2 ± 0.97

* Value of x at intercept corresponds to the $\log_{10}$ of the mean breeding age of females (4.61 years).

Table 2.2 : Date of Return to the Colony of Males and Females in relation to Breeding Age

Mean Date of Return

Breeding Age (years)	Females	Males	Difference (days) Female - Male
1	83.4	77.1	6.3
2	68.9	65.4	3.5
3	65.0	59.4	5.6
4	58.6	55.2	3.4
5	51.5	53.3	-1.8
6	50.5	47.8	2.7
7	46.3	44.4	1.9
8	46.2	43.7	2.5
9-11	41.0	36.0	5.0
12-19	31.2	22.9	8.3
All Birds	56.1	55.5	0.6

S.D. and Sample Sizes

Breeding Age (years)	Females	Males
1	29.5 (86)	32.1 (125)
2	30.9 (165)	31.9 (187)
3	32.3 (144)	29.5 (169)
4	31.4 (130)	30.6 (131)
5	30.4 (118)	33.4 (112)
6	32.3 (84)	32.2 (78)
7	33.2 (74)	32.0 (63)
8	35.3 (61)	31.2 (46)
9-11	32.8 (118)	25.3 (94)
12-19	26.4 (78)	20.3 (39)
All Birds	34.2(1058)	33.2(1044)

years of his study. It has been found here that, although there is no consistency in the size of the difference between the date of return of males and females, with increasing breeding age, it is amongst the oldest age group that the difference between the sexes is greatest and it is these birds which tend to return to the colony first. Nelson (1978) also found that, on average, male Gannets of a particular age group returned before females and that it was the oldest males which were first to return to the breeding colony. Spurr (1975) and Warham (1974) observed the same in Adélie and Fiordland Crested Penguins.

In the Kittiwake, with the exception of some of the oldest birds, it is the males which normally hold the nest site and so there may be a selective pressure on these birds to return earlier to the colony. The fact that, on average, females tend to mate with males younger than themselves (Chapter 3) suggests that there may be a degree of synchrony in the date of return of the two members of the pair, which is not evident here.

2.2.3 Date of Return and Nest Site Location

Data presented in Table 2.3 show that, on average, birds of both sexes which nest in the centre of the colony return approximately 5 days earlier than those which breed on the edge and that this difference is significant (Females : $t = 2.46$, $N = 1058$, $P < 0.02$; Males : $t = 2.30$, $N = 1044$, $P < 0.05$). The centre-edge effect is most marked amongst first breeders and in females breeding for the second time, where it is significant ($t = 2.66$, $N = 165$, $P < 0.02$). In all other age groups, the difference between date of return to the centre and edge is less than four days and in one (birds with a breeding age of 5-7 years) the overall trend is actually reversed. The synchrony of return amongst birds of the same age (as measured by the standard deviation) tends to be greater amongst those nesting in the centre, although in all cases differences are small.

Table 2.3 : Date of Return to the Colony of Males and Females in relation to Breeding Age and Nest Site Location

Mean Date of Return

Breeding Age (years)	Females			Males		
	Edge	Centre	E-C*	Edge	Centre	E-C*
1	87.6	79.5	8.1	81.9	72.5	9.4
2	74.4	61.9	12.5**	66.1	64.7	1.4
3-4	63.7	60.4	3.3	58.7	56.5	2.2
5-7	47.7	51.6	-3.9	47.8	50.4	-2.6
8-19	41.0	38.1	2.9	36.7	34.5	2.2
All Birds	58.9	53.7	5.2**	58.2	53.4	4.8**

Standard Deviation and Sample Sizes

1	29.0 (42)	29.7 (44)	33.1 (61)	30.6 (64)
2	32.1 (92)	28.1 (73)	33.7 (88)	30.4 (99)
3-4	32.7 (127)	31.4 (147)	31.1 (144)	29.0 (156)
5-7	31.4 (125)	32.0 (151)	33.7 (99)	32.2 (154)
8-19	33.0 (104)	31.4 (153)	26.7 (55)	27.0 (124)
All Birds	35.2 (490)	33.1 (568)	34.4 (447)	32.1 (597)

* E-C : Difference between date of return of birds of the same age nesting in centre and edge of the colony.

** Indicates that the difference is significant at the 5% level.

Coulson (1968) suggested that there was greater competition for central nest sites in the colony at North Shields. This would be expected to increase the selective pressure on all birds, but in particular first breeders (which have no nest site from the previous year) to return earlier to this part of the colony. In addition, this may also lead to more synchronised return in the centre, although any difference in synchrony of return to the two parts of the colony may also be explained in terms of the lower divorce rate found amongst central nesting birds (Coulson 1972) since divorce is often associated with the asynchronous return of the two members of the pair (see below).

Differences in the date of re-occupation of the centre and edge of a colony has also been reported in the Gannet (Nelson 1978) although it might also be expected in other colonial species where the age structure of birds breeding in each part differs, for example, the Shag (Coulson 1971).

2.2.4 Date of Return and Pair Status

The change in date of return of the same individual in consecutive years is shown in Table 2.4, data being first separated according to whether the bird had retained the same mate as in the previous breeding season, or changed, either through divorce or as a result of the death of the old mate. (This method removes any effect of age or nest site location, without the loss of sample size.) On average, birds which retain the same mate return to the colony 9-10 days earlier in the present year than in the last. A similar change is found amongst both males and females which divorce. Females whose mates have died since the previous breeding season do not show such a marked difference. However, in the corresponding group of males, the reverse is true.

Although there is no significant difference between the three means for each sex, the data suggest that females whose mates have died

Table 2.4 : The Difference in Date of Return of the same Individual between the Present Year and the Last in relation to Pair Status

	Females			Males		
	Same Mate	Change Mate		Same Mate	Change Mate	
		Death	Divorce		Death	Divorce
Mean Difference (days)	+10.5	+4.6	+9.0	+9.1	+15.1	+10.8
N	415	92	121	390	80	101
S.D.	25.7	27.7	30.1	26.3	25.7	22.3

Difference in Date of Return = (Date of Return Last Year - Date of Return This Year) may be returning later in the present year than corresponding groups of birds which have divorced or retained the same mate. Since it seems unlikely that an individual female would know that its mate had died, unless the two birds overwintered together, I would suggest that this result reflects a difference in the behaviour of birds upon their return. Upon arrival at the colony the birds either re-occupy their old nest site or, usually as a result of change of mate, move to a new site (Section 3.5.1). Male Kittiwakes normally retain the nest site but once the pair is formed, the female will aid in its defence. Old pairs and males will then show greater site tenacity than unattached females. At this time of the year, when birds are easily disturbed, it is less likely therefore that these females would be seen on any particular visit.

2.2.5 Between Year Variation in Date of Return to the Colony

With the exception of only one year (1969)[**], the mean date of return of all birds breeding at North Shields has advanced progressively since the mid-1950s (Figure 2.1). This change corresponds to the progressively earlier return of the first birds to arrive back, reported by Wooller (1973). Changes in the size and age structure of the population over the same period have been discussed in the previous chapter. The number of breeding birds in the colony increased to a peak in 1967, since when there has been a slow but continuous decline to date. This decline has not, however, affected the date of return of the birds, which has continued to advance. Although the mean breeding age of birds reached a peak in 1969, since when it has remained fairly constant, there is a

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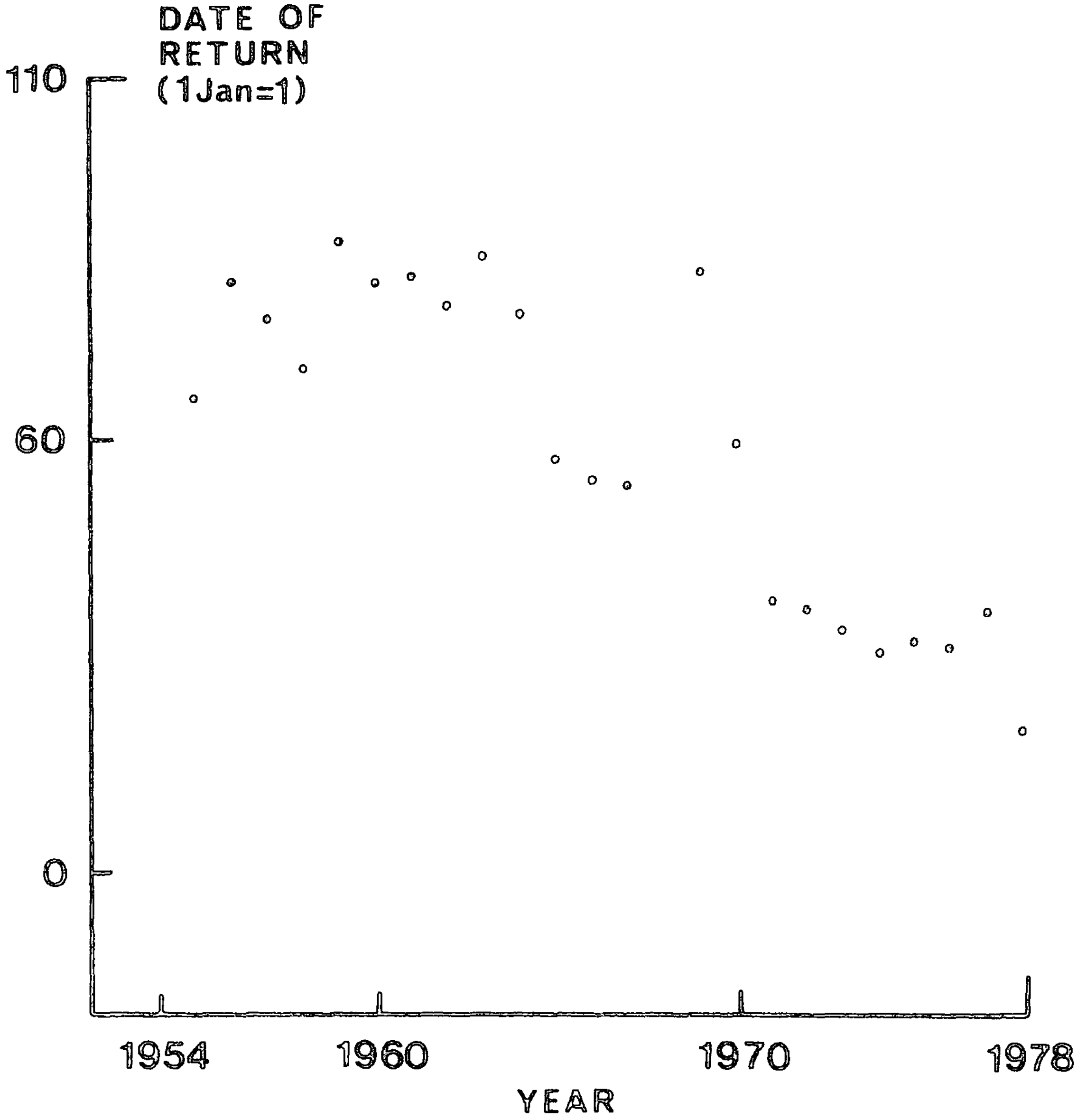
[**] 1969 was also a year in which laying was unusually late at North Shields. The possible reasons for this are discussed in Section 4.5, Chapter 4.

Figure 2.1 : Annual variations in the mean date of re-occupation of the colony. The mean date of return of the breeding population has advanced significantly over the period of this study (Slope = -2.61 ± 0.34, $r = -0.86$, $p < 0.001$)



significant correlation between the mean date of return of each sex in each year and the mean breeding age of the birds (Table 2.5). Multivariate analysis, the results of which are also shown in Table 2.5, has shown that age is the only factor to have a significant or independent effect upon date of return of the population as a whole.

These data show that size itself does not affect the date of re-occupation of the colony, as would be implied from Darling (1938) and in fact, birds are now returning to North Shields at the same time as in some of the larger colonies at nearby Marsden, many of which contain over ten times the number of birds. The concept of nest density, which has also been shown to affect time of breeding in the Gannet (Nelson 1967) and the Kittiwake (Coulson and White 1960), is hard to apply to the colony at North Shields, since nests are fairly evenly spaced throughout. Wooller (1973) found a correlation between the percentage of window-ledges with two nests and the total number of breeding birds in the colony. However, the data show that even this gross measure of density has no effect. The changing age structure of the population does influence this aspect of the breeding biology of the birds however, as was suggested by Coulson and White (1956).

2.3 Relative Date of Return of the Members of the Pair

2.3.1 Pair Status and the Difference in Date of Return between the Two Members of the Pair

Table 2.6, part 1, shows the mean difference in date of return between members of pairs in relation to whether the pair was newly formed in the present year or whether the same mate had been retained from the previous breeding season. In addition, a corresponding value is given for pairs from the previous year which return to the colony, but divorce.

Table 2.5 : Multivariate Analysis - Annual Variations in Date of Return to the Colony

Males

Correlation Matrix

	Colony Size	Male Age	Return Date
Colony Size	-	0.75*	-0.37
Male Age		-	-0.65
Return Date			-

N = 23 *Correlation significant at 1% level

Regression Model

Date of Return = -13.7 (Male Breeding Age) + 110.9

S.E. Slope = ±3.50, $P < 0.001$

Females

Correlation Matrix

	Colony Size	Female Age	Return Date
Colony Size	-	0.75*	-0.32
Female Age	-	-	-0.65
Return Date			-

N = 23 *Correlation significant at 1% level

Regression Model

Date of Return = -13.0 (Female Breeding Age) + 117.0

S.E. Slope = ±3.24, $P < 0.001$

(For each variable, data used in analysis are mean values for each year)

Table 2.6 : Relative Date of Return of the Two Members of the Pair in relation to Pair Status

1. Difference in Date of Return between Members of the Pair (Days)

	Same Pair	New Pair	Divorcing Pair
Mean	12.6	16.6	23.9
N	493	226	119
S.D.	15.9	19.1	21.6

2. Order of Return within the Pair

	Same Pair	New Pair	Divorcing Pair
Male Returns First	26%	35%	50%
Female Returns First	35%	34%	33%
Pair* Returns Together	39%	31%	17%
Sample Sizes	493	226	119

* Members of the pair first seen in the colony within 4 days of each other (see text).

The data clearly show that pairs retaining the same mate return to the colony with a higher degree of synchrony than pairs to be formed in the present season and that divorce is associated with asynchrony of return. The spread of values about each mean, as measured by the standard deviation, also reflect the degree of synchrony. These values follow the same trend as that of the means. All three means are significantly different from each other.

2.3.2 Pair Status and Order of Return

The size of the standard deviations associated with each mean in Table 2.6, part 1, indicate that the members of some pairs return to the colony at the same time irrespective of the status of the pair. In addition, data presented in this table do not reflect the order of return of males and females in the pair although it has been shown to be of importance in the maintenance of the pair bond in Adélie Penguins (LeResche and Sladen 1970). In Table 2.6, part 2, the percentage of pairs in which either the male or female returns to the colony first, or in which the two birds return together (i.e. within 4 days of each other[**]) is shown in relation to the status of the pair.

The proportion of pairs in which the two individuals return at the same time is greatest amongst birds which have bred together previously and retained the same mates. Even amongst pairs formed in the present year, however, 31% contained birds which were first seen in the colony either on the same, or on consecutive visits, suggesting that the pair is first formed,

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[**] During the period when the birds were returning, visits were made to the colony every 3-4 days. If a pair had returned together, but one of the partners had been missed on the first visit, there was a chance that it would be seen on the next.

or re-formed, either before the birds arrive back at the colony, or soon after their return. LeResche and Sladen (1970) suggested that it is within the first few days after returning that the pair bond is 'strengthened' in Adélie Penguins, although comparative data are not available for the Kittiwake. In divorcing pairs, 17% return to the colony at the same time, showing that not all divorce can be accounted for in terms of asynchrony of return.

Amongst pairs formed in previous years which stay together, a higher proportion of females return to the colony before their mates. This reflects the fact that, on average, females tend to mate with males which are younger than themselves owing to the differential mortality rates between the sexes (Coulson and Wooller 1976). There is no difference between the percentage of males and females which return first in newly-formed pairs, but males tend to return to the colony before females amongst pairs which divorce.

Spurr (1975) stated that in Adélie Penguins the female returned to the colony before the male in only 3% of pairs, and LeResche and Sladen (1970) found that in all cases where pairs were reunited it was the male which returned first, whereas in all cases where the female returned first, divorce followed. They suggested that this was because females rarely remained alone at the nest site but paired as soon as they arrived, whilst males often occupied a territory for a long period before pairing. The same cannot be true of the Kittiwake since amongst divorcing birds there was an increase in the percentage of pairs in which males returned first.

Without knowing more about the methods of mate selection in the Kittiwake, which would require a behavioural study, it would be inappropriate to make further comments upon these results, although it is evident that this bird differs from the Adélie Penguin in that order of return of the two members of the pair is of less importance to the stability of the pair bond.

2.3.3 Relative Breeding Ages of the Members of the Pair and Difference in Date of Return to the Colony

The difference in the breeding ages of the two members of the pair may have a marked effect upon the relative date of return of the birds. It has been shown that birds return progressively earlier as they get older and that within a particular age group, on average, males return to the colony before females. This would suggest that pairs containing birds of a similar age may return with a greater degree of synchrony than pairs of birds with widely differing breeding ages. In addition, in this latter group, a combination of young males and old females should show greater synchrony than old males paired with young females.

Data presented in this form are shown in Table 2.7 (young birds being defined as those with a breeding age of between 2 and 5 years and old birds, those with a breeding age of over 5 years) and have been arranged to show the effect of pair status upon the relationship. The only group which conforms to the expected pattern discussed above is that of pairs newly formed in the present year, the greatest synchrony being shown by pairs of old birds. (The standard deviations about each mean also conform to the trends expected.)

Amongst pairs formed in earlier years, which stay together, there is greater synchrony in each of the four age groups than in corresponding groups of newly-formed and divorcing pairs. (The difference in the synchrony of return of the two members of the pair in relation to pair status, which is shown in Table 2.6, part 1, is clearly not, therefore, a function of the relative breeding ages of the birds.) In addition, there is little difference between each of the four age groups in these birds, showing that the relative ages of the members of the pair do not affect synchrony of return to such an extent, although pairs of old birds which stay together do return with a significantly greater degree of synchrony than pairs of young birds ($t = 2.13$, d.f. = 366, $p < 0.05$).

Table 2.7 : The Difference in Date of Return between the Members of a Pair in relation to Pair Status and the Breeding Ages of the Two Birds

	Same Pairs		New Pairs		Divorcing Pairs	
Male Age	Young	Old	Young	Old	Young	Old
Female Age	Mean Difference in Date of Return (days)					
Young	14.2	12.9	17.5	23.3	26.7	21.0
Old	12.3	10.7	14.8	11.5	17.5	23.1
	S.D. and Sample Sizes					
Young	16.3 (208)	18.1 (39)	17.2 (74)	23.8 (34)	23.0 (61)	22.9 (20)
Old	15.5 (85)	15.1 (160)	20.4 (54)	13.2 (24)	18.1 (21)	17.2 (15)

Young male or female is a bird with a breeding age of 2-5 years

Old male or female is a bird with a breeding age of 6-19 years

2.3.4 Date of Return and Divorce

Asynchrony of return to the colony between the two members of the pair has been suggested as a factor which may result in divorce although 17% of pairs which undergo divorce contain birds which return to the colony at the same time. Observations have shown that in some pairs which return together and later divorce, one or both birds disappear for a period of time after the first sighting.

In Table 2.8 the difference in the date of return of the two members of the pair has been calculated from the date on which the birds were first seen in the colony and also from their second sighting. These data are presented for birds which retain the same mate and those which divorce. There is no difference in the degree of asynchrony of return, calculated from the first and second sightings of birds which retain the same mate. Amongst birds which divorce, however, the difference in date of return between the two members of the pair is greater when calculated from the second sighting than it is for the first. This result, although not significant, does suggest that the disappearance of one member of the pair shortly after its return may be another factor which could result in the break-up of the pair bond. This finding may reflect a lower drive in one member of the pair to remain at the site or with the old mate, or could result from the behaviour of a bird towards its former partner.

2.4 Discussion

At the end of the winter period Kittiwakes return from the sea and re-occupy their breeding colonies. The birds show both mate and site fidelity but in certain pairs a divorce or death may occur, resulting in one or both members of the pair taking a new mate and changing site. The first birds to arrive back at the colony have a choice of the

Table 2.8 : The Difference in Date of Return between the Members of Pairs which Stay Together and those which undergo Divorce. Calculated from the First and Second Sightings of the Birds

	Mean Difference in Date of Return (days)	
	First Sighting	Second Sighting
Birds retaining same mate	13	13
Birds undergoing divorce	24	27
	S.D. and Sample Sizes	
Birds retaining same mate	16 (493)	14 (445)
Birds undergoing divorce	22 (119)	26 (113)

First Sighting - Difference calculated from dates on which each bird was first seen at the colony.

Second Sighting - Difference calculated from the dates of the second occasion when each bird was seen.

available nest sites and since it is normally the male which retains the site, there may be a selective advantage for these birds to return first, as indeed they do, on average, within each age group. Older individuals return before younger birds and, on average, the centre of the colony, where competition is greatest (Coulson 1968), is re-occupied before the edge. In this situation, and since older birds change mate or site less frequently, the first arrivals back are often those birds returning to the same mates and sites as in the previous year. (Wooller 1973 stated that early arrivals show more site fidelity.) There is less confrontation, therefore, between these birds upon their arrival. It is only later that the younger birds and in particular, first breeders return, many of which are looking for new mates and nest sites amongst those which have not yet been taken. In this way young birds, which in general are less successful breeders, are not in direct competition for nest sites with older, more successful individuals. In a situation of a limited number of nest sites Wynne-Edwards (1962) suggested that this was a method by which colony size is limited. Having said this, however, in all years there has remained a number of nest sites in the colony which were unused throughout the breeding season.

Overall, the mean date of return of the entire colony has advanced progressively over the period of this study, reflecting in part changes in the age structure of the population. Over the past ten years, however, while the mean age of birds in the colony has remained relatively constant, date of return has continued to advance. It seems very unlikely that this results from any consistent change in an environmental stimulus and I can only suggest that there may be some aspect of the breeding season in the previous year which may have produced this result. The date on which birds leave the colony at the end of the breeding season has not been considered in this work. Any relationship between date of leaving and subsequent date of return may explain some of the variation found here.

Amongst pairs newly-formed in the present year the difference in date of return between the two birds is related to their relative breeding ages. In pairs of birds which survive from the previous breeding season, asynchrony of return is associated with divorce.

There are two aspects in the consideration of the time at which birds return to their breeding colony; one is the actual date of return of the individuals, and the other, the relative date of return of the two members of the pair. Multivariate analysis of all the factors studied (Tables 2.9 and 2.10) shows that breeding age is the only one to have a significant independent effect upon the date of return of males and females and suggests that divorce is the only factor associated with the difference in date of return between the members of a pair. In studies carried out by LeResche and Sladen (1970) on the Adélie Penguin, it was suggested that early return of birds was essential for the securing of nest sites, while synchrony of return within the pair was essential to the maintenance of the pair bond. It would appear that similar factors operate in the Kittiwake although, as discussed earlier, certain differences exist between the two species with respect to the importance of the order of return of males and females.

Table 2.9 : Multivariate Analysis - Factors associated with the Date of Return of Experienced Birds

Regression Models

Females : Date of Return = -41.4 (Lg. Breeding Age) + 80.3

$r = -0.33$, $N = 663$, $P < 0.001$

S.E. Slope = ±4.56, $P < 0.001$

Males : Date of Return = -44.4 (Lg. Breeding Age) + 80.1

$r = -0.38$, $N = 641$, $P < 0.001$

S.E. Slope = ±4.28, $P < 0.001$

Variables included in the Analysis

Date of Return to the Colony

Nest Site Location - 0 = edge 1 = centre

Success Last Year* - 0 = fledged 0 chicks last year

1 = fledged at least one chick last year

Same Mate or Divorce - 0 = divorce

1 = same mate

Log. Breeding Age of Bird

*It will be shown in the next chapter that pairs which fail to fledge any chicks in a particular season are more likely to undergo divorce before the next year than those which fledge at least one.

Table 2.10 : Multivariate Analysis - Factors associated with the Difference in Date of Return between Members of the Pair

Regression Model

Difference in Date of Return = -10.3 (Same Mate or Divorce) + 22.5

$r = -0.24$, $N = 566$, $P < 0.02$

S.E. Slope = ±1.77, $P < 0.001$

Variables included in the Analysis

Difference in Date of Return between Members of the Pair (days)

Difference in Breeding Age between Members of the Pair :

female breeding age - male breeding age

Success Last Year :	0 = fledged no chicks
	1 = fledged at least one chick
Same Mate or Divorce :	0 = divorce
	1 = same mate

CHAPTER 3 : THE PAIR BOND

3.1 Introduction

For any monogamous species of bird in which both sexes are involved with incubation and chick rearing it is evident that:

1. A degree of co-operation is necessary between the two members of the pair.
2. The breeding activities of the two birds must be synchronised to facilitate this co-operation.

Coulson (1966, 1972) has shown that Kittiwakes forming a pair for the first time in the present year breed later and less successfully than pairs formed in previous years. Similar results have been found in other species: Adélie Penguins (LeResche and Sladen 1970, Penney 1968); Red-billed Gulls (Mills 1973); Ring Doves (Erickson and Morris 1972) and Yellow-eyed Penguins (Richdale 1957). Austin (1945), working with Common Terns found pairs retaining the same nest site or territory from one season to the next to be more successful. However, several workers have shown a close correlation between nest site and mate fidelity, a point which is discussed further.

Change of mate occurs for one of two reasons in the Kittiwake. Firstly, if one member of the pair returns to breed and the other is assumed to have died (DEATH) and secondly, if both birds return to the colony but breed with new mates (DIVORCE).

Despite the initial setback to breeding which is associated with change of mate it has been suggested that, in the long run, a method by which 'incompatible' pairs can be split up may be advantageous to the future breeding of the members of those pairs.

In a long-lived bird such as the Kittiwake the status of the pair bond may have a significant effect upon the breeding of the birds. It is, therefore, important that the factors associated with the duration of the pair be investigated and linked to the relationship between date of return to the colony and divorce, which was outlined in the previous chapter.

3.2 Duration of the Pair Bond

One pair of birds at North Shields has remained together for a total of 14 consecutive breeding seasons. However, the data presented in Figure 3.1 (which shows the duration of all pairs formed before 1969) indicate that over 50% of pairs remain together for only one year. The proportion of birds which retain the same mate from one year to the next increases with the age of the pair bond (see Appendix 3.1). This result would initially suggest that the association between two individuals over a number of years may enhance the probability that the two birds breed together in the future, although it is necessary to investigate the factors which are associated with age, such as mortality and divorce rate, before this effect can be looked at.

In several different species the pair bond has been found to last for a number of years; these include the Gannet (Nelson 1978), the Red-billed Gull (Mills 1973) and the Yellow-eyed Penguin (Richdale 1957).

3.3 Breeding Age of Members of the Pair

Table 3.1 shows the breeding ages of all males and females forming pairs at North Shields. There is a wide range of differences between the breeding ages of partners. However, there is a strong tendency for birds to mate with a partner of a similar breeding age,

Figure 3.1 : The duration of the pair bond

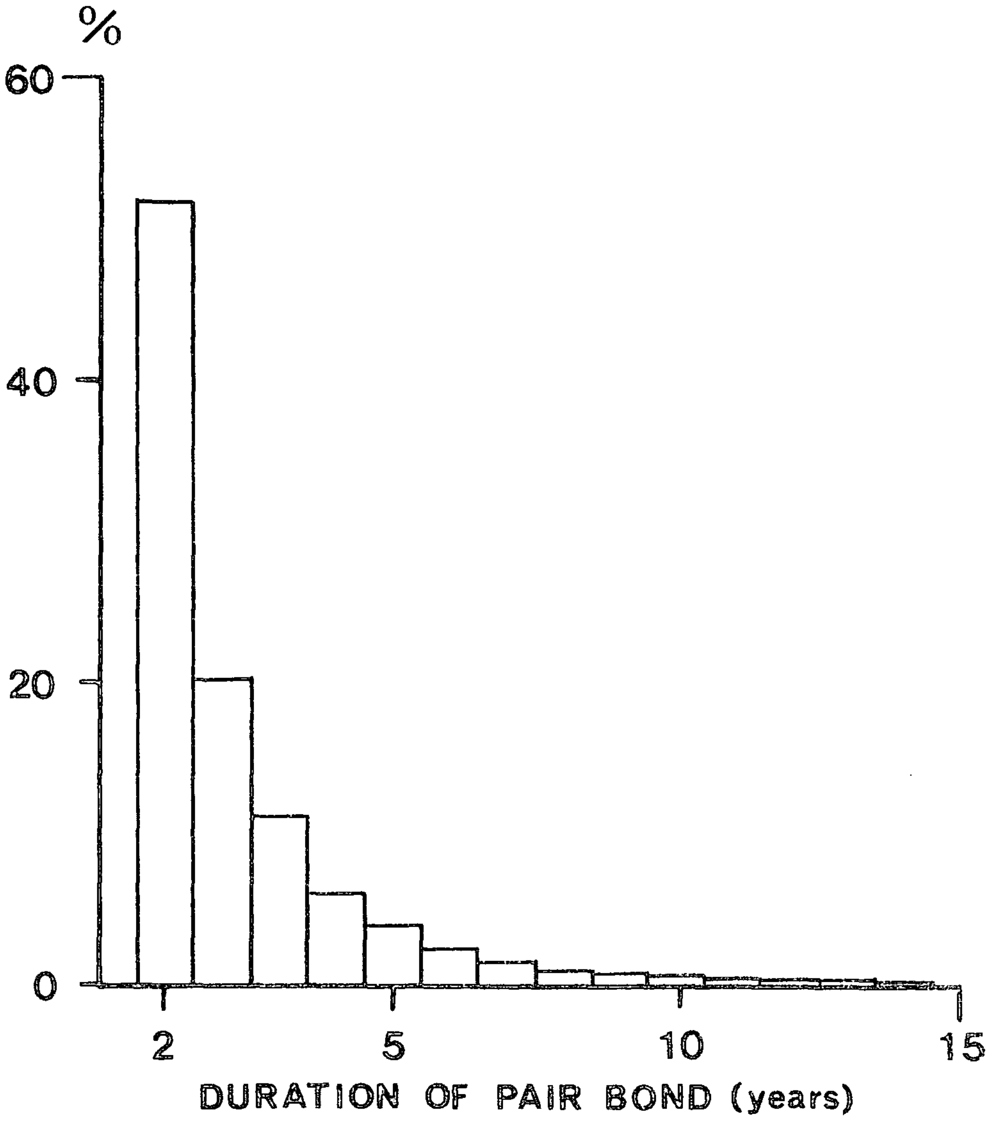


TABLE 3.1 : The Frequency of Occurrence of All Pairs, grouped according to the Breeding Ages of the Male and Female Birds

Age male																			
18					1														
17				1															
16	1		1																
15	1	1							1						1				
14	1							1	1			1	1	1					
13						1	3	2		1	1	2	1		1				
12		1				2	3	1	1	1	2	2	1	2					
11	2		2	1	3		1	3	1	2	2	2	2		1	2			
10	1	2	1	4		2	5	1	4	7	2	3		1	4				
9	2	2	2	2	2	7	2	6	9	2	3		2	4		1	1		
8	2	2	3	4	8	2	9	11	1	5		2	2		1	1			
7	3	4	4	7	6	13	17	5	4	2	4	4	3	1	1				
6	6	5	8	10	17	20	6	5	3	7	3	4	1	1	1				
5	11	13	13	17	23	13	8	3	7	2	4	1	4	1	1				
4	17	19	26	37	15	11	6	10	4	5	2	3	1	1				1	
3	25	27	55	20	15	11	13	8	8	6	6	3	1		1		2		
2	45	74	32	19	16	15	6	5	6	2	3	2	1	1		1	1		
1	191	44	28	21	20	7	6	11	2	3	3		1	3		2		1	
Age female	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19

as shown in Figure 3.2. A similar association has been found in the Red-billed Gull and in the Arctic Tern (Mills 1973, Coulson and Horobin 1976). Coulson (1966) produced the same data as shown in Table 3.1, incorporating all the pairs which had been formed up to that time. He found that 52% of pairs were formed between birds of exactly the same breeding age and that 72% contained birds whose ages differed by a maximum of one year. The corresponding values obtained from Table 3.1 are 30% and 51% respectively. Even amongst female first breeders the proportion nesting with a male breeding for the first time has dropped from 80% to 62%, indicating that the stability of the pair bond and/or the age structure of the breeding population may have changed since 1966. Table 3.2 shows the relative breeding ages of members of pairs during the year in which the pair was formed. This removes any effect caused by the inclusion of several sets of data for the same pair, for each year in which they bred together. The overall pattern which emerges from this table is different from that found in Table 3.1, since older birds especially are seen to be taking new partners which are much younger than themselves. The mean breeding age of new mates taken by males and females of a particular breeding age is given in Figure 3.3. The results show that as birds get older, the difference in age between themselves and their new mate increases. The effect is such that in the oldest breeding age groups, birds are taking new partners which, on average, are younger than those taken by some less experienced birds, the results being more marked amongst females. The data available to Coulson in 1966 did not show this effect so clearly and he only noted the tendency of older females to take younger partners when changing mate. Coulson (1966) explained these results in terms of differences between the sexes in the number of new birds entering the colony, whilst Mills (1973), who found similar results in Red-billed Gulls, was able to attribute the differences to

Figure 3.2 : Difference in breeding age between the two members of the pair (female age - male age)

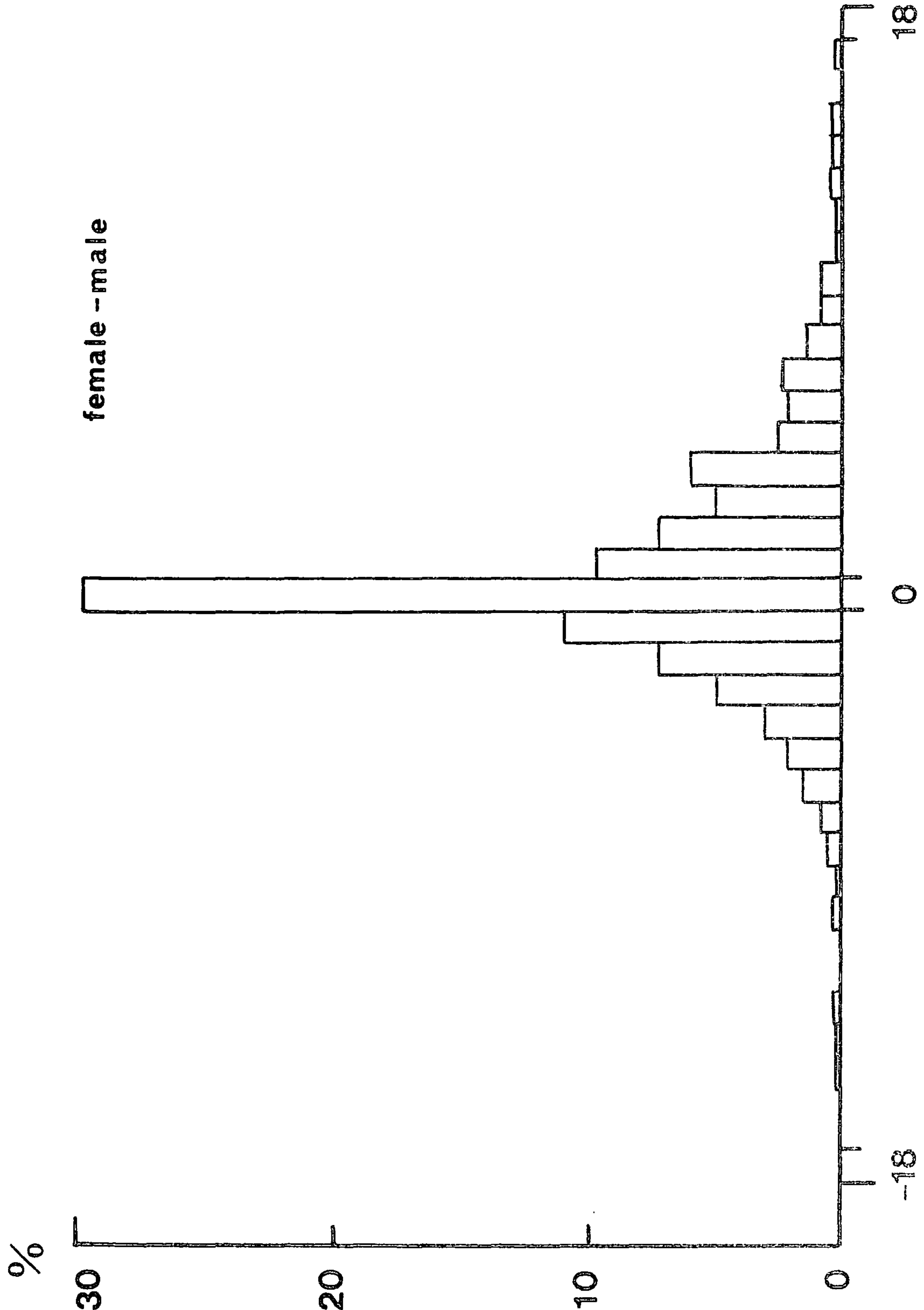
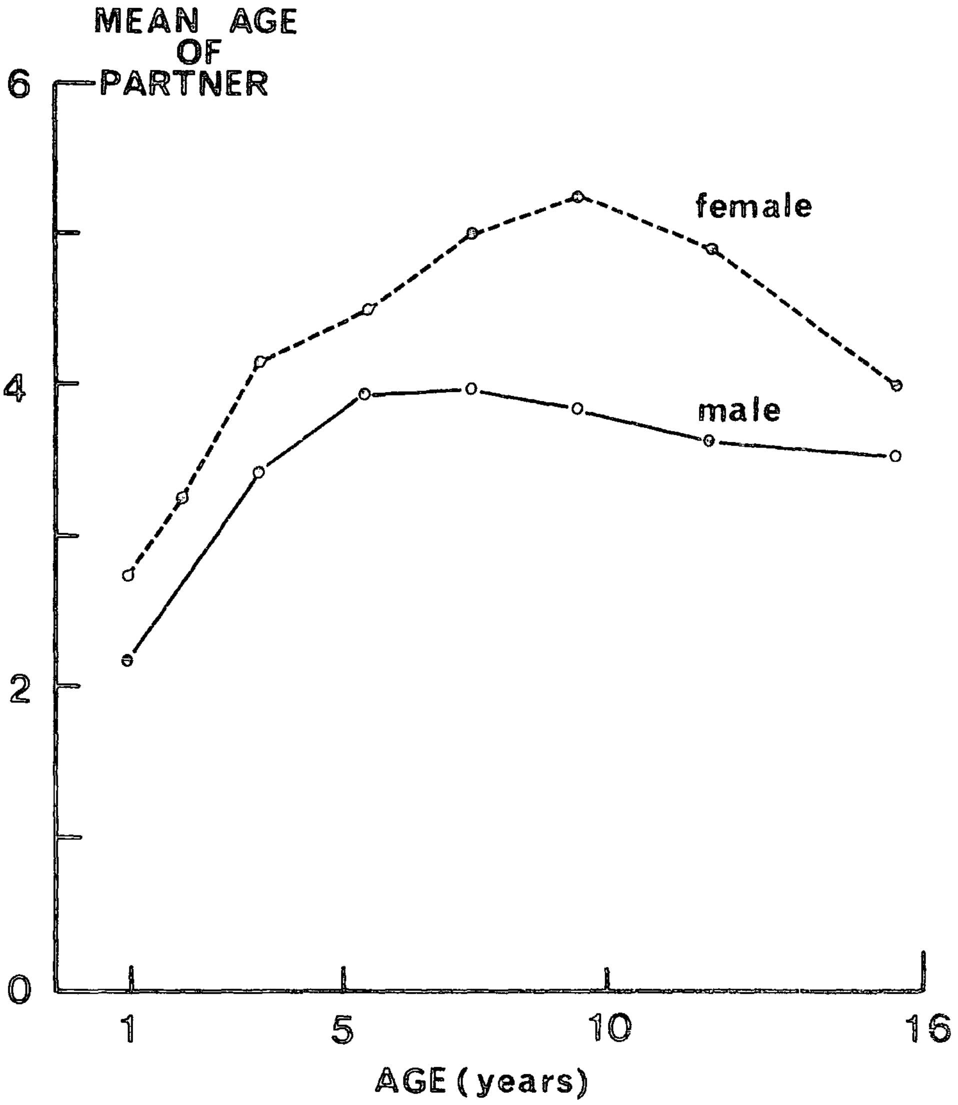


TABLE 3.2 : The Frequency of Occurrence of Newly Formed Pairs, grouped according to the Breeding Ages of the Male and Female Birds

Age male																			
16	1																		
15	1																		
14	1																		
13						1	1	1											
12		1				1	3												
11	2		1	1	1														
10	1	1		4		1	1								1				
9	2	2		1		1			2					1					
8	2	1	2	4	4	2	1			1						1			
7	3	3	4	4	2	7	2	2				1	1						
6	6	3	3	5	6	4		1	2	2		1							
5	11	7	7	6	3	4	5	2	2			1	1		1				
4	17	13	13	7	3	6	3	4	1		2	1	1	1					
3	25	7	16	8	6	4	6	4	5	2	3	2					1		
2	45	23	13	8	6	10	4	4	1	2		1	1			1			
1	191	44	28	21	20	7	6	11	2	3	3		1	3		2		1	
Age female	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19

Figure 3.3 : The mean breeding age of new partners taken by birds of differing ages following change of mate



a higher survival rate amongst females. In the previous chapter it was shown that birds of a particular age group return to the colony at a similar time at the start of the breeding season. This would explain why many pairs are formed between birds of a similar breeding age, especially if, as has been suggested, the pair bond is formed soon after the birds' arrival. Wooller and Coulson (1977) have confirmed that, on average, male Kittiwakes breed for the first time at a younger age than females. They have also shown (Coulson and Wooller 1976) that the survival of Kittiwakes declines with age and that within a particular age group males have a higher mortality than females. These results explain why, for birds of both sexes, the difference in age between an individual which changes mate and its new partner,increases with the age of the bird. In addition, they explain why this effect is more marked amongst females.

Table 3.3 shows the source of new partners taken by birds which change mate. Males and females both take similar proportions of new mates from birds which missed breeding in the previous year or which had divorced their old mates. Differences between the sexes are apparent in the relative proportions of birds which had not bred before and birds whose mates have died since the previous breeding season. The differences reflect the different mortality rates and rates of recruitment between the sexes outlined above.

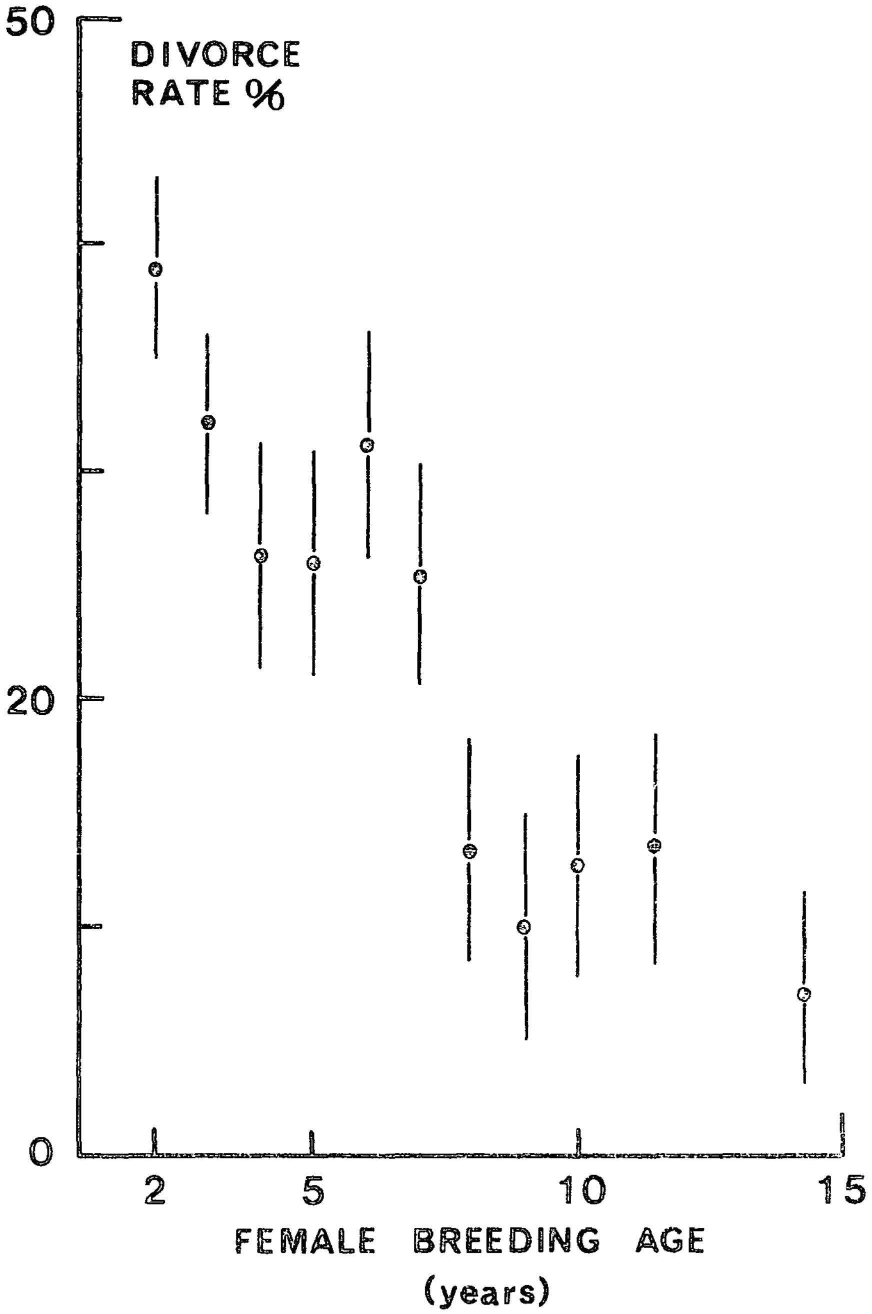
3.4 Factors affecting the duration of the Pair Bond

Figure 3.4 shows that the divorce rate amongst pairs surviving from one year to the next declines with increasing female breeding age. The same relationship exists for males also, since there is a close correlation between the breeding ages of the two members of the pair. The overall trend is progressive; however, there is a suggestion of a 'step' in the divorce rate between birds breeding for seven and eight years.

TABLE 3.3 : The Sources of a New Mate for Male and Female Kittiwakes which have already bred

New Mate	Male	Female
Bird which has not bred before	25%	37%
Bird which missed breeding last year	12%	13%
Bird whose previous mate had died	22%	12%
Bird which has divorced previous mate	41%	39%
Total Sample	358	300

Figure 3.4 : The relationship between the divorce rate (± 1 S.E.) of pairs surviving from one year to the next and female breeding age (years)



Since both survival and divorce decrease with age, it is likely that the cause of the break-up of the pair bond may change as birds get older. Figure 3.5 shows this relationship clearly; as birds get older the pair bond becomes more likely to be broken up by the death of a mate than through divorce.

Very few long-term studies have been made on other species which would provide comparable data. Mills (1973) noted that in Red-billed Gulls a higher proportion of older birds retained the same mate than did young birds, a similar situation to that found in Adélie Penguins (Richdale 1957, LeResche and Sladen 1970) and in Common Terns (Austin 1945). In none of these studies, however, was it possible to separate the effects of mortality and divorce from the overall values for change of mate.

3.4.1 Length of the Existing Pair

Earlier it was suggested that the pair bond may be 'self-prolonging', i.e. the longer the pair remains together, the greater the probability that it will do so in the future. In Table 3.4 the data have been arranged to show the relationship between female breeding age, age of pair bond and the probability that the pair will undergo divorce before the next year. Ignoring the relationship between age and divorce, which has been discussed above, the results show that within a particular age group, pairs which were formed in the present year are more likely to split up through divorce than pairs which were formed earlier. This relationship becomes more marked in older birds where, amongst females with a breeding age of more than ten years, divorce has not occurred in any of the pairs which were formed before the present year. In nearly all age groups, pairs which were formed more than one year ago are even less likely to undergo divorce than pairs formed last year. On average, the stability of the pair bond is therefore enhanced by the prior association of the two birds.

Figure 3.5 : The percentage of females which change mate either as a result of 'divorce' or as a result of the death of last year's partner (mortality) in relation to breeding age

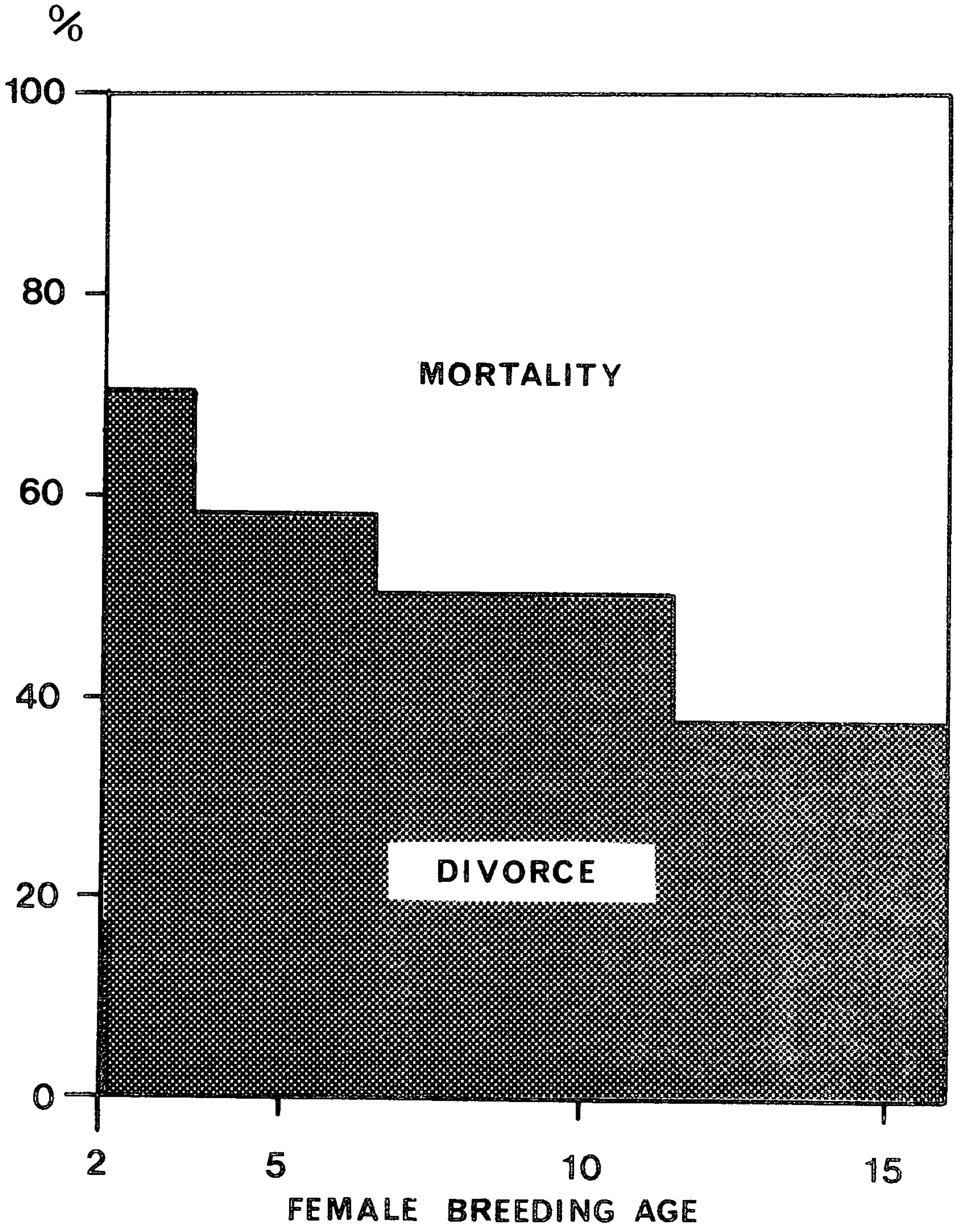


TABLE 3.4 : Probability of a Pair Undergoing Divorce before Next Year in relation to Female Breeding Age and the Age of the Pair Bond

Probability of divorce next year

Pair first formed	Female breeding age now (years) 1	2	3	4 and 5	6 and 7	8 to 11	12 to 18
This year	0.39	0.41	0.43	0.30	0.32	0.21	0.25
Last year	-	0.23	0.33	0.33	0.23	0.07	0.00
Two or more years ago	-	-	0.11	0.24	0.09	0.10	0.00

Sample Sizes

Pair first formed							
This year	152	70	47	67	48	47	12
Last year	0	52	24	45	26	31	5
Two or more years ago	0	0	28	64	43	69	28

Stettner *et al*. (1971) suggested that the length of the pair bond relationship in Bobwhite Quail affected its duration, and Erickson (1976) showed the same for Ringed Turtle Doves. In these situations, however, the breeding cycle is much shorter than in the Kittiwake and the prior association may have only lasted for a short period.

3.4.2 Between Year Variations in Mortality Rates and Divorce

Coulson and Wooller (1976) have shown that mortality rates of Kittiwakes breeding at the North Shields colony vary from year to year and that there has been an overall decline in the survival of breeding adults over the period of study. 264 birds out of a total of 658 (40%) which changed mate took new partners from pairs which had divorced. Amongst males and females whose mates had died since the previous breeding season, 31-35% of pairs were formed with individuals which had divorced their mates. Although this in itself is not evidence that bereaved birds cause the break-up of surviving pairs, it does suggest that in years when mortality is high, the divorce rate may be high also. The correlation between the divorce and mortality rates for the years 1960 to 1978 is positive and significant ($r = 0.49$, $N = 19$, $P < 0.05$). The slope of the regression of annual adult mortality (x) on annual divorce rate (y), 0.84 ± 0.37, is significantly greater than zero ($P < 0.05$). This suggests that in years when mortality causes more change of mate, increased divorce reinforces this effect, even though in years of high mortality fewer pairs survive to undergo divorce.

3.4.3 Breeding Success and Pair Bond Stability

Coulson (1966) found that pairs of Kittiwakes which failed to fledge at least one chick in a particular breeding season were more likely to undergo divorce than successful pairs and similar results have been reported in other species including the Fulmar, the Red-billed Gull and the Skylark (Macdonald 1977, Mills 1973, Delius 1965).

In Table 3.5 (which shows the probability of a pair of birds which survive from one season to the next undergoing divorce in relation to the breeding success in that season) data have been broken down according to the breeding age of the female member of the pair. The results show a consistent though not significantly higher divorce rate amongst birds which fail to fledge at least one chick in all age groups except females breeding for at least the eighth year. This indicates that the association between success and subsequent divorce is not a function of the relationship between breeding age and both divorce rate and breeding success. Ignoring the relationship between divorce rate and breeding age, which was discussed earlier, it can be seen from the data presented that the difference in the probability of divorce between successful and unsuccessful pairs declines with increasing female breeding age, showing that amongst the oldest birds the stability of the pair bond is unaffected by success of breeding.

3.5 Factors associated with the Pair Bond

3.5.1 The Relationship between Site and Mate Fidelity

Many passerines as well as larid species have been found to remain faithful to the same nest site or territory from one breeding season to the next; for example: the Song Sparrow (Nice 1937); the Skylark (Delius 1965); the Common Tern (Austin 1949); the Fulmar (Macdonald 1977); the Herring Gull (Drost *et al.* 1961, Parsons 1971); the Kittiwake (Wooller 1973) and the Red-billed Gull (Mills 1973). Data have been presented to show that site fidelity increases amongst older birds (Austin 1949, Richdale 1957), that birds which retain the same site as in the previous season are more

TABLE 3.5 : The Probability of a Pair undergoing Divorce before Next Year in relation to Female Breeding Age and Breeding Success this Year

Probability of Divorce Next Year

Number of Chicks fledged this Year	Female Breeding Age this Year			
	1	2-3	4-7	8-19
a. None	0.49	0.34	0.29	0.11
b. At least one	0.36	0.29	0.25	0.11
Difference (a - b)	0.13	0.05	0.04	0.00

Sample Sizes

Number of Chicks fledged this Year	Female Breeding Age this Year			
	1	2-3	4-7	8-19
a. None	35	32	34	27
b. At least one	114	185	248	144

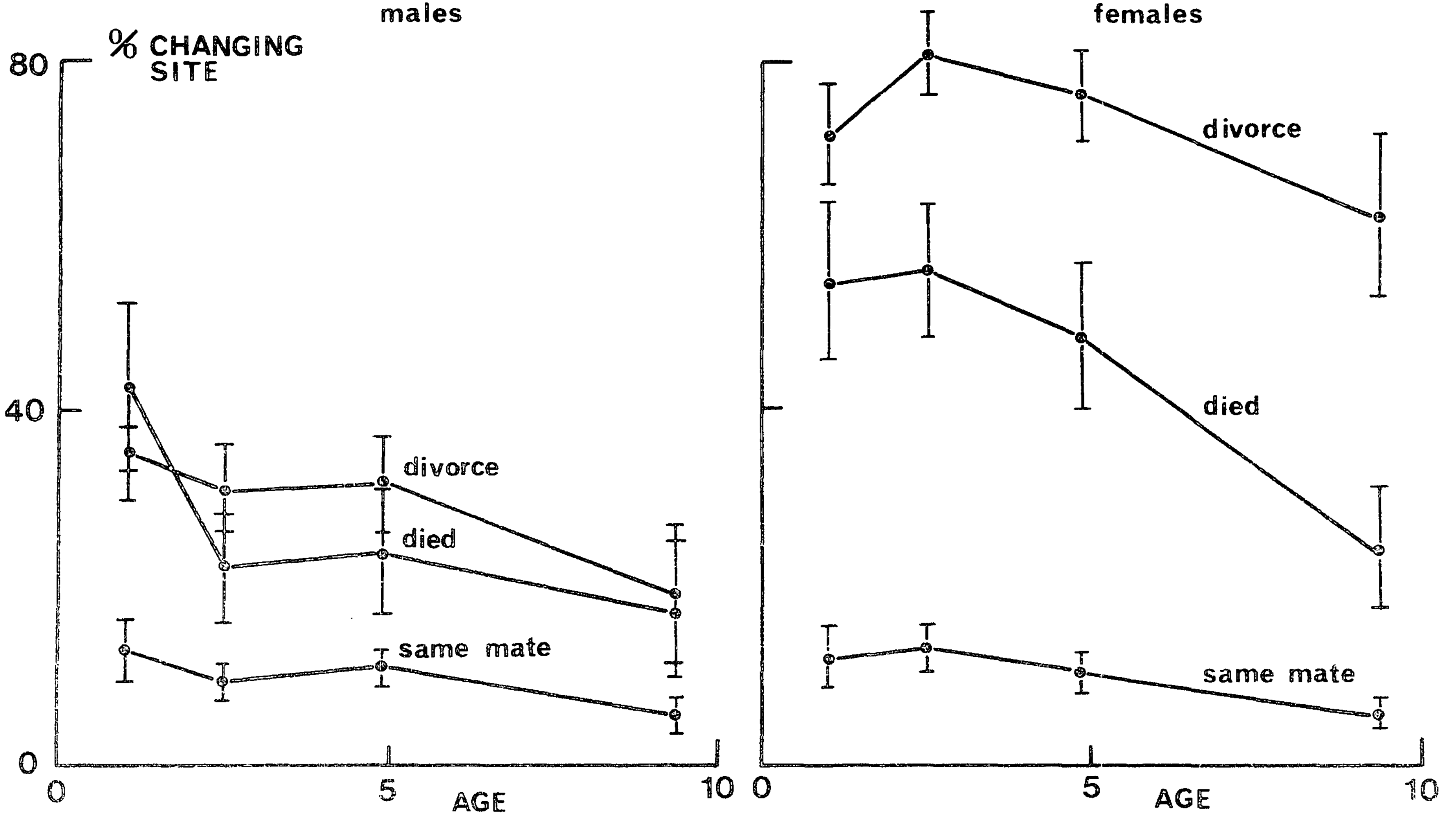
successful than those which change site (Austin 1945) and that following poor breeding a bird is more likely to move to a new site or territory (Darley *et al.* 1977, Nolan 1966, Richdale 1957, von Haartman 1949).

There are, then, similarities between the factors associated with the maintenance of the pair bond and the factors associated with nest site fidelity. Controversy exists as to whether nest site fidelity arises out of mate fidelity, or if pairs re-mate simply because they return to the same nest site year after year.

Figure 3.6 shows the relationship between breeding age, pair status and nest site fidelity. Only 10% of pairs which retain the same mate from one year to the next change site. On average, males which change mate are three times more likely to change site at the same time than pairs which stay together and in females this effect is even more marked (6 times). Females, whose mates die, move site significantly less often than females which divorce (46%, n = 142 : 75%, n = 224 : $X_1^2 = 32.1$, $P < 0.001$). In males too, a move is more likely in the year following a divorce, although here the difference is not significant. The differences between the sexes reflect the fact that it is the male Kittiwake which normally retains the nest site. Change of site is more frequent amongst birds which divorce since both members of the pair return and are able to try to retain the nest site whereas in pairs in which one member has died, the remaining bird only faces competition from other members of the colony which have not previously owned the site.

The effect of age upon the proportion of birds which change sites is more marked amongst females. The relationship in part reflects the difference in age between the members of the newly-formed pair, i.e. the oldest females are paired with males much younger than themselves. It is these old females which retain and defend the nest site in direct contrast to younger birds, amongst whom the male partner retains the nest site

Figure 3.6 : The percentage of birds changing site between one year and the next (± 1 S.E.) in relation to age, sex and the status of the pair bond


males
% CHANGING SITE
80
40
0
divorce
died
same mate
0
5
10
AGE
females
divorce
died
same mate
0
5
AGE
10

and both members of the pair defend it. Age has no significant effect upon the proportion of pairs retaining the same mate which move to a new site, although there is a slight tendency for older birds to move site less often.

The proportion of pairs which change site from one year to the next is related to sex, breeding age and pair status. A total of 61 birds which retained the same mate as in the previous year moved to a new nest site to breed. In 77 of the pairs in which divorce occurred, both birds moved to a new site. In all therefore, a total of 138 pairs of birds returned to the colony, but moved to new sites and out of these 44.2% retained the same mate as in the previous year. If, as has been suggested by some workers, the pair is re-formed because both birds returned to the old nest site, the proportion of birds which change site but retain the same mate would not be expected to differ significantly from that expected if the two birds moved to the same new site by chance. It is hard to estimate the average number of available nest sites to which the birds might move at the start of the breeding season. The probability of the two members of an old pair moving by chance to the same new site in a particular year is related to the probability of each leaving the old site in that year (X) divided by the total number of available sites (Y) squared, i.e. $P = X/Y^2$. If, for the sake of this discussion, the probability of both birds moving site in a particular year is 0.1, as suggested by the data, and the number of available nest sites is 10 (a value which must, of necessity, be an educated guess), then only one in every 1000 pairs would be expected to re-mate, by chance, following change of site. Without having a more accurate estimate of the number of available sites it can be seen that the proportion of pairs moving site which retain the same mate is significantly higher than that expected by chance. A figure of 0.44, as has been found in this study, could only arise if there were only one or two new sites to which the birds could move.

The results presented here do not imply that the nest site does not affect the maintenance of the pair bond but rather that it is not the primary reason why pairs of birds remain together in successive years. It has been shown in the previous chapter that pairs in which the two individuals return to the colony at widely differing times at the start of the breeding season are more likely to divorce. The nest site may be regarded as a focal point in the colony for a particular pair of birds, which ensures that they are brought into close proximity to each other soon after their return, thereby ensuring the re-formation of the pair bond. In a colony such as North Shields, which is small and where all the nests are widely spaced, this factor may not be as significant as in other larger colonies where nests are more closely packed.

3.6 Discussion

This study has investigated various factors associated with the duration of the pair bond amongst Kittiwakes breeding at North Shields. The majority of pairs are made up of individuals of a similar breeding experience. Older birds which change mate, however, tend to pair with younger partners, the difference in age between the members of the newly-formed pair increasing as the birds get older. The divorce rate of pairs and the survival rate of individuals decreases in older birds in such a way that mortality gradually replaces divorce as the major cause of the break-up of the pair. Within the colony as a whole in years of high mortality the divorce rate is high also, although the divorce rate of an individual pair is inversely related to its age. Divorce is more likely to occur in the year following unsuccessful breeding by a pair containing young birds, although the effect of breeding success upon the subsequent survival of the pair bond declines in older birds. It has been shown that in the Kittiwake site fidelity and mate fidelity are linked, site fidelity being associated with breeding age, sex and pair status. In the previous chapter a simple mechanism for divorce was proposed in terms of the relative date of return of the two members of the pair.

In the evolution of breeding systems the pair bond must have developed as a method of maximising an individual's reproductive output, whilst minimising the effort required to achieve this. LeResche and Sladen (1970), in a study of Adélie Penguins, point out the obvious savings in time and energy of not having to search for a new mate if the pair bond is retained from the previous breeding season.

Trillmich (1976a) found that individual Budgerigars show a high degree of variation in their behavioural patterns. In this study it was found that individual Kittiwakes tend to lay at a particular time in the breeding season (Section 4.3.1). Since it is necessary for the two members of the pair to adapt their behaviour and perhaps even modify their physiological rhythms in order to achieve successful breeding, the relationship between the two partners must be complex. This idea is strengthened by the fact that in various species of birds the two members of the pair have been shown to recognise one another as individuals, either through vocalisation (Wiley 1976, Wooller 1978) or through structural or behavioural differences (Macdonald 1977, Thorpe 1968) even after long periods of separation.

Behavioural and physiological changes would take a long time to develop and so there are obvious advantages in retaining the same mate from one breeding season to the next. Whilst the pair bond must be 'firm', allowing time for partners to adapt their own behaviour and learn to anticipate the behaviour of their mates (Trillmich 1976b), it must also be flexible, to allow the dissolution of 'incompatible' pairs. Younger birds especially, which fail to fledge at least one chick in a particular breeding season, have been shown to have a higher divorce rate than successful breeders, although amongst older individuals this effect disappears. Meanwhile, both unsuccessful breeding and divorce is more common amongst younger birds. LeResche and Sladen (1970) and Coulson and Wooller (in press) have suggested that younger birds are better able to adapt to their partners than older individuals. Because of this it can be envisaged how a strategy may have evolved whereby older, more successful birds which are less able to adapt their behaviour retain the same mate from one year to the next and therefore breed more successfully and with a lower 'energy cost'. Meanwhile, unsuccessful birds, and particularly young ones, are able to change mate with the chance of forming a new pair with a more 'compatible' partner.

The status of the pair bond can have a significant effect upon both the time of breeding and the subsequent success of individual pairs, and hence the colony as a whole. It has been shown here that the factors associated with the duration of the pair bond are complex, as is the very nature of the pair bond itself. Much more work is required into this aspect of the breeding biology of birds since over 90% of all birds are monogamous (Lack 1968) and in many species survival rates are such that both members of the pair will return to breed in consecutive seasons. In particular, more information is required about the behavioural mechanisms associated with the formation or re-formation of the pair bond, in order to explain the relationships found here, and by LeResche and Sladen (1970) and Penney (1968), between date of return to the colony and divorce.

CHAPTER 4 : DATE OF LAYING

4.1 Introduction

The onset of breeding, as measured by the date on which birds lay the first egg of the clutch, has received much attention in studies of avian biology. Like date of return, differences in the time of breeding between colonies have been explained in terms of the effects of social stimulation and colony size (Darling 1938) and the effect of the age structure of the different populations (Coulson and White 1960). A third theory, proposed by Orians (1961) following work carried out on Redwinged and Tricoloured Blackbirds, suggested that variations in the peak of laying observed in different populations of the same size resulted from geographical variation in the ecological factors associated with the nesting area.

Studies at North Shields by Coulson (1966) and Coulson and White (1958a) have shown that various parameters in the population affect the date of laying of individual birds, including breeding age and the stability of the pair bond, whilst studies at nearby cliff colonies of Kittiwakes enabled colonial differences to be examined. It is now possible to carry out a similar study within a single colony, thereby removing one possible source of variation, as envisaged by Orians (1961).

Coulson and White (1961) showed that date of laying had a significant effect upon clutch size in the Kittiwake, although they also found that certain females tended to lay the same number of eggs in different years. This would suggest that individual females may show a tendency to lay at a similar time in different breeding seasons, a trend which is also found in Yellow-eyed Penguins (Richdale 1957). Since much of the variation in clutch size observed by Coulson and White could be explained in terms of individual differences, it is hoped to attribute much of the unexplained variation in date of laying to this factor also.

Throughout this chapter, between year variations in the time of breeding are discussed with respect to the calendar date of laying, whilst within year variations and changes in the date of laying of individual females are discussed with respect to the 'relative date of laying'. The relative date of laying of a bird is the deviation (in days) of the laying date of that individual from the mean for the whole colony in the same year. (A positive relative laying date indicates that the bird has laid before the mean.)

4.2 Within Year Variations in the Time of Breeding

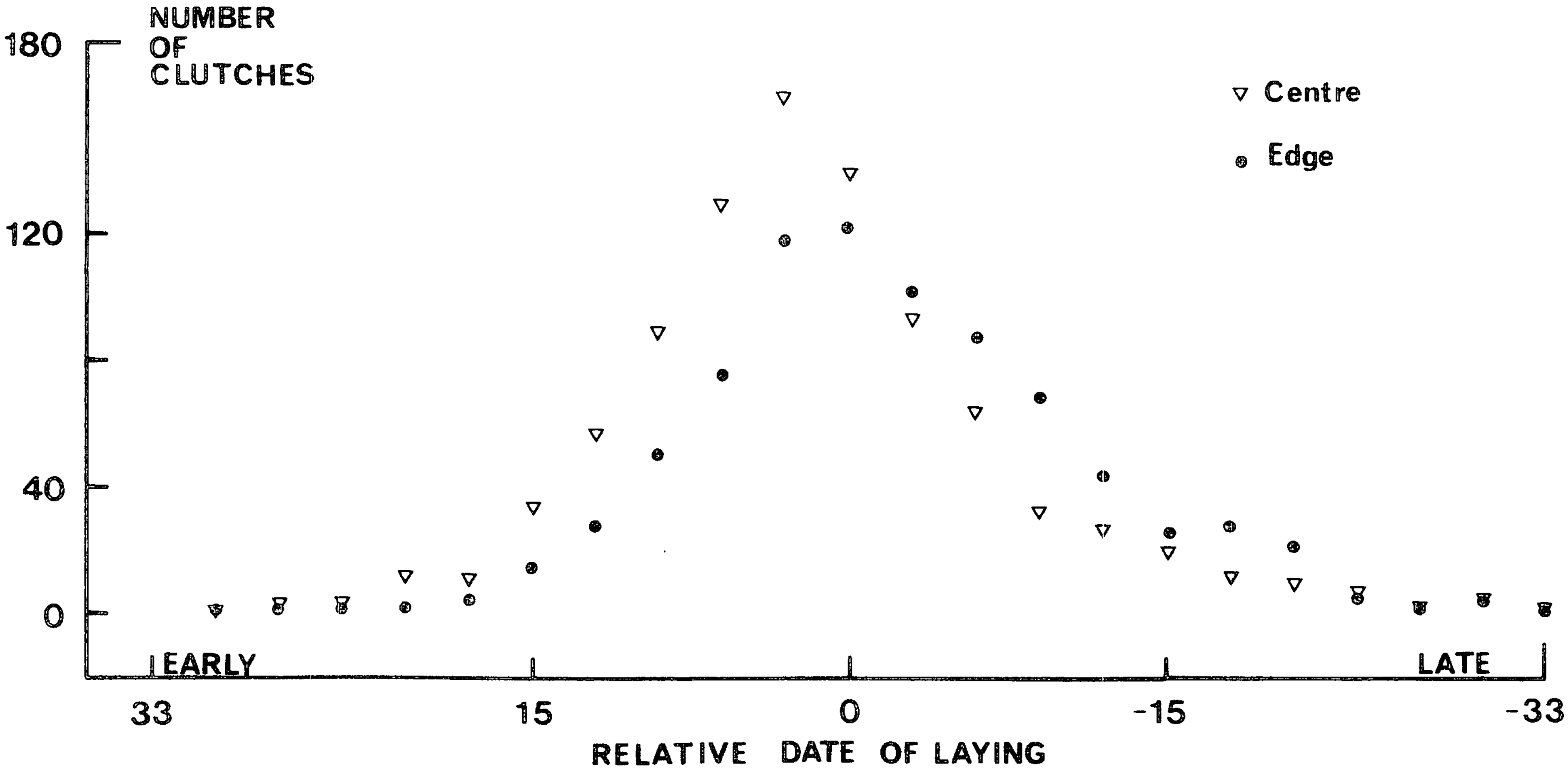
4.2.1 Pattern of Egg Laying

The pattern of egg laying of all birds which have bred at North Shields since 1954, for which date are available, is shown in Figure 4.1. (Separate lines have been drawn for birds nesting in the centre and on the edge of the colony.) In the Kittiwake, as in most other colonial nesting species, e.g. the Black-headed Gull (Patterson 1965), the California Gull (Vermeer 1970), the Herring Gull (Parsons 1975a), the Ring-billed Gull (Ryder 1975) and the Shag (Potts 1966), the pattern of laying approximates to a normal distribution. At North Shields this has a slight positive skew of 0.4 days, indicating that, on average, more clutches are started after the mean date of laying for the colony. During the 25 years in which laying dates have been recorded for all breeding birds, the earliest egg was produced on 18 April, whilst the last was laid on 20 June. All 1725 clutches included in this study were laid within a 63 day period, with a mean of 18.7 May (S.D. ± 9.4 Days).

4.2.2 Nest Site Location and Date of Laying

The mean date of laying of birds nesting in the centre of the colony was 17.0 May (S.D. ± 9.2, N = 919). On the edge, birds breed,

Figure 4.1 : The pattern of egg-laying of birds nesting in the 'centre' and on the 'edge' of the colony


NUMBER OF CLUTCHES
180
120
40
0
▽ Centre
● Edge
EARLY
LATE
33
15
0
-15
-33
RELATIVE DATE OF LAYING

on average, 3.6 days later ($\bar{x}$ = 20.6, S.D. = 9.2, N = 806) and this difference is highly significant (t = 8.1, d.f. = 1723, $P < 0.001$).

Despite a difference in the total number of birds which have bred in the two parts of the colony, the spread of laying in each is the same: 63 days in the centre, 62 on the edge. This suggests that there may be limits outside which birds find it impossible to lay, a point which is discussed further below. The two lines presented in Figure 4.1 show that the pattern of laying in the centre and the edge is similar also, with simply a shift of 1-3 days to the right (later) amongst birds nesting on the edge.

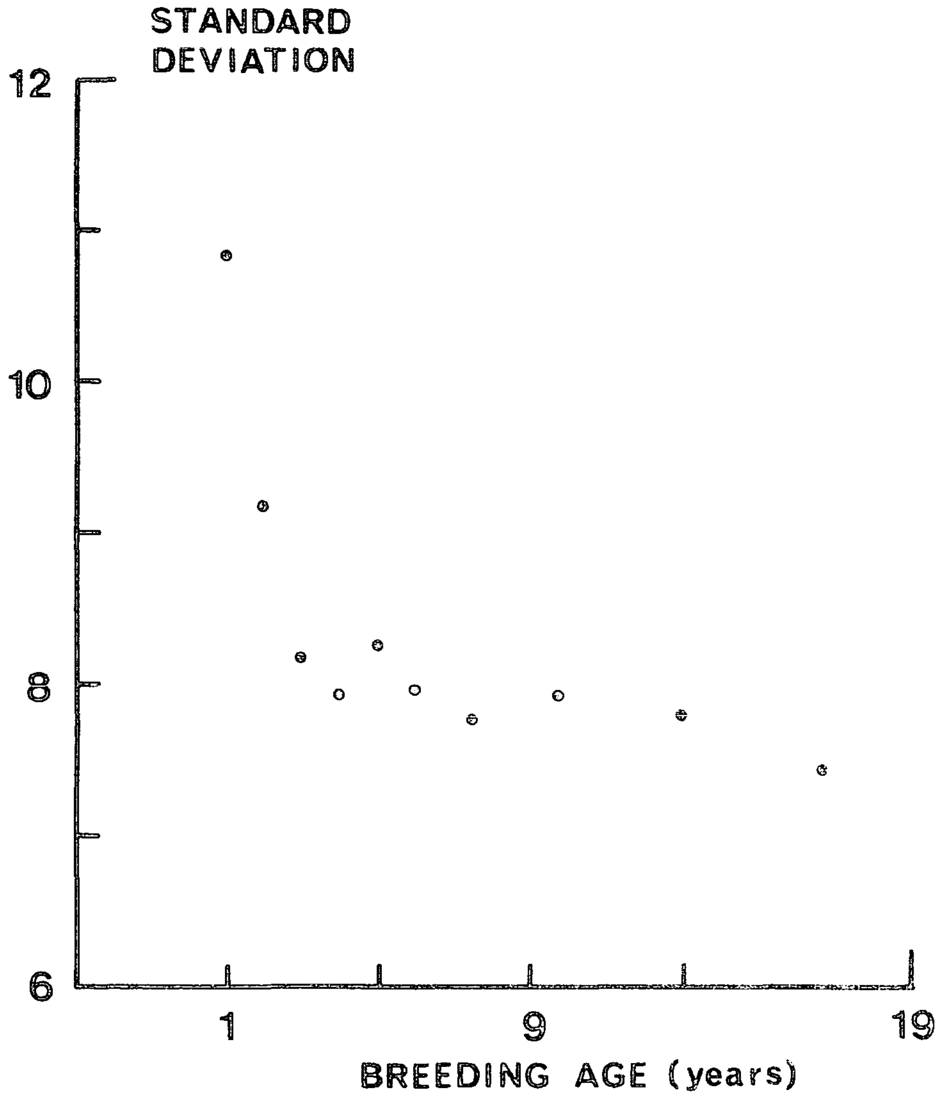
4.2.3 Breeding Age and Date of Laying

The relative date of laying of females of differing ages is shown in Table 4.1. The data indicate that whilst, on average, first breeders lay 3.2 days later than experienced birds, a difference which is significant (t = 5.25, d.f. = 1605, $P < 0.001$), there is no significant change in relative date of laying amongst females which have previously bred on at least one occasion. In Figure 4.2 the spread of laying about each mean (as measured by the standard deviation) is seen to decline as female breeding age increases, the effect being more marked in birds breeding for the first, second or third time. On average, therefore, there is a tendency for birds to lay progressively closer to the mean date of laying for the colony as a whole as they get older. Similar results were obtained if data were broken down by male breeding age, reflecting the close correlation between the ages of the two members of the pair.

TABLE 4.1 : Relationship between Female Breeding Age and Relative Date of Laying

Female Breeding Age (years)	Relative Date of Laying Mean	S.D.	N
1	-2.11	10.85	380
2	0.88	9.19	223
3	1.27	8.17	188
4	1.25	7.95	155
5	1.28	8,27	135
6	2.21	7.98	108
7-8	0.53	7.78	171
9-11	0.85	7.95	148
12-15	0.67	7.82	82
16-19	-0.88	7.45	17
2-19	1.06	8.21	1227

Figure 4.2 : The Synchrony of Laying (as measured by the standard deviation) of Different Age-Groups of Females. The mean relative date of laying of females of differing ages does not change significantly after the year of first breeding, although synchrony of laying within each age-group increases amongst older birds

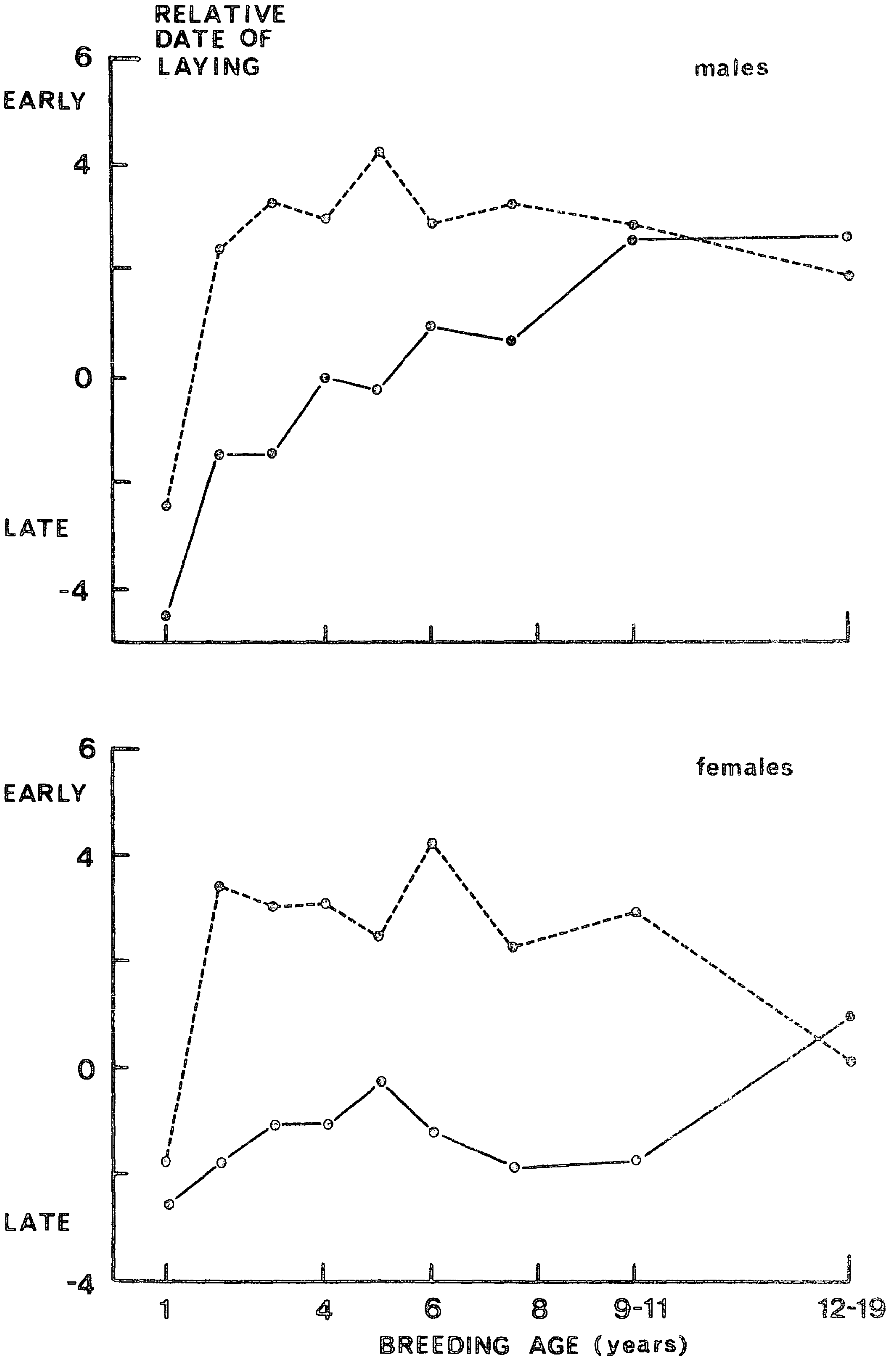


4.2.4 Breeding Age, Nest Site Location and Date of Laying

In Figure 4.3 the relationship between relative date of laying and breeding age is shown for males and females nesting in the centre and edge of the colony. Nest site location has no significant effect upon the mean date of laying of first breeders. Amongst experienced females with a breeding age of less than 11 the difference between the date of laying of birds nesting in the centre and edge of the colony is significant in all but one age group (Appendix 4.1). In the oldest females (11-19 years), however, there is again no significant difference between the mean date of laying of birds in each part of the colony and while those nesting in the centre lay significantly later than other experienced birds ($t = 2.87$, d.f. = 676, $P < 0.01$), on the edge this trend is reversed, although not significant. Amongst males nesting on the edge of the colony, date of laying advances progressively with increasing age (for at least 9 years after first breeding) and this trend is significant ($r = 0.25$, $N = 734$, Slope $= 6.34 \pm 0.92$). The trend shown by males nesting in the centre of the colony is similar to that of females.

To summarise, on the edge of the colony there is a tendency for birds to breed earlier in the season as they get older (although this is only significant amongst males). In the centre, amongst experienced birds, the overall trend is reversed and more marked amongst females. The advancement of breeding with increasing age, recorded in Red-billed Gulls and Shags (Mills 1973, Potts 1966) has been explained in terms of the time taken for the male to bring its mate into breeding condition, as well as the time required for the female to gather food for herself and the speed with which she responds to the courtship of the male. (These points are discussed further below.) Data have never been presented, however, to show that older birds lay later. Since this trend was only found in

Figure 4.3 : The relationship between relative date of laying and breeding age (years) amongst males and females nesting in the 'centre' (-----) and on the 'edge' (———) of the colony


RELATIVE DATE OF LAYING
6
EARLY
4
0
LATE
-4
males
6
EARLY
4
0
LATE
-4
females
1
4
6
8
9-11
12-19
BREEDING AGE (years)

central nesting birds, which are the earliest to lay in the colony, any factor which prevents birds laying progressively earlier would also result in more synchronised laying of the colony as a whole. Coulson and Dixon (1979), Darling (1938), Nelson (1967) and others have suggested that social stimulation within the colony could bring this about.

4.2.5 Change of Mate and Date of Laying

Females which change mate tend to lay later than females which have retained the same mate as in the previous breeding season (Table 4.2). The effect is more marked in birds which change mate through divorce, and the difference is significant amongst those breeding on the edge of the colony ($t = 2.01$, $N = 387$, $P < 0.05$). Males show no consistent trend and there is no difference in either the centre or the edge between those which retain the same mate and those whose old mates have died. Divorcing males nesting in the centre of the colony breed, on average, 0.6 days later than those which retain the same mate, whilst on the edge this trend is reversed, although in both cases the differences are not significant. Differences between the date of laying of birds which change mate through divorce and those whose mates have died, will be related to the age structure of birds making up each group, since death replaces divorce as the major cause of the break-up of the pair in older birds.

4.2.6 Breeding Age, Nest Site Location, Pair Status and Laying Date

In Figure 4.4 the relationship between breeding age (of males and females) and date of laying has been broken down to separate the effects of pair status and nest site location, revealing a marked difference in the trends shown by each sex.

Breeding experience has no effect upon the date of laying of females nesting in the centre of the colony which retain the same mate,

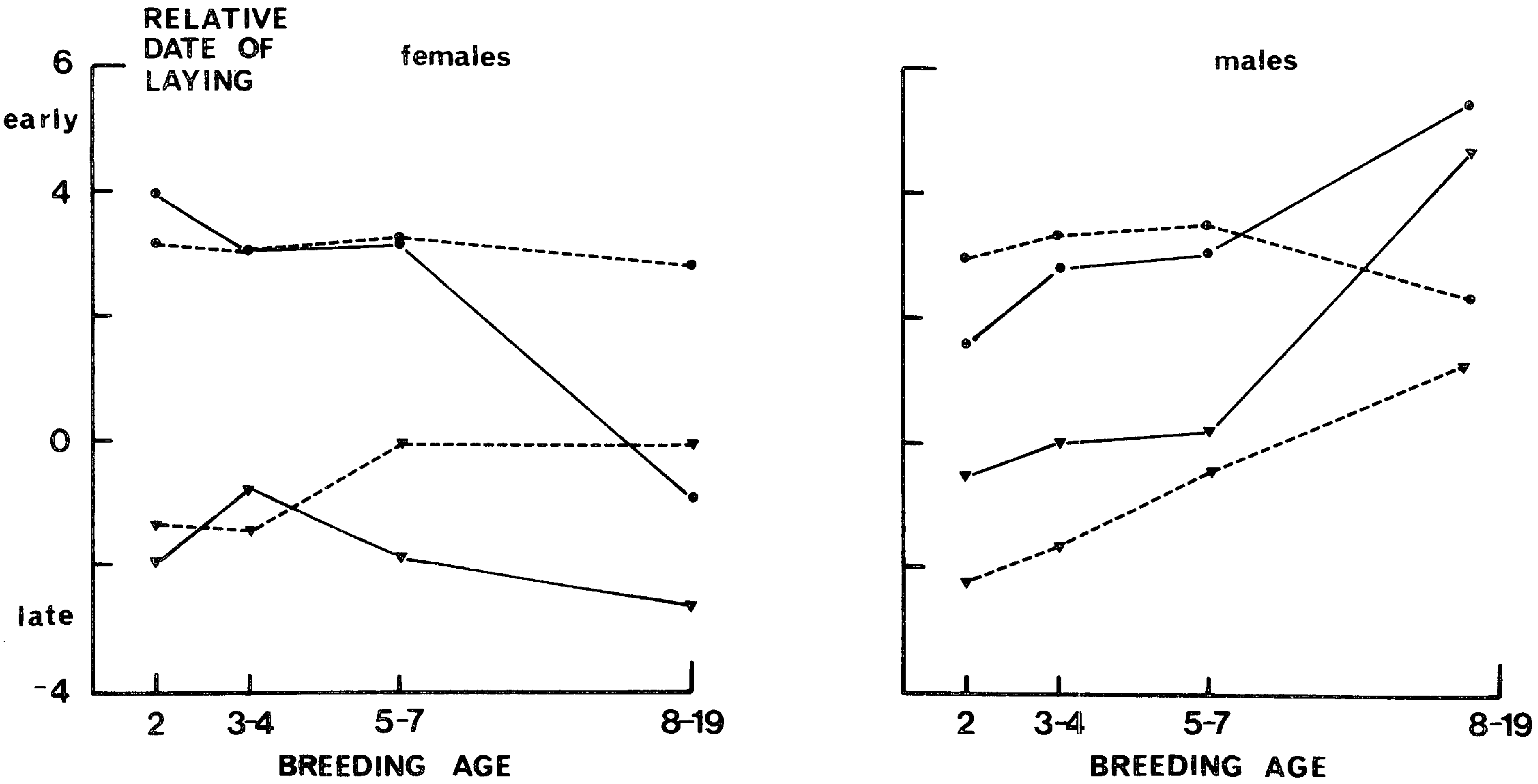
TABLE 4.2 : Relative Date of Laying of Birds in relation to Pair Status and Nest Site Location

		Same Mate	Change Mate	
			Death	Divorce
FEMALES				
	$\bar{x}$	-0.55**	-2.09	-2.33**
EDGE	N	267	71	120
	S.D.	7.80	8.95	8.15
	$\bar{x}$	3.06	3.48	1.88
CENTRE	N	393	77	125
	S.D.	7.01	9.66	8.04
MALES				
	$\bar{x}$	-0.55	-0.58	0.41
EDGE	N	267	52	81
	S.D.	7.80	9.42	7.83
	$\bar{x}$	3.06	3.19	2.47
CENTRE	N	393	81	96
	S.D.	7.01	9.36	8.06

** Significant Difference $t = 2.01$, d.f. $= 385$, $P < 0.05$

Figure 4.4 : The relationship between relative date of laying and breeding age (years) for males and females grouped according to both nest site location and pair status

Centre	Nest/ Same	Mate	○----○
Centre	Nest/Change	Mate	○——○
Edge	Nest/ Same	Mate	▽----▽
Edge	Nest/Change	Mate	▽——▽


RELATIVE DATE OF LAYING
6
early
4
0
late
-4
females
males
2
3-4
5-7
8-19
BREEDING AGE
2
3-4
5-7
8-19
BREEDING AGE

but those which change mate lay progressively later as age increases. These two trends are reversed amongst females nesting on the edge of the colony, although the net effect is the same; as breeding age increases, so does the size of the difference between the date of laying of birds which retain the same mate and those which change. Amongst younger birds, in some age groups, females which change mate actually lay, on average, earlier than those with the same mate, a finding which has also been reported in the Shag (Potts 1966).

Breeding age has no effect upon the date of laying of males retaining the same mate in the centre of the colony, but all other groups show a progressive advancement in time of breeding as age increases. In all age groups on the edge of the colony, males changing mate breed consistently earlier than those retaining the same mate, and this difference increases with age. In the centre, amongst older birds, a corresponding difference exists. However, on average, younger birds which retain the same mate breed earlier than those which change.

Differences found here between the sexes suggest that the breeding experience of both the male and female may independently affect the date of laying of the pair, and data presented below show that the relative breeding ages of the two birds can explain much of the variation found in this section.

4.2.7 Relative Breeding Ages of Members of the Pair and Date of Laying

In Table 4.3 the data have been broken down to show the effects of the relative breeding ages of the two members of the pair upon relative date of laying, data being first grouped according to nest site location and pair status.

With the exception of two groups (pairs of first breeders and old males mated with first breeding females nesting in the centre),

TABLE 4.3 : Relative Date of Laying of Pairs in relation to Pair Status, Nest Site Location and the Breeding Ages of the Male and the Female

		Edge			Centre		
		Male Age (years)					
	Female Age (years)	1	2-5	6-19	1	2-5	6-19
		Mean Relative Date of Laying					
CHANGE MATE	1	-4.36	2.16	4.43	-3.82	4.12	0.62
	2-5	-2.41	-0.45	3.00	1.35	2.93	5.16
	6-19	-6.41	-2.35	0.36	-0.47	0.08	4.34
SAME MATE	2-5		-1.21	0.83		3.56	1.86
	6-19		-2.06	1.12		3.58	2.66
		S.D. and Sample Sizes					
CHANGE MATE	1	9.78 (102)	9.90 (55)	5.59 (7)	11.92 (101)	9.18 (51)	8.44 (13)
	2-5	8.27 (73)	9.72 (69)	8.42 (22)	9.34 (51)	8.01 (86)	8.32 (32)
	6-19	8.40 (17)	8.17 (51)	4.01 (11)	6.87 (23)	8.43 (40)	9.63 (35)
SAME MATE	2-5		7.87 (124)	8.07 (18)		7.82 (158)	3.58 (36)
	6-19		7.38 (51)	7.56 (76)		6.97 (60)	6.79 (150)

a number of trends emerge from this table. Amongst all birds which change mate, females of a particular breeding age lay progressively earlier as the age of the male partner increases. However, males of a particular age breed progressively later as the age of the female increases. The trend associated with increasing female age is less marked than that of increasing male breeding age and, on average, differences between groups are greater amongst birds nesting on the edge of the colony than in the centre. Birds retaining the same mate show no consistency with respect to the relative breeding ages of the two members of the pair and there is no consistent or significant difference between the date of laying of corresponding age groups of birds in relation to pair status.

The age of the male, as well as the female member of the pair, has been shown to affect date of laying in various species, including the Laysan Albatross (Fisher 1969), the Red-billed Gull (Mills 1973), Ring-billed Gull (Ryder 1975) and the Shag (Potts 1966). However, these papers showed a general advancement in date of laying with increase in the breeding age of either partner. Possible reasons for the earlier laying of older birds have been outlined above. However, the data presented here show that while these may be applicable to the male Kittiwake, the female is not necessarily brought into breeding condition earlier as she gets older. Both LeResche and Sladen (1970) and Coulson and Wooller (in press) have suggested that older individuals are less able to adapt to their new mates than younger birds. This would explain why males of a particular age breed progressively later as the age of the female increases, if the pair is newly formed. If this is correct, it would imply that the ideas proposed by Coulson and Wooller and LeResche and Sladen are only applicable to the female, in the Kittiwake at least.

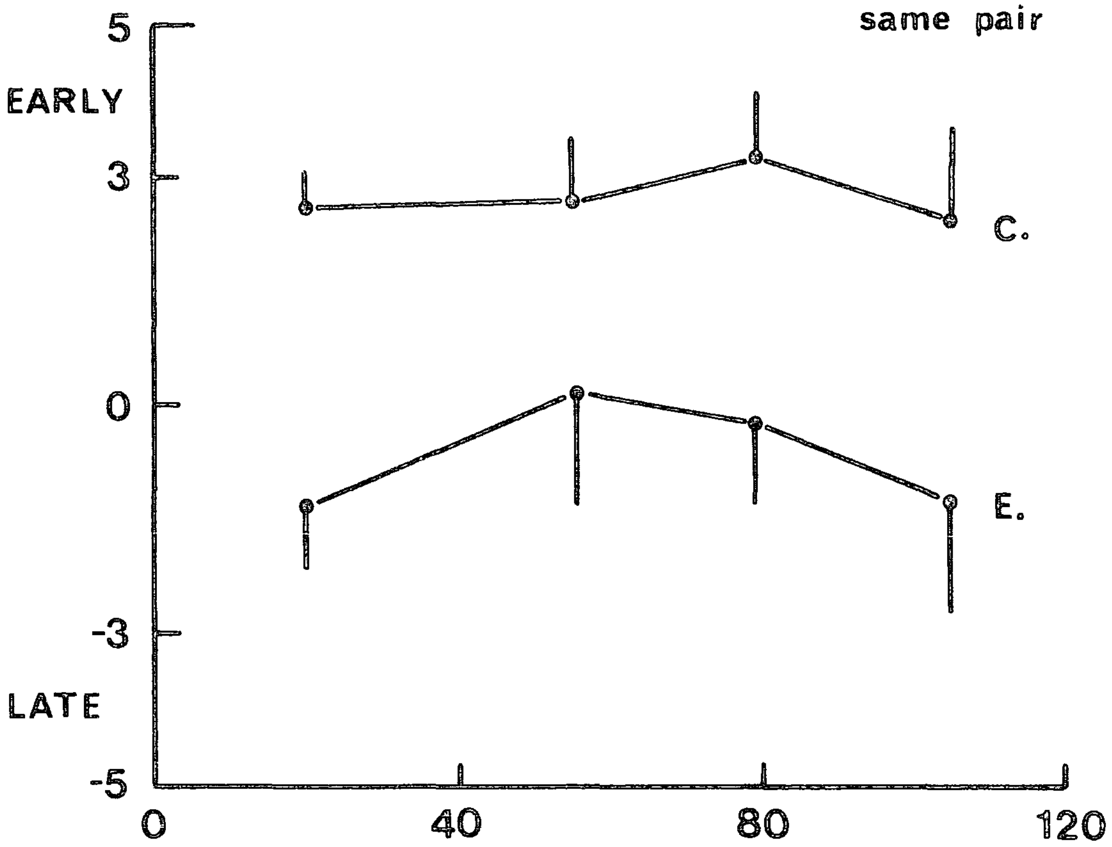
Change of mate has been shown to have no consistent or significant effect upon date of laying if the effect of the relative breeding ages of the two members of the pair is removed. In the previous chapter it was shown that although birds tend to mate with a partner of the same breeding age, as the age of birds which change mate increases, so does the difference in age between the members of the newly formed pair. This trend would explain why the difference in date of laying between birds which change mate and those which retain the same mate increases amongst older individuals. In addition, the same logic would explain why, amongst females of a particular breeding age group, those which change mate tend to lay later than those retaining the same mate, whilst in males the opposite is true.

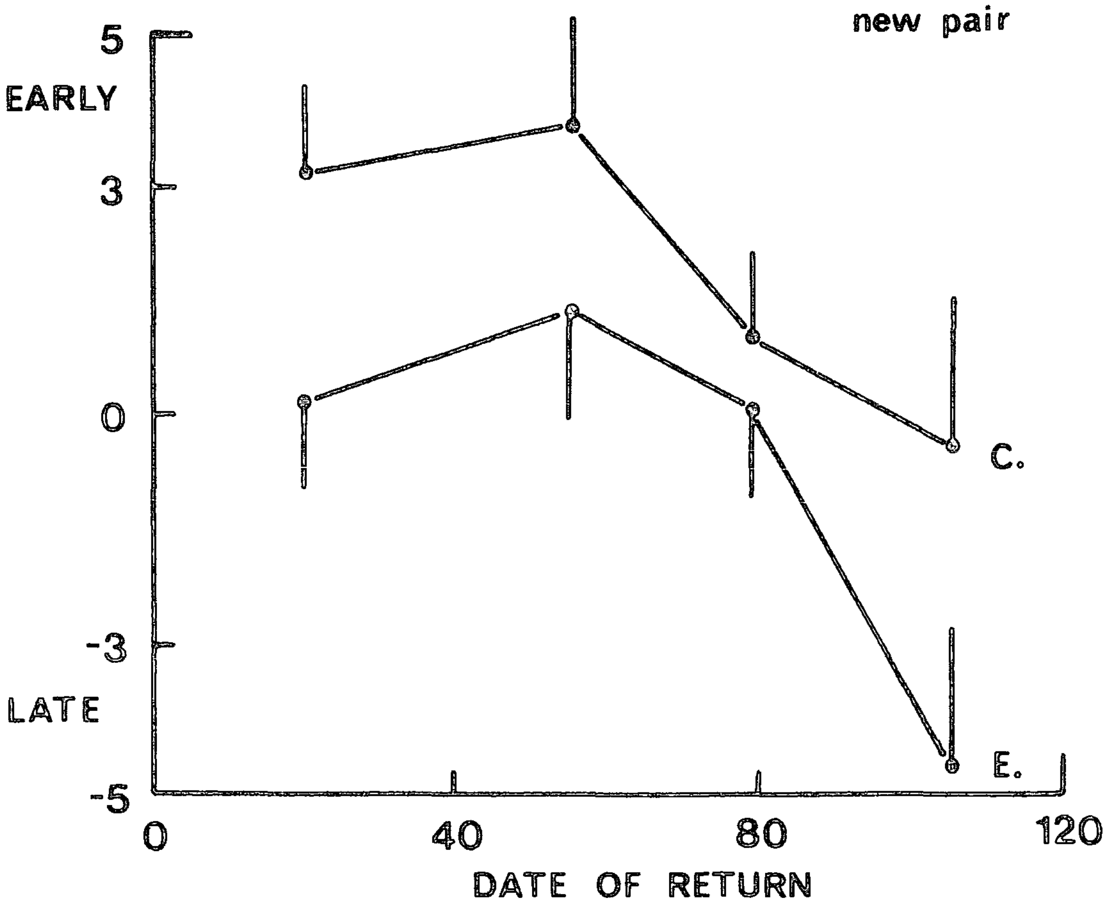
4.2.8 Date of Return to the Colony and Date of Laying

Coulson and White (1958a) found a significant positive correlation between the mean date of return of members of pairs breeding at North Shields and the date of laying of the birds. In an earlier paper (Coulson and White 1956) they found a similar relationship for the mean date of return and time of breeding of different colonies. In view of the close correlation between breeding age and date of return it is likely that this resulted from differences in the age structure of each population.

In the present analysis mean date of return to the colony was found to have no effect upon the subsequent date of laying of the birds if the pair was formed in previous years (Figure 4.5). In pairs newly formed in the present year, date of return does not affect the laying date of those arriving back early in the new year. Amongst those which return, on average, after 13 February, there is a progressive delay in laying associated with later return. One factor which has not been

Figure 4.5 : The relationship between relative date of laying (± 2 S.E.) and date of return to the colony for pairs grouped according to both nest site location (centre/edge) and pair status (same/new)


same pair
5
EARLY
3
0
-3
LATE
-5
0
40
80
120
C.
E.


new pair
5
EARLY
3
0
-3
LATE
-5
0
40
80
120
DATE OF RETURN
C.
E.

included in this analysis is the effect of date of return upon the probability that the pair will breed at all; it is likely that the late return of some birds will result in failure to breed (see Coulson and White 1958a).

The effects discussed here may be explained in two ways. Firstly, the change in the relative breeding ages of the members of the pair following change of mate. The difference in age between members of the newly formed pair increases amongst older birds; this should affect the mean date of return of the pair as young birds return later. Amongst females, this change in relative ages also causes later laying. A second explanation of these results lies in the availability of nest sites. Change of mate is often associated with change of site, especially in the female. The number of available nest sites in the colony would be expected to decline as more and more birds return. Late returning pairs in search of a nest site would therefore face greater competition (particularly from first breeders which return late and have no nest site from the previous year) and this could further delay the time taken for pair formation and subsequent laying.

Central nesting birds returning at a particular time in the year spend less time at the colony before laying than those on the edge, irrespective of the status of the pair, and in some cases this difference is significant (Appendix 4.2). Because of the compressed nature of the breeding season in comparison to the time over which birds return to the colony, late arriving individuals also spend less time at the colony before laying than those which return earlier. Coulson and White (1958a),Coulson and Horobin (1976) and Nelson (1967) all found similar results, explaining them in terms of the effect of social stimulation within the colony. Although this will be discussed at length further, it is introduced now as a possible explanation of the differences between the centre and edge of the colony recorded here.

4.3 Individual Variation in Date of Laying

A tendency for individual females to lay at a similar time in different breeding seasons has been found in the Pigeon Guillemot (Drent 1965) and the Yellow-eyed Penguin (Richdale 1957). In addition, Davis (1975) found a significant correlation between the date of laying of individual pairs of Herring Gulls in consecutive years, and comparable results have been obtained for the Great Tit (Jones 1973), the Lesser Black-backed Gull (Brown 1967) and the Manx Shearwater (Harris 1966). Much of the variation in date of laying in the Kittiwake remains unexplained after the effects of the most obvious factors (such as breeding age, pair status and nest site location) have been removed. As a result, the data have been re-analysed in order to investigate and remove any effect of individual variation.

4.3.1 Laying Dates of Individual Females

The relative date of laying in each season of all females breeding at North Shields which have survived for at least 15 years is shown in Table 4.4. Even from this simple form of data presentation it can be seen that certain individuals are consistently late layers, whilst others breed early in the season. Despite year-to-year variations there is a difference of almost 16 days between the mean date of laying of the birds at the two extremes (204.4917, 204.4874). The mean date of laying of various pairs of birds in this table are significantly different from each other.

4.3.2 Between Female Variation in Relative Date of Laying

Data from experienced females which have bred in the colony for at least two years were subjected to an analysis of covariance**,

** Analysis carried out using a Biomedical Computer Programme (BMDO4V), details of which are found in Dixon 1975.

TABLE 4.4 : Relative Date of Laying in Each Year of Individual Females which attempted to breed in at least Fifteen Seasons

Ring No. of Female	Breeding Age																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Mean	S.E.	N
EC11330	-7	5	2	5	0	4	-2	-2	-2	3	-6	-3	-2	-5	-11	-1.4	1.21	15
EC11778		14	4	8	-2		-6	-1	-2	-5	1	3	0	-5	1	0.8	1.55	13
202.0006	0		3	-7	7	3	-12	0	-2	1	1	1	1	-1	-1	-0.4	1.21	14
202.8402		5			9		3	-6	11		7	8	12	10	12	7.1	1.73	10
202.8794	-13	-3	-3	3	-2	3	0	3		8	-6	1	1	-9	-1	-1.3	1.44	14
204.4067	-4	-3	-3	8	7	4	6	-4	1	0	-6	0		7	2	1.1	1.26	14
204.4075	14			16	5	7	11	11	8	2	3		-21	11	3	5.8	2.76	12
204.4874		14	8	10	14	10	14	16	13	13	13	8	-10	2	11	9.7	1.79	14
204.4875		0	4	6	5	14	5	12	15	13	8	14	9	11	3	8.5	1.27	14
204.4892	14	4	4	14	2	8	5	7	5	13	1	1	1	-5	3	5.1	1.38	15
204.4917	-18		-12	-3	-4	-2	-3	-4	-7	0	-14	-5	1	-9	-6	-6.1	1.45	14

the results of which are presented in Table 4.5. Over 39% of the variation in relative date of laying in the colony can be explained in terms of individual differences between females after any effects of nest site location, pair status and the breeding age of the female and her mate have been removed.

Falconer (1964) points out that the 'within-individual' component is entirely environmental in origin, whilst the 'between-individual' component is partially environmental and partially genetic. The ratio of the 'between-individual' component to the total phenotypic variance measures the correlation between the repeated measurements of the same individual and is known as the repeatability of the character.

$$\text{Repeatability} = \frac{(\text{variance of 'between' group })}{(\text{variance of 'between' + variance of 'within'})}$$

The repeatability of relative date of laying in this sample of female Kittiwakes is 0.76, indicating a marked tendency amongst individuals to lay at a particular time in the breeding season in different years, irrespective of annual variations in proximate factors.

4.3.3 The Consistency in Date of Laying of the Same Female in Consecutive Breeding Seasons

There is a significant positive correlation between the date of laying of the same females in consecutive breeding seasons ($r = 0.32$, $N = 1071$, $P < 0.001$). This relationship remains, irrespective of whether the bird has changed mate or not over the same period although, as might be expected, the correlation is higher amongst females which have retained the same mate ($r = 0.38$, $N = 657$, $P < 0.001$) than amongst those which change ($r = 0.24$, $N = 414$, $P < 0.001$).

TABLE 4.5 : Results of Analysis of Covariance showing the degree of variation in relative date of laying within the colony which can be attributed to the tendency of some females to breed consistently earlier in the season than others (after any effect of the proximate factors listed below has been removed)

	Sum-Squares	d.f.	Variance
Between bird	31850.77[a]	195	163.337[x]
Within bird	48342.97	933	51.815[y]
Total	80193.74[b]	1128	71.094

$F(195,933) = 3.16 \quad P < 0.01$

r^2 Individual Differences between Females = a/b = 0.397

Repeatability = x/(x+y) = 0.759

Factors included as covariates:

Pair Status : 0 = change mate, 1 = same mate

Nest Location : 0 = edge, 1 = centre

Log_{10} Breeding Age : of male and female

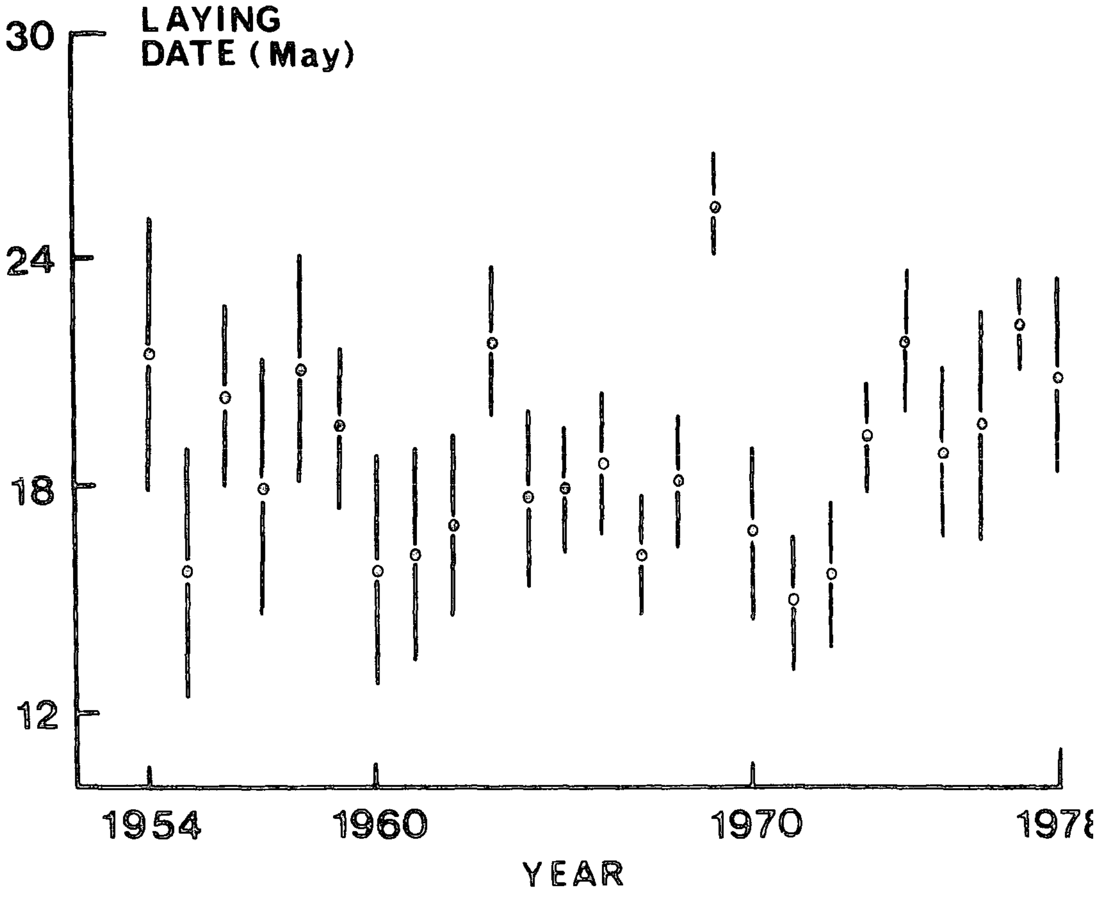
When females change mate the age of their new partner is often different from that of the old and this is found to have a marked effect upon the change in date of laying of the bird. There is a significant positive correlation between the change in breeding age of the male partner and the corresponding change in date of laying of the female. ($r = 0.19$, $N = 378$, $P < 0.001$). The slope of the relationship (0.57 ± 0.15) which is significantly different from zero ($P < 0.001$) indicates that if the female takes a new partner which is older than the previous mate, the bird will tend to lay earlier in the present breeding season than it did in the last.

Female Kittiwakes, therefore, show a tendency to lay at the same time in different breeding seasons although this is modified amongst birds which change mate, especially by the breeding experience of the male.

4.4 Between Year Variation in Date of Laying

The timing of the breeding season at North Shields (as measured by the mean date of laying of the birds) has changed very little over the period 1954-1978, with only one year, 1969, significantly later than the rest (Figure 4.6). The difference between the mean date of laying of the earliest and latest years is only 10 days, which is less than one third of the spread of laying within an average year. There has been no consistent pattern to changes in the timing of the breeding season although up to 1972 there was a tendency for birds to breed progressively earlier. Since then, however, there has been a rapid reversal of this trend and in 1978, on average, birds were breeding as late as in the early 1950s, soon after the colony's formation. There is no correlation between changes in the mean date of laying of the colony in each year and any of the corresponding changes in colony size or age composition discussed earlier.

Figure 4.6 : Annual variation in the mean date of laying (± 2 S.E.) of Kittiwakes breeding in the colony at North Shields



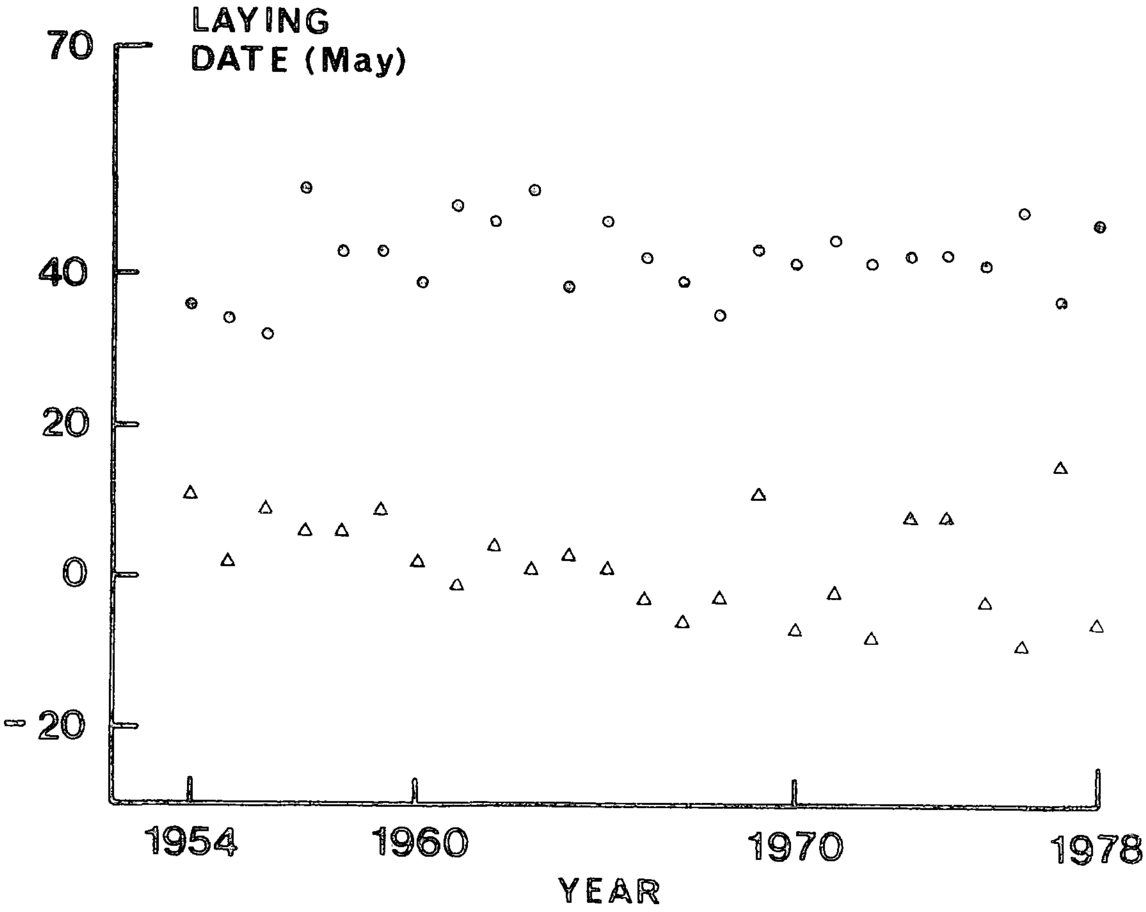
The dates of laying of the first and last clutches produced in each year are shown in Figure 4.7. With the exception of four years (which will be discussed in the next section), the laying date of the first egg in each year has advanced steadily since 1954. The date on which the last clutch was started has shown no corresponding change and has remained constant in all years, with the exception of 1954, 1955 and 1956 when the colony was small. The length of the breeding season has therefore increased during the period of this study. The regression of date of laying of the first egg in each year (x) on the variance about the mean date of laying of the whole colony (y) gives the relationship:

$$y = -3.21x + 88.32 \quad (N = 25,\ r = -0.67)$$

The slope of the relationship -3.21 ± 0.71 is significantly different from zero ($P < 0.001$), indicating that in late starting years breeding is more synchronised. There is, however, no correlation between the spread of laying in a particular year (or the variance) and colony size.

Earlier in this chapter it was shown that the pattern of laying at North Shields approximates to a normal distribution with a slight positive skew, indicating that, on average, more clutches are started after the mean. Since there has been a consistent change in the date of laying of the first egg in the colony, which has not been followed by a corresponding change in either the mean or the date of laying of the last, it seems likely that the pattern of laying will have changed also. The slope of the regression describing the relationship between date of laying of the first egg in each year and the degree to which the pattern of laying is skewed from the normal, 0.05 ± 0.02 ($N = 25$, $r = 0.54$) is significantly different from zero ($P < 0.05$). In late starting years there is a positive skew of up to two days. However, as the start of the breeding season advances, the pattern of laying becomes progressively

Figure 4.7 : Variation in the date of laying of the first (△) and last (•) clutches produced in each year. Over the period of this study there has been no consistent or significant change in the date of laying of the last clutch. However, with the exception of four years (▲), discussed in the text, date of laying of the first clutch has advanced progressively and significantly (Slope = -0.72 ± 0.10, r = -0.86, p < 0.001)



closer to that of a normal distribution, and in the earliest starting years the breeding season is negatively skewed, but by only 0.2 days. This indicates that the proportion of birds laying during the first half of the breeding season is lower in years when breeding starts later. In addition, the relative consistency in both the mean date of laying and the date on which laying ends suggests that the pattern of laying in the second half of the season remains similar in all years.

4.5 Years in which the Onset of Breeding was 'Unusually Late'

In four years during this study, 1969, 1973, 1974, 1977, the date of laying of the first egg of the season was later than that expected from the overall trend discussed in the previous section. In these years, the mean date of laying of the colony was delayed also, although this was only marked in 1969.

Colony size, the age structure of the breeding population and date of return showed no consistent changes in these years which could account for the delay in breeding (although in 1969 the mean date of return of the birds was much later than that expected from the overall trends shown by the colony (Figure 2.1, Chapter 2). The survival rate of breeding birds from North Shields over the winter periods 1968/1969 and 1973/1974 was lower than in any other year for which data are available (see Coulson and Wooller 1976). This could have affected the time of breeding in one of two ways. Firstly, because in years of high mortality the divorce rate of surviving birds is high also, resulting in more pairs splitting up (change of mate in general resulting in later breeding). Secondly, in years when mortality is high, the physical condition of surviving birds may be generally 'poorer' so that they require more time to come into breeding condition, although there was no evidence of this from the body weights of first breeders caught in each year.

In 1968 a bloom of toxin-producing dinoflagellates resulted in a Red Tide along parts of the Durham and Northumberland coast (Ayres and Cullum 1978). Large numbers of seabirds, particularly Shags, died as a result and in various other species breeding was affected (Coulson *et al.* 1968, Coulson and Horobin 1976). Although the effect upon the Kittiwake was not as marked as in other species, it is likely that this may be a factor which contributed to the higher mortality rate of birds in the following winter. In 1973 and 1974, though, the levels of paralytic shellfish poisoning (a measure of the occurrence of toxin-producing dinoflagellates) were lower than in most years (Ayres and Cullum 1978) so it is unlikely that this could have resulted in the low survival of birds before the 1974 season. It is possible that some other factor such as weather conditions or food availability in the wintering area could have affected both the survival and physical condition of the birds. However, since the birds from North Shields disperse throughout the North Atlantic (Chapter 1), it is impossible to investigate this theory. None of the factors discussed so far could be used to explain late breeding in 1973 and 1977, although conditions in the wintering area which did not affect survival could be involved. Meteorological data from two stations within two miles of the colony (Tynemouth : Temperature, Rainfall, Snow; and South Shields : Wind Speed) revealed no adverse weather conditions during March, April and May of each year since 1966 which could be correlated with the onset of breeding.

4.6 Discussion

Several factors have been found to affect date of laying of birds breeding at North Shields. These include the location of the nest site, the breeding ages of the two members of the pair, the status of the pair and, for birds breeding together for the first time in the present year, the mean date of return of the two individuals. The results of a multivariate analysis (Table 4.6) show that although there is only a significant correlation between relative date of laying and nest site location and male breeding age, once the effect of these two variables is removed from the relationship the effect of female breeding age becomes significant. Birds nesting in the centre tend to breed before those on the edge and, within the pair, increase in male age tends to result in earlier laying, whilst increase in female age results in progressively later laying. The delay in breeding, associated with change of mate, which has in the past been thought to result from the time required for courtship in unfamiliar birds, has now been shown to arise from changes in the relative breeding ages of the two members of the pair. Individual females tend to breed at a similar time in the season in consecutive years, but it appears that the actual date of laying is influenced by the breeding age of the male partner.

In previous papers (Coulson 1966, Coulson and White 1958a) it was suggested that female Kittiwakes tend to lay earlier as they get older, although the effect was less marked amongst experienced birds. It was found here, however, that both males and females lay progressively closer to the mean date of laying of the colony with increasing breeding age. This situation arises because birds nesting on the edge of the colony lay earlier as they get older, whilst those in the centre breed slightly later. It is as a result of this that colony synchrony is maintained.

Changes in the timing of the breeding season in different years are thought to be linked both to environmental conditions after the birds return to the colony and to the possible effects of adverse weather conditions or food availability in the wintering areas, although neither could be proved. In one particular year (1969) late breeding was

TABLE 4.6 : Multivariate Analysis - Factors associated with Variations in the Relative Date of Laying of Experienced Birds

Correlation Matrix

	Relative Date of Laying	Female Age (Log)	Male Age (Log)	Nest* Site Location	Pair Status **
Relative date of laying	-	-0.02	0.15	0.23	0.07
Female Age (Log)		-	0.41	0.06	0.18
Male Age (Log)			-	0.14	0.40
Nest Site Location*				-	0.08
Pair Status**					

Regression Model

Dependent Variable = Relative Date of Laying

Variable in Equation	Regression Coefficient	Standard Error	P
Nest Location	+ 3.53	0.47	< 0.001
Male Age (Log)	+ 4.18	0.79	< 0.001
Female Age (Log)	- 3.14	0.96	< 0.002

C = -1.04 N = 1184 r = 0.28

* Nest Site Location : 0 = Edge 1 = Centre

** Pair Status : 0 = Change 1 = Same

correlated with high winter mortality and late return, and it was suggested that this may have resulted, directly or indirectly, from a bloom of toxin-producing dinoflagellates in the previous year.

It is generally accepted that birds have evolved to breed at the time of year when environmental conditions (e.g. food supply, Lack 1954) are most favourable for the production of offspring. The factors which affect the variation in date of laying of individuals within the breeding season is poorly understood, although there are two main theories at present. Perrins (1970) presented data on the Great Tit which suggested that the date of laying of females is related to the time at which the bird obtains enough food for egg formation. Mills (1973) explained variations in the date of laying of Red-billed Gulls (which were positively related to the breeding ages of both the male and the female) in terms of the foraging ability of the birds and the rôle of courtship feeding. Coulson *et al.* (1969) stated that there was no evidence of any food shortage at North Shields, and they and other writers have shown date of laying to be independent of food supply; Herring Gull (Parsons 1975a), Slender-billed Shearwater (Serventy 1963) and Swallow-tailed Gull (Harris 1969).

Lofts and Murton (1968) outlined the evidence for a photoperiodic control of some avian breeding cycles and Parsons (1975a) suggested that day length was likely to be the most important environmental cue co-ordinating the endogenous events prior to egg laying. Courtship has been shown to affect the final growth phase of the ovaries in Ring Doves (Lehrman 1964) and so the time of courtship will have a direct effect upon date of laying. Mills (1973) found that the development of the testis in young Red-billed Gulls was slower than in older birds and it was suggested that this could affect the timing of the onset of courtship through the effect of gonadal hormones upon the hypothalamus. Further, male pigeons with inactive gonads do not normally respond to the displays of females (Carpenter 1933a,b), while inexperienced female Ring Doves have been shown to be less responsive to courtship by males than experienced individuals (Lehrman and Wortis 1960). These relationships are complicated by the suggestion made earlier that older females which change mate may take longer to adapt to their partners than younger individuals. In general, though, it would appear that the date of laying is influenced by the speed with which individual males and females respond both to environmental cues and to the courtship of their partners and this in turn will vary with the breeding ages of the members of the pair. In addition, although there is no evidence to support this idea, it is very likely that individual birds will also vary in the speed of their response. This would explain why some female Kittiwakes tend to be consistently early or late layers.

These effects explain changes in date of laying with breeding age but they do not explain why the relationship between these two factors is different in the centre and edge of the colony. It has been suggested that some form of stimulation from other birds in the colony may be necessary to facilitate egg laying and that this effect may not only speed up the onset of breeding but may also be the reason why Kittiwakes are unable to breed as solitary nesters (Coulson and Dixon 1979). If it is accepted that some form of 'social stimulation' is necessary to facilitate pre-copulatory behaviour patterns, it is possible to explain some of the variation in date of laying in the two parts of the colony in these terms.

Birds which return late in the new year spend less time at the colony before breeding than those which arrive back earlier. During the period of return the number of birds at the colony gradually increases (Wooller 1973) as does the number of occupied nest sites. Late returning birds are, therefore, exposed to a higher level of 'social stimulation' from the colony than those which return earlier. The centre of the colony is, on average, re-occupied before the edge and in the same way, at any particular time, the level of stimulation within this part of the colony will be greater. This may explain why, on average, amongst pairs which return at the same time, those nesting in the centre lay consistently earlier than those on the edge. (Although this result could also reflect a difference in 'quality' of the birds found in each part, as suggested by Coulson 1968.) The importance of social stimulation as a stimulus for breeding may give a clue to the tendency for birds nesting in the centre to lay slightly later, and not earlier, as they get older. Although these birds may respond more rapidly to environmental cues and to the behaviour of their mates, any behavioural stimulus from other birds in the colony will be lacking since these birds are physiologically the most 'advanced'. As a result, there may be a limit to how early a pair of birds can breed.

The result of this explanation suggests that there may be two different mechanisms operating in the colony which control the time of breeding. Early nesters respond more rapidly to environmental cues and their mates, but are delayed in their laying by the lack of social stimulation within the colony. Late laying (normally young) birds respond less rapidly to environmental changes but encounter a higher degree of social stimulation from the colony. Obviously this theory is entirely speculative. However, it would explain the degree of synchrony in the colony which was observed.

When Darling (1949) first proposed the idea of social stimulation he made no attempt to quantify it. In a recent paper by Coulson and Dixon (1979) different types of behaviour exhibited by Kittiwakes which involve the participation of several members of the colony were described, such as the gathering of nesting material. In addition, behaviours such as the greeting ceremony of birds returning to their mates in the colony which evoke responses from neighbouring birds were quoted as factors which could act as a form of social stimulation. Due to the close proximity of neighbouring nests it is likely that any pre-copulatory displays made by one pair of birds may act as a stimulus to others at nearby nests, which may not evoke an immediate response, but which may speed up the onset of courtship in those birds. This type of communication, occurring over short distances, would explain why small sub-units within colonies are more synchronised, with the result that there is more synchrony within the colony as a whole (Coulson and White 1960).

To summarise, although day length is thought to be a proximate factor controlling the date of laying of some birds, including the Kittiwake, differences in the speed with which birds respond to this stimulus, which is related both to individual differences, breeding age and the effect of social stimulation, result in the variation in date of laying of the birds within the colony. The importance of the role of social stimulation may vary from one bird to another, causing some to lay earlier, whilst preventing others from doing so, thereby maintaining synchrony within the colony.

CHAPTER 5 : CLUTCH SIZE

5.1 Introduction

The mean clutch size of Kittiwakes breeding at North Shields has been found to vary from year to year, between 1.92 and 2.17 eggs per pair (Wooller 1973). On average, pairs of birds nesting in the centre of the colony produce larger clutches than those on the edge (Coulson 1968) and birds retaining the same mate tend to lay more eggs than those which change (Coulson 1966). Finally, clutch size tends to increase with female breeding age and, even amongst birds of the same age, shows an overall decline through the breeding season (Coulson and White 1961). In view of the inter-relationships which have been shown to exist between all these factors, an attempt will be made here to separate the effects of each.

Although clutch size was found to be primarily determined by date of laying, Coulson and White (1961) noted a tendency for some individual females to lay clutches of three in a number of consecutive years when, on average, 73% of birds laid only two eggs. They suggested therefore that some of the unexplained variation in the colony may have been related to factors which had a genetic basis, although they stated that the direct relationship between clutch size and date of laying was independent of genetics. This was in contrast to Koskimies (1957) who suggested that the consistency of both laying date and clutch size in the Velvet Scoter arose from a pair of linked genes. Lack (1948) noted that clutches laid by particular female Starlings in successive years varied less in size than those of the colony as a whole and suggested that this apparent consistency may have been due to some hereditary factor. Perrins and Jones (1974) felt that if clutch size had evolved through natural selection it may be assumed to have a genetic basis. In view of these findings, data will be re-analysed to look at the effects of changes in proximate factors such as date of laying upon changes in the number of eggs laid by the same individual in different years.

5.2 Within Year Variation in Clutch Size

The modal clutch size laid by Kittiwakes is two eggs. At North Shields the mean clutch size produced over the period of this study was 2.05 eggs, clutches of one and three comprising only 9.8% and 14.6% respectively of the total (1730 clutches). Only three nests have ever been found containing four eggs and in two of these cases more than one female is known to have used the site. As a result, all three clutches of four have been excluded from the analysis.

The mean number of eggs laid by each pair at North Shields is greater than that reported for other Kittiwake colonies: 1.85 (Maunder and Threlfall (1972); 1.80 Barrett (1978); 1.84 Swartz (1966); 1.96 Belopol'skii (1961); 1.89 Uspenski (1956). These differences are discussed further below. However, it should be pointed out that while in other studies egg loss may have occurred prior to counts being made, the frequency of visits made to North Shields and the nature of the colony is such that clutch size estimates are very accurate here.

5.2.1 Nest Site Location, Pair Status and Clutch Size

Data presented in Table 5.1 show that experienced females nesting in the centre of the colony lay significantly larger clutches than those on the edge ($\chi^2_2 = 21.19$, $P < 0.001$), a similar result to that obtained by Coulson (1968). In addition, females which retain the same mate as in the previous breeding season lay significantly larger clutches, on average, than those which change ($\chi^2_2 = 35.06$,

TABLE 5.1 : The Clutch Size of Experienced Females Nesting in the Centre and Edge of the Colony in relation to Pair Status

Pair Status and Nest Location		Size of Clutch				
		1 %	2 %	3 %	Mean	Sample Size
Edge		7.8	78.2	14.0	2.06	528
Centre		4.0	72.9	23.1	2.19	678
Change		6.6	81.7	11.7	2.05	531
Same		4.9	70.1	25.0	2.20	675
Edge	Change	7.4	81.0	11.6	2.04	258
Edge	Same	8.1	75.6	16.3	2.08	270
Centre	Change	5.9	82.4	11.7	2.06	273
Centre	Same	2.7	66.4	30.9	2.28	405

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$P < 0.001$). Mills (1973) found the same effect in Red-billed Gulls, as did Coulson (1972) in an earlier paper on the Kittiwake. Coulson also showed that change of mate due to the death of a partner is associated with a greater reduction in clutch size than change through divorce, although in this work no difference was found between the mean clutch size of each group (Divorce : 2.05 eggs, $N = 245$; Death : 2.05 eggs, $N = 149$).

Change of mate amongst birds nesting on the edge of the colony results in a 2% reduction in clutch size in comparison with those which have retained the same mate. In the centre of the colony the effect of change of mate is more marked, resulting in a 10% reduction in clutch size which is significant ($\chi^2_2 = 35.00$, $P < 0.001$). This means that while pairs in both the centre and edge which change mate lay clutches of a similar size, amongst those which retain the same mate, birds nesting in the centre of the colony lay significantly larger clutches than those on the edge ($\chi^2_2 = 26.44$, $P < 0.001$) showing that both nest location and pair status have a compounding effect.

At the edge of the colony, pairs which change mate lay proportionately fewer clutches of three eggs, with a corresponding increase in the proportion of two egg clutches. In the centre this effect is accompanied by an increase in the proportion of clutches of one egg.

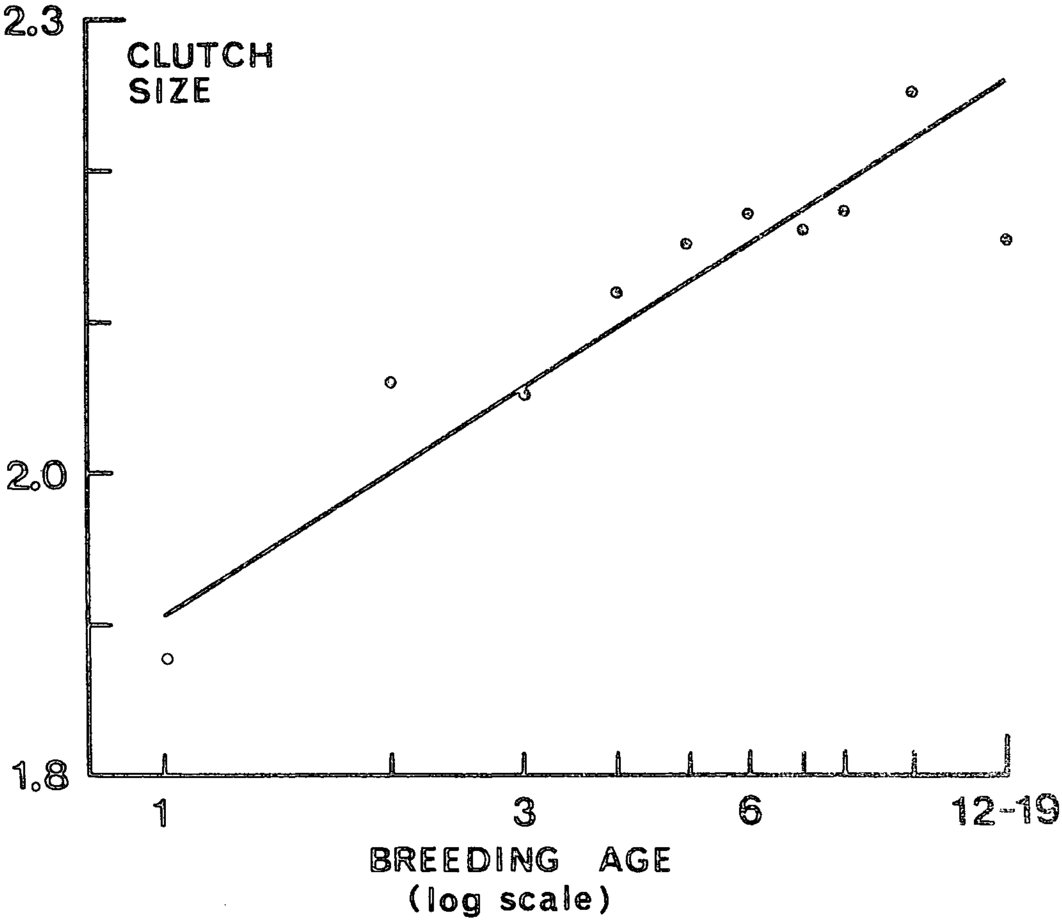
5.2.2 Breeding Age and Clutch Size

Clutch size increases with female breeding age, reaching a peak amongst birds which have previously bred for between 8 and 10 years (Figure 5.1). The change is most marked and significant between females breeding for the first and second time ($\chi^2_2 = 25.45$, $P < 0.001$). Amongst experienced birds there is no significant difference between the mean

Figure 5.1 : The relationship between clutch size and female breeding age (years) described by the regression equation:

$$y = 0.308 \log_{10} x + 1.909$$

$r = 0.24$ $p < 0.001$ $N = 1610$



clutch size of consecutive or even alternate age groups of birds. (The clutch size distribution of each age group is shown in Appendix 5.1.)

The equation describing the relationship between female breeding age (x) and clutch size (y) is:

$$y = 0.308 \log_{10}x + 1.909$$

$$r = 0.24,\ P < 0.001,\ \text{S.E. Slope} = \pm 0.03,\ N = 1610$$

A similar relationship exists with respect to male breeding age, reflecting the close correlation between the breeding ages of the two members of the pair.

$$y = 0.347 \log_{10}x + 1.908$$

$$r = 0.25,\ P < 0.001,\ \text{S.E. Slope} = \pm 0.03,\ N = 1608$$

Data published in earlier papers on the Kittiwake (Coulson 1966, Coulson and White 1961) included very few old birds and so a peak in clutch size was not found. In other species the association between clutch size and breeding age is varied. In both the Shag and the White Stork no correlation could be found between these two factors (Potts 1966, Hornberger 1943). In Great Tits, age was found to have no effect after year of first breeding (Perrins 1965, van Balen 1973). In Arctic Terns and Herring Gulls, clutch size was not found to increase significantly after 3-5 breeding seasons (Coulson and Horobin 1976, Duncan 1978), whilst in Red-billed Gulls and Ring-billed Gulls no increase was found following the fourth year of breeding (Mills 1973, Haymes and Blokpoel (in press)). In the Kittiwake, the increase in clutch size with breeding age continues for a greater number of years than in many other species, including long-lived seabirds. This reflects the fact that Kittiwakes show very little change in egg size with increasing breeding age, unlike these other seabirds (Coulson *et al.* 1969).

Figure 5.2 shows the relationship between clutch size and female breeding age for birds nesting in each part of the colony, in relation to the status of the pair. In all but one group there is a progressive increase in clutch size with age although this tails off slightly amongst birds which have changed mate. First breeders in both the centre and edge of the colony lay the smallest clutches, there being no difference between the two parts of the colony. Within a particular age group there is no significant difference between the mean clutch size of birds changing mate in the centre and either group of birds on the edge. Pairs retaining the same mate, nesting in the centre of the colony, lay consistently and significantly larger clutches than birds of the same age in any of the other groups.

Coulson (1966) suggested that amongst pairs which retain the same mate there is a greater increase in clutch size with breeding age than in those which change. The results presented here, which also take into account the effects of nest site location, do not disagree with the earlier work, although the relationship is seen to be more complex.

In Table 5.2 data have been arranged to show the percentage of one, two and three egg clutches laid by each of the groups of birds which were used in Figure 5.2. First breeders lay the largest proportion of one egg clutches. Amongst older birds there is a slight decline in the proportion of one egg clutches produced as age increases, except in birds retaining the same mate and nesting at the centre of the colony, which lay very few clutches of one in all age groups. In general, changes associated with an increase in age result from a gradual decline in the proportions of two egg clutches produced and a corresponding increase in the proportions of clutches of three, although here again birds nesting in the centre with the same mate show no such trends.

Figure 5.2 : **The relationship between clutch size and female breeding age (years) for birds grouped according to both nest site location and pair status**

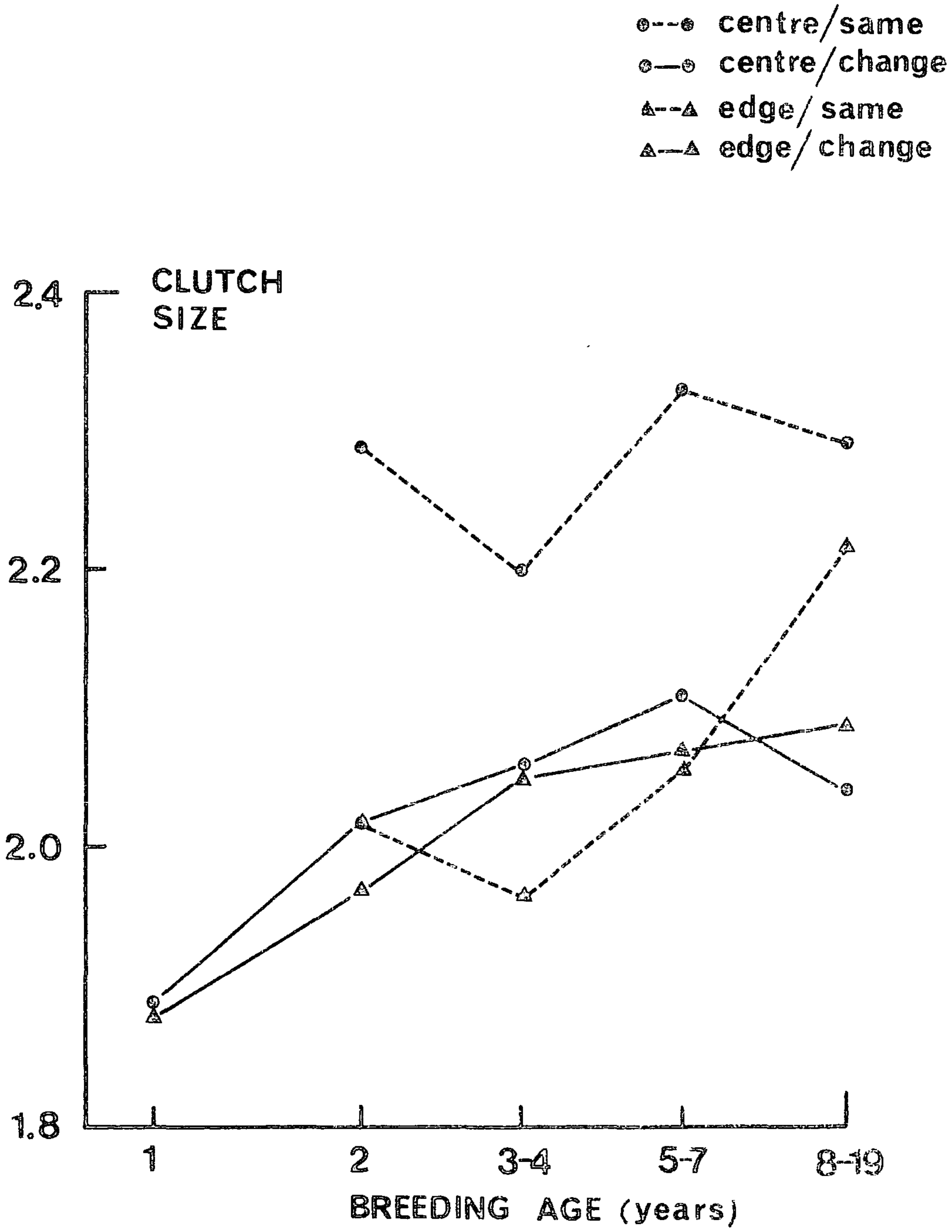


TABLE 5.2 : The Percentage of One, Two and Three Egg Clutches laid by Birds of Differing Ages in relation to the Status of the Pair and Nest Site Location

	Pair Status and Nest Location		Female Breeding Age (years)				
			1	2	3-4	5-7	8-19
ONE EGG CLUTCH	Edge	Change	16.4	10.9	6.1	7.2	4.7
	Edge	Same		11.1	10.6	8.3	4.6
	Centre	Change	15.7	7.0	4.5	6.9	5.5
	Centre	Same		2.0	2.0	3.4	2.9
TWO EGG CLUTCH	Edge	Change	78.9	81.3	82.9	78.3	81.4
	Edge	Same		75.6	81.8	77.8	69.0
	Centre	Change	79.7	84.2	85.4	75.3	85.2
	Centre	Same		66.7	75.8	60.2	65.0
THREE EGG CLUTCH	Edge	Change	4.7	7.8	11.0	14.5	13.9
	Edge	Same		13.3	7.6	13.9	26.4
	Centre	Change	4.6	8.8	10.1	17.8	9.3
	Centre	Same		31.3	22.2	36.4	32.1
SAMPLE SIZES	Edge	Change	171	64	82	69	43
	Edge	Same		45	66	72	87
	Centre	Change	172	57	89	73	54
	Centre	Same		51	99	118	137

Differences in the numbers of eggs laid by birds in relation to nest site location and pair status are not, therefore, a direct result of the age structure of the birds making up each group.

5.2.3 Breeding Ages of Both Members of the Pair and Clutch Size

In Table 5.3 the mean number of eggs laid by pairs of birds is shown in relation to the status of the pair and also the breeding ages of both the male and female partner. Clutch size increases with the breeding age of each partner. The largest clutches are, therefore, laid by pairs of old birds, whilst the smallest are produced by pairs of first breeders (clutch size distribution given in Appendix 5.2). There is a consistent and, in some cases, significant reduction in clutch size associated with change of mate amongst corresponding age groups of birds.

Changes in clutch size with breeding age do not result from the direct effect of date of laying since the trends found here do not correspond to those in Table 4.3, Chapter 4, and, similarly, the effect of pair status is independent of both breeding age and date of laying. Data have not been broken down by centre and edge, thereby maintaining sample sizes, but the overall trends remain, after the effect of nest site location is removed, although they are less marked.

5.2.4 Date of Laying and Clutch Size

Clutch size increases during the first quarter of the breeding season, reaching a peak amongst birds nesting 7-10 days before the mean date of laying for the colony as a whole. Thereafter, there is a gradual decline as the season progresses. This relationship may be described by the polynomial expression:

$$\text{Clutch Size} = -0.0696 + 0.0719(x) - 0.00056(x)^2$$

(where x = Relative Date of Laying + 50 days)**

$r = 0.35,\ N = 1606,\ P < 0.001$

** adding 50 to the relative date of laying removes the problem of squaring a negative number.

TABLE 5.3 : The Mean Clutch Size produced by Different Pairs, grouped according to the Breeding Ages of the Two Birds and Pair Status

Mean Clutch Size and Sample Sizes

			Male Breeding Age		
			1	2-5	6-19
Change Mate	Female Breeding Age	1	1.83 (206)	1.98 (106)	2.15 (20)
		2-5	1.99 (124)	2.04* (155)	2.07 (55)
		6-19	2.05 (40)	2.09 (91)	2.13 (46)
Same Mate	Female Breeding Age	2-5		2.14* (282)	2.24 (54)
		6-19		2.19 (111)	2.27 (225)

* Significant difference : $\chi^2_2 = 6.04$, $P < 0.05$

Clutch size distribution for each group is shown in Appendix 5.1

Coulson and White (1961) found that the average clutch size laid by Kittiwakes at North Shields declined in a linear fashion throughout the breeding season by approximately 9% per week. The corresponding decline in other seabird species is lower; Herring Gull (5-6%), Red-billed Gull (3%) and Ring-billed Gull (2%) (calculated from data in Parsons 1975a, Mills 1973, Chardine 1978). The change is more marked in the Kittiwake, in the same way that the variation in clutch size with breeding age was greater, reflecting again the fact that this species tends to show less variation in egg size than other seabirds (Coulson *et al.* 1969).

The initial rise in clutch size during the early part of the breeding season has only been recorded in birds producing two broods a year; for example, the Robin (Lack 1946) and the Song Thrush and Mistle Thrush (Snow 1955), although papers on the Kestrel (Cave 1968) and the Red-billed Gull (Mills 1973) contain data for single-brooded species which show a slight increase at the beginning of the season but which were too small to warrant discussion. With increased sample sizes, particularly for clutches laid early in the year, it is possible that a more marked rise may be recorded in these and other species.

5.2.5 Date of Laying, Female Breeding Age and Clutch Size

In Table 5.4 data have been broken down to separate the effects of both female breeding age and date of laying. The tendency for an increase in clutch size amongst older birds is maintained within a group of females breeding at a particular time in the year. Similarly, the overall pattern of an initial increase in clutch size, followed by a gradual decline through the breeding season, is found in each age group, although the initial rise is less marked amongst younger birds and first breeders. (Coulson and White (1961) noted that the decline

TABLE 5.4 : The Relationship between Relative Date of Laying and Clutch Size amongst Females of the Same Age

Relative Date of Laying	Female Age (years)				
	1	2	3-4	5-7	8-19
	Mean Clutch Size				
+30 → +16 (early)	2.00	2.00	2.00	2.25	2.00
+12 → +16	2.00	2.18	2.18	2.18	2.48
+ 6 → +11	2.04	2.25	2.24	2.36	2.25
0 → + 5	2.02	2.12	2.10	2.24	2.27
- 1 → - 6	1.82	2.00	2.04	2.07	2.18
- 7 → -10	1.85	1.87	1.86	2.00	1.92
-11 → -15	1.81	1.91	1.85	1.67	2.06
-15 → -33 (late)	1.49	1.55	1.80	1.64	1.77
	S.D. amd Sample Sizes				
+30 → +16	15	7	6	8	4
+12 → +16	19	11	22	22	21
+ 6 → +11	57	48	62	58	57
0 → + 5	97	69	128	133	115
- 1 → - 6	73	51	74	72	73
- 7 → -10	40	15	21	18	24
-11 → -15	32	11	20	12	16
-15 → -33	47	11	10	14	13

in clutch size through the breeding season was more pronounced amongst older birds.) The two effects of date of laying and female breeding age are, therefore, independent of each other. This independence has also been shown in Pied Flycatchers and Red-billed Gulls (von Haartman 1967, Mills 1973).

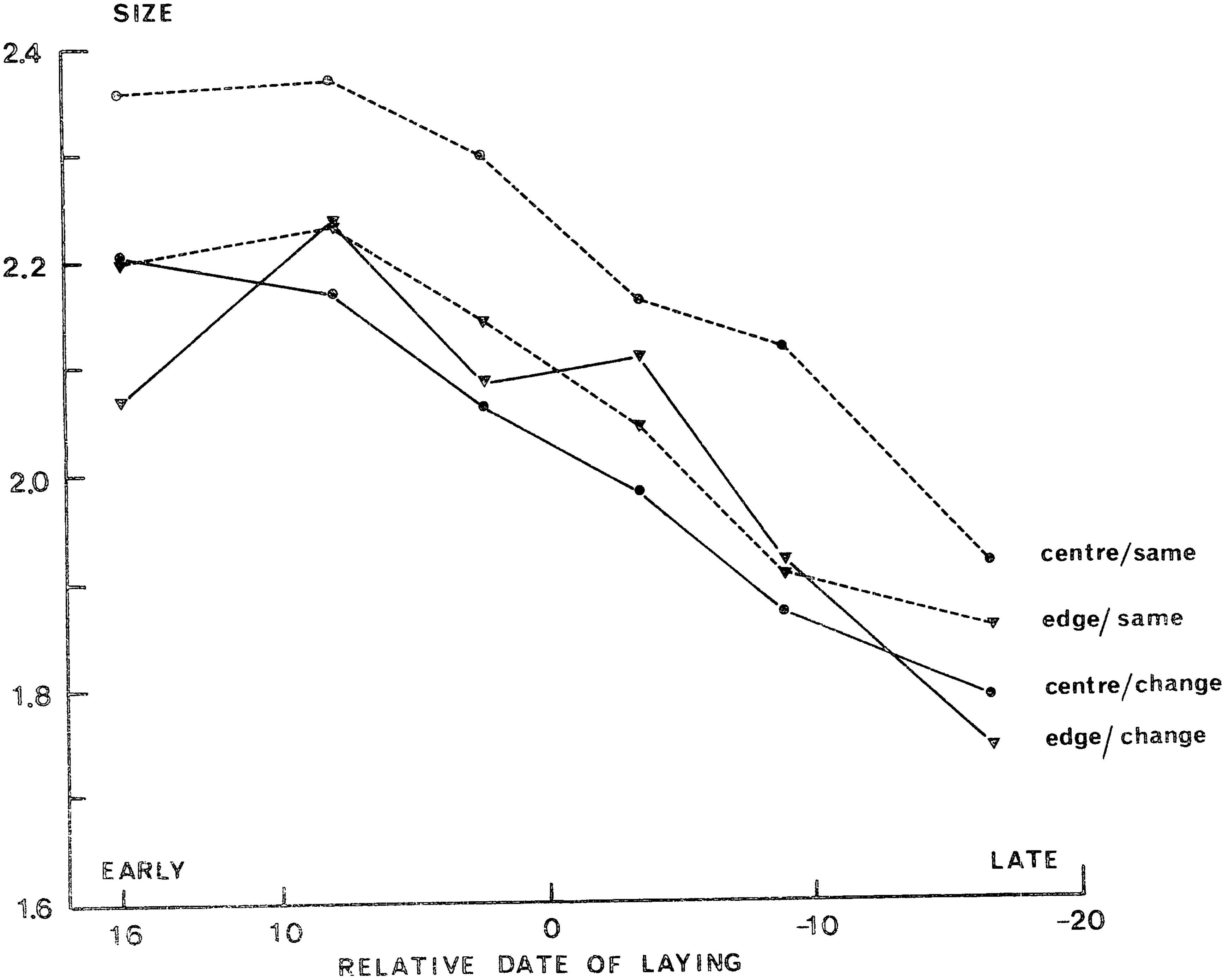
The progressive decline in clutch size through the breeding season (Coulson and White 1961) could in part be explained in terms of the breeding age structure of the birds nesting at different times since it was thought that, overall, date of laying advanced with breeding age. Since in the last chapter it was shown that older birds tend to breed towards the middle of the season, many of the earliest layers will be young birds or first breeders. This tendency will, therefore, enhance the initial rise in clutch size at the start of the season, which is recorded for the colony as a whole.

5.2.6 Date of Laying, Nest Site Location, Pair Status and Clutch Size

The relationship between clutch size, pair status and nest site location is independent of date of laying amongst experienced females (Figure 5.3) and at all times in the breeding season birds nesting in the centre of the colony which have retained the same mate lay consistently larger clutches than the other three groups.

The distribution of laying dates of the four groups (defined by nest site location and pair status) is such that centre birds retaining the same mate constitute a higher proportion of pairs which lay before the mean: 39% (759) c.f. 23% (446) of pairs laying after the mean. The larger clutches laid by the group 'centre-same' will therefore independently enhance the initial rise in clutch size at the beginning of the season, in addition to the effect of the changing age structure of birds laying at different times.

Figure 5.3 : The relationship between clutch size and relative date of laying for experienced females grouped according to both nest site location and pair status


SIZE
2.4
2.2
2.0
1.8
1.6
EARLY
LATE
16
10
0
-10
-20
RELATIVE DATE OF LAYING
centre/same
edge/ same
centre/change
edge/ change

5.2.7 Changes in the Number of Clutches of each size laid at different times in the Breeding Season

The pattern of laying of one, two and three egg clutches all approximate to a normal distribution (Figure 5.4). The distribution of two egg clutches extends throughout the breeding season and has a mean of 19 May (the same as that of all eggs laid in the colony). Three egg clutches are all started within a 36 day period, mainly during the first half of the season; in fact, 74% of the total are laid before the colony mean. One egg clutches do not appear until 6 May, 17 days after the start of the breeding season and the spread of laying in this group is large. In most years the first clutches laid in the colony contain only two eggs, whilst the last often only contain one.

5.2.8 Multivariate Analysis of Within Year Variations in Clutch Size

Multivariate analysis shows that clutch size is primarily correlated with date of laying (Table 5.5) although this is modified by the independent effects of pair status, nest site location and female breeding age. Although there is a significant correlation between male age and clutch size, this is found to result from the close correlation between the breeding ages of the two members of the pair, and any effect of male age disappears when the variable log. female breeding age is entered into the analysis.

Only 12% of the variation can be explained in terms of these factors, making apparent the need to investigate the effect of individual differences between females.

Figure 5.4 : The Pattern of Laying of Clutches of One, Two and Three Eggs

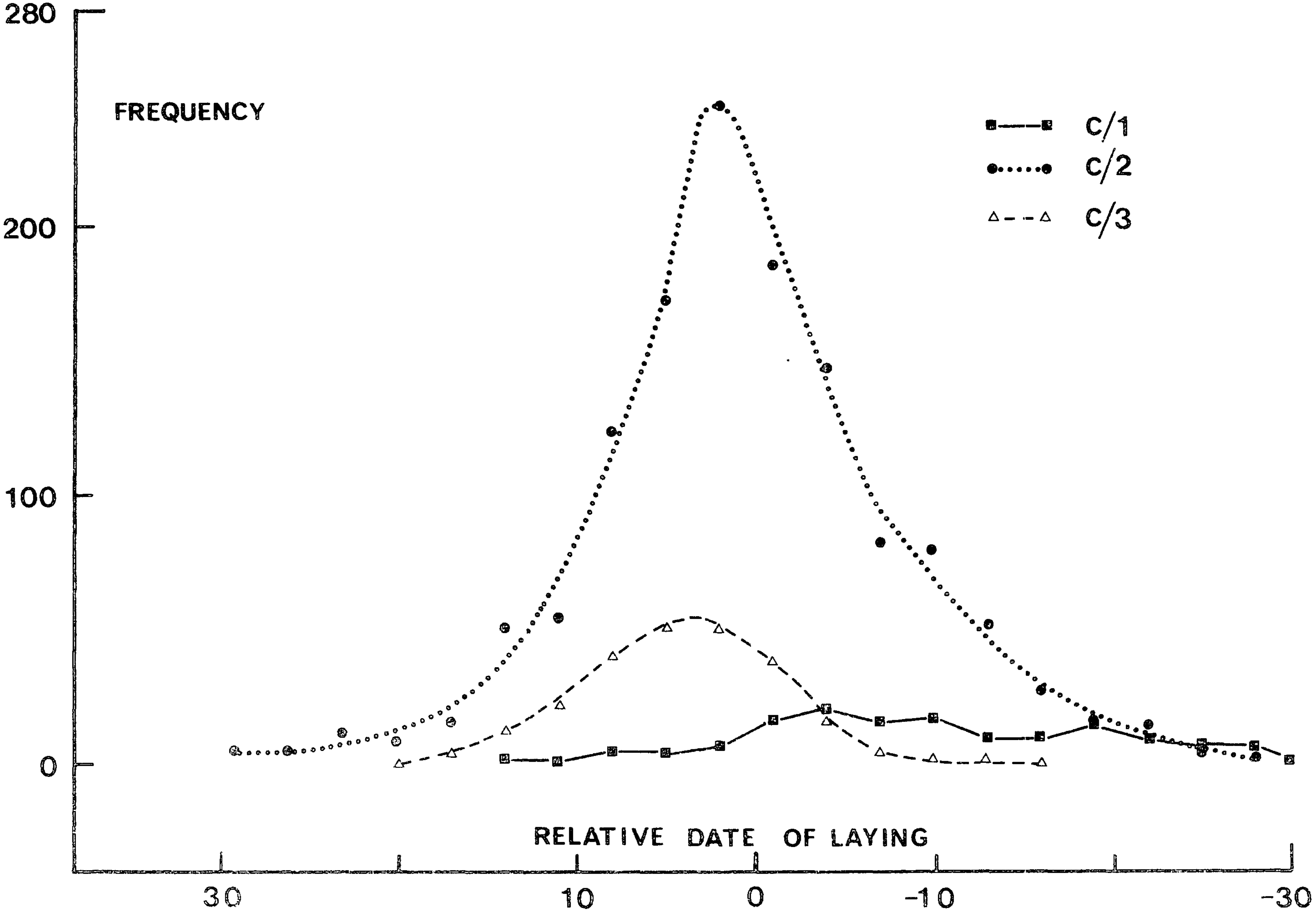

280
200
100
0
FREQUENCY
C/1
C/2
C/3
RELATIVE DATE OF LAYING
30
10
0
-10
-30

TABLE 5.5 : Multivariate Analysis - Factors associated with Variations in the Number of Eggs laid by Experienced Females

Correlation Matrix

	Clutch Size	Nest Location	Pair Status	Female Age ($\log_{10}$)	Male Age ($\log_{10}$)	Date	Date^2
Clutch Size	-	0.14	0.15	0.11	0.15	0.27	0.25
Nest Location		-	0.08	0.06	0.14	0.23	0.23
Pair Status			-	0.18	0.40	0.07	0.05
Female Age ($\log_{10}$)				-	0.41	-0.02	-0.03
Male Age ($\log_{10}$)					-	0.15	0.14
Date						-	0.99
Date^2							-

Regression Model

Dependent Variable = Clutch Size

Variables in Equation	Regression Coefficient	Standard Error	P
Date	0.062	0.011	< 0.001
Pair Status	0.103	0.027	< 0.001
Date^2	-0.0005	0.0001	< 0.001
Female Age ($\log_{10}$)	0.153	0.052	< 0.01
Nest Location	0.063	0.027	< 0.02

C = 0.054 N = 1183 r = 0.34

Pair Status : 0 = change mate 1 = same mate
Nest Location : 0 = edge nest 1 = centre nest
Date = Relative Date of Laying +50

5.3 Individual Variation in Clutch Size

5.3.1 Number of Eggs laid by Individual Females in Successive Years

Certain individual Kittiwakes have been found to lay clutches of three eggs in successive breeding seasons (Coulson and White 1961). To illustrate this tendency data have been broken down (in Table 5.6) to show the number of eggs laid in each year by twelve females which have bred at North Shields for at least 15 years. Although, on average, 76% of birds in the colony lay clutches of two eggs, certain of these individuals are seen to lay clutches of three eggs in a number of years (Female 204.4875 laid three egg clutches in 13 out of 14 years.) The mean clutch size varies between 1.93 in two cases, to a maximum of 2.93. Over 15 years, therefore, one female in this small group has laid fifteen more eggs than two others.

To quantify the amount of variation in clutch size which can be accounted for in terms of individual differences, data from experienced females which have bred at least twice have been subjected to an analysis of co-variance technique described in Section 4.3.2 of the previous chapter (Table 5.7). After removing any effect of breeding age, pair status, nest location and date of laying, individual differences between females account for 39% of the remaining variation in clutch size. The repeatability of this factor is 0.75, showing a marked tendency for females to lay the same number of eggs in different years.

5.3.2 Pair Status and the Number of Eggs laid by the Same Female in Consecutive Years

A comparison of the number of eggs laid by the same female in consecutive breeding seasons shows that 72% of birds lay the same clutch size in each year. 15% of birds lay larger clutches in the present year,

TABLE 5.6 : Consistency in the Number of Eggs Laid by Individual Females in Different Years

																Totals				%
Breeding Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	C/1	C/2	C/3	mean	C/2
							Number of Eggs in Clutch													
Ring Number																				
EC 11330	2	3	2	2	2	3	2	3	3	3	3	2	2	2	2	0	9	6	2.40	60
EC 11778	-	2	2	2	2	-	2	2	2	3	2	2	2	2	2	0	12	1	2.08	92
202.0006	1	-	2	2	2	3	2	2	2	2	2	2	2	2	3	1	11	2	2.07	79
202.8402	-	2	-	-	3	2	2	2	2	-	2	2	2	3	3	0	8	3	2.27	73
202.8794	2	2	2	2	2	2	2	2	-	3	2	2	2	2	2	0	13	1	2.07	93
204.4067	2	3	3	3	3	3	3	3	3	3	2	3	-	1	2	1	3	10	2.64	21
204.4075	2	-	-	3	3	2	2	2	2	2	3	-	2	3	2	0	8	4	2.33	67
204.4874	-	2	2	2	2	2	2	2	2	2	2	2	2	2	2	0	14	0	2.00	100
204.4875	-	3	3	3	3	3	3	3	3	3	2	3	3	3	3	0	1	13	2.93	7
204.4892	2	2	2	2	1	2	2	2	2	2	2	2	2	2	2	1	14	0	1.93	93
204.4917	2	-	2	2	2	2	2	2	2	2	2	1	2	2	2	1	13	0	1.93	93

TABLE 5.7 : Results of Analysis of Covariance - showing the degree of variation in clutch size in the colony which can be attributed to the tendency of some females to lay consistently larger clutches than others (after data have been corrected for the proximate factors listed below)

	Sum-Squares	d.f.	Variance
Between bird	90.051^a	195	0.4618^x
Within bird	142.419	931	0.1530^y
Total	232.470^b	1126	0.2065

$F(195,931) = 3.02$ $P < 0.01$

r^2 Individual Differences between Females $= a/b$ $= 0.387$

Repeatability $= x/(x+y)$ $= 0.751$

Factors included as covariates:

Pair Status : 0 = change mate, 1 = same mate

Nest Location : 0 = edge, 1 = centre

Log_{10} Breeding Age : of male and female

Relative Date of Laying

whilst 13% lay smaller clutches. This effect, which is independent of whether the bird retained the same mate as in the previous year, or changed mate, reflects both the large proportion of birds which lay two egg clutches and the annual increase in clutch size with breeding age.

By looking at the percentage of birds laying a particular clutch size in the previous year which produce one, two or three eggs in the present year (Table 5.8), the effect of change of mate emerges. Change of mate results in a slight increase in the proportions of birds which lay one egg clutches in the present year. However, its effect is more marked in the relative proportions of two and three egg clutches produced.

5.3.3 Change in Laying Date and Change in Clutch Size of Individual Females breeding in Consecutive Years

The correlation between the change in relative date of laying of a female in two consecutive years and the corresponding change in clutch size is positive and highly significant. Amongst females which retain the same mate, however, the correlation is lower ($r = 0.24$, $N = 656$, $P < 0.001$) than amongst individuals which change ($r = 0.38$, $N = 414$, $P < 0.001$). The slopes of the relationships indicate that later laying results in a reduction in clutch size (Same mate: 0.015 ± 0.003; Change mate: 0.019 ± 0.002) and there is no significant difference between the slopes in relation to pair status although the reduction in clutch size is slightly greater amongst birds which change.

Multivariate analysis (Table 5.9) shows that only the change in date of laying has a significant independent effect upon clutch size and suggests that for individual females differences in the number of eggs laid, associated with change of mate, result from the tendency for birds which change mate to lay later than those which retain the same mate.

TABLE 5.8 : The Number of Eggs Laid by the Same Female in Consecutive Breeding Seasons[**] in relation to whether the Bird changed Mate or not over the corresponding period

Change Mate Since Previous Year

		Clutch Size This Year			
		1	2	3	N
Clutch Size Last Year	1	11.4	82.9	5.7	35
	2	6.9	84.0	9.1	331
	3	4.0	64.0	32.0	50

Same Mate as Previous Year

		Clutch Size This Year			
		1	2	3	N
Clutch Size Last Year	1	6.1	84.8	9.1	33
	2	5.4	79.9	14.7	477
	3	2.1	34.2	63.7	146

[**] Data show the percentage of birds laying a particular clutch size in the previous year which produce one, two or three eggs in the present year.

TABLE 5.9 : Multivariate Analysis - Factors associated with Changes in the Number of Eggs laid by the Same Female in Consecutive Years

Regression Model

Change in Clutch Size = 0.021 + 0.017 (Change in Relative Date of Laying)

$r = 0.29$, $N = 1032$, S.E. Slope = 0.002

Variables included in the Analysis

Change in Clutch Size = clutch size this year - clutch size last year

Change in Male Age = age of this year's mate - age of last year's mate

Female Breeding Age ($\log_{10}$)

Pair Status : 0 = change mate 1 = same mate

Change in Relative Date of Laying = relative date of laying this year - relative date of laying last year

5.4 Between Year Variations in Clutch Size

Various explanations have been proposed for the annual variations in clutch size observed in single populations (reviewed in Klomp 1970). In studies on the Kittiwake, time of breeding and food availability have been the major factors linked to these changes (Barrett 1978, Belopol'skii 1961).

At North Shields the mean clutch size laid in each year has shown an overall decline since data were first collected in 1954 (Figure 5.5). Despite large variations in clutch size found between different age groups of birds and in relation to date of laying, the difference between the minimum and maximum annual means over the period of 25 years (1.94-2.17) is only 12%. There is a significant correlation between the mean date of laying of the colony in each year, and the resultant mean clutch size ($r = -0.60$), the relationship being described by the equation:

$$\text{Clutch Size} = 2.36 - 0.016\,(\text{Date of Laying})$$

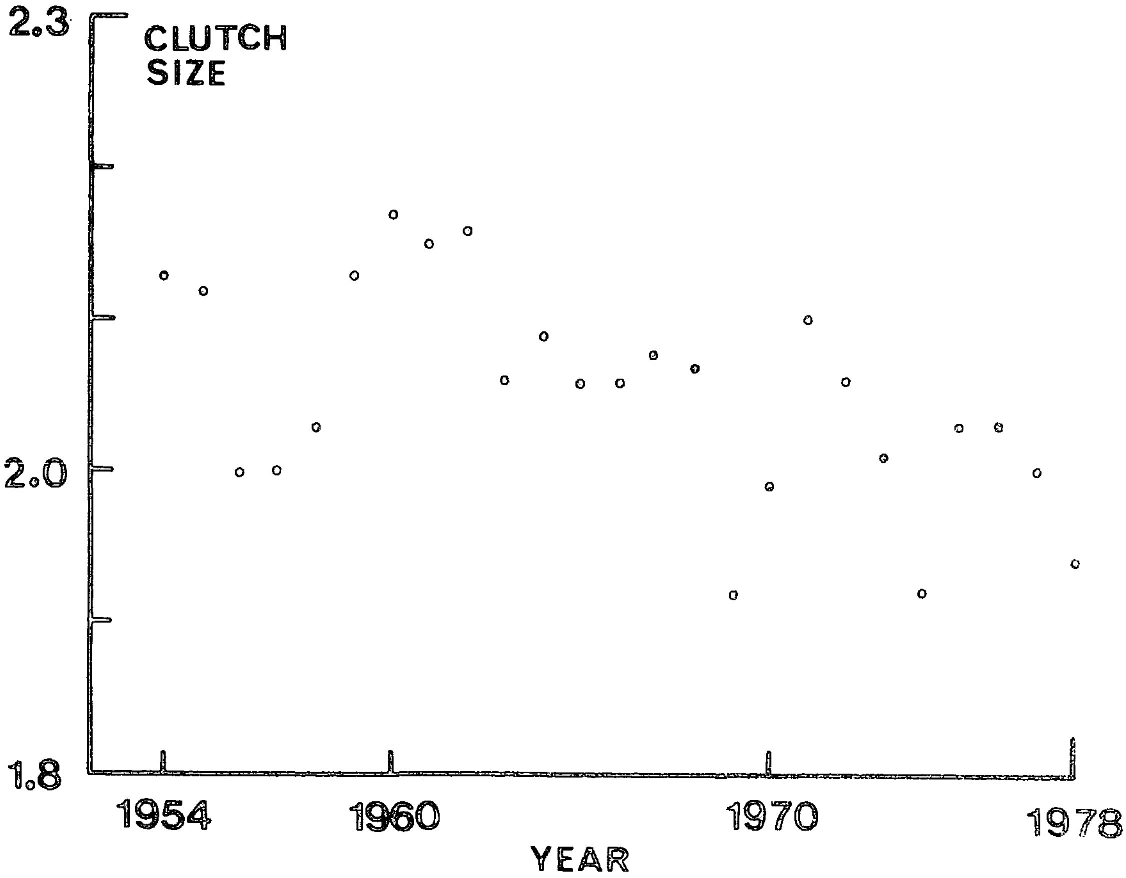
$$N = 25,\ \text{S.E. Slope} = 0.005$$

Annual variations recorded here are less marked than those reported by Belopol'skii (1961) for a colony of Kittiwakes in Arctic Russia (1.53-2.33 in only four years). In part, this may reflect the apparent stability of food supplies at North Shields and the consistency in time of breeding in different years. However, it also results from the fact that the decline in clutch size in relation to date of laying is more rapid in more northerly colonies (see below).

5.5 Variations in Clutch Size between Different Colonies

At the beginning of this chapter details were given of the mean clutch size recorded in different Kittiwake colonies throughout

Figure 5.5 : Annual variation in the mean number of eggs laid per pair by Kittiwakes nesting in the colony at North Shields. The mean clutch size has shown a significant decline over the period of this study (Slope = -0.012 ± 0.003)



the North Atlantic and along the Russian Coast. Barrett (1978), reviewing geographical differences in the timing of breeding in the Kittiwake, noted that, overall, the birds breed later in the northern parts of their range, and these differences were attributed to the fact that spring starts earlier and is warmer in the south. Local variations in the onset of breeding have been related both to differences in the age structure of populations and to food availability (Barrett 1978, Belopol'skii 1961, Coulson and White 1956). Colonial variations in clutch size follow similar trends and there is a significant correlation between the mean date of laying recorded in different colonies and the resultant mean clutch size: $r = -0.85$, $N = 5$, $P < 0.05$ (data used in this calculation are given in Appendix 5.3). In addition, despite the fact that data have been collected in a number of different ways, and in some cases means have been calculated from ranges of values, the regression line describing the relationship is very similar to that calculated from between year variations in the colony at North Shields.

Between Colonies : Clutch Size = 2.21 - 0.012 (Date of Laying)
N = 5, S.E. Slope = 0.003
Between Years (at N.S.) : Clutch Size = 2.36 - 0.016 (Date of Laying)
N = 25, S.E. Slope = 0.005

Geographical variation of clutch size in the Kittiwake is seen, then, to be related to the time of breeding in different colonies. Change in day length is generally accepted to be a proximate factor which is related to the seasonal decline in clutch size. Coulson and White (1961) suggested that it should be possible to test this hypothesis by looking at the relationship between clutch size and time of breeding for colonies in more northern regions where the increase in day length is more rapid. Data presented in Table 5.10 show the annual variations

TABLE 5.10 The Relationship between Date of Laying of the First Egg and Clutch Size in Different Years for Colonies in North Norway and Russia

Colony	Year	Mean Clutch Size	Laying Date of First Egg (in May)	Source of Reference
Hekkingen Norway	1974	1.89	15	Barrett (1978)
	1975	1.52	25**	
	1976	1.81	22	
Runneskholmen Norway	1974	1.98	21	Barrett (1978)
	1975	1.64	26	
	1976	1.80	24	
Karlov Islands East Murman	1937	2.33	11	Belopol'skii (1961)
	1938	1.53	26	
	1939	1.74	27	

** The first egg laid on Hekkingen in 1975 was in fact produced on 9 May. However, after three clutches had been started, laying ceased until 25 May.

Mean date of laying in this year, 2 June, was much later than that recorded for the colony in 1974 (26 May) in mean clutch size and date of laying of the first egg* in three colonies of Kittiwakes in north Norway (Latitude 69°N)** and Arctic Russia (Latitude 70°N). The regression equation describing the relationship between date of laying (x) and clutch size (y) in these colonies is:

$$y = -0.039x + 2.67, \quad r = -0.86, \quad N = 9$$

The slope of the relationship (-0.039 ± 0.008) is significantly steeper than that recorded for annual variations in clutch size at North Shields ($t = 2.44$, d.f. $= 32$, $P < 0.05$). In fact, the decline in clutch size with date of laying is twice as rapid in these colonies than in north east England, reflecting the more rapid change in day length.

5.6 Discussion

Clutch size has been shown to be primarily determined by date of laying, both within an individual year, between years and between different colonies. Unlike many other single brooded species which show a progressive decline in clutch size through the breeding season, an initial rise during the first quarter of the season was found in this study. Female breeding age has been shown to have a significant independent effect upon clutch size and, within individual pairs, this is modified, although not significantly, by the age of the male partner.

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* Belopol'skii (1961) gives only the date of laying of the first egg laid in each year, and not the mean.

** Latitude of North Shields Colony 55°N

The effects of pair status and nest site location appear to result primarily from the large clutches laid by birds nesting in the centre of the colony which have retained the same mate as in the previous breeding season. The distribution of laying dates of pairs in relation to all these factors (discussed in the previous chapter) independently enhance the pattern of change in clutch size through the breeding season.

Individual females exhibit a tendency to lay the same number of eggs in different years. In part, this results from the fact that the birds breed at a similar time in different seasons although analysis has shown that this tendency remains after any effect of date of laying is removed. For the Kittiwake at least the idea that clutch size and date of laying are controlled by a pair of linked genes (Koskimies 1957) is incorrect.

Lack (1954) suggested that clutch size in nidicolous species of birds has evolved to that which produces the largest number of surviving offspring. This idea has since been modified to take into account the effect of chick production upon adult survival (Charnov and Krebs 1974) since many birds lay fewer eggs than is most productive. These workers have, therefore, proposed the concept of 'optimal clutch size' instead of 'maximum clutch size'. The Kittiwake is an example of a species in which the modal clutch size is not the most productive (Section 7.2.4). Most gulls lay clutches which normally contain three eggs, whilst Kittiwakes usually only lay two. Cullen (1957) proposed that this is linked, not to the effect of clutch size upon adult survival, but rather to adaptations associated with the cliff-nesting habit of the bird. Chick loss through falling from the nest is an important cause of mortality in the Kittiwake (Section 7.2.2) and although no evidence could be found to support the idea, it seems likely that this would be a more frequent cause of death in larger broods. In addition, predation is less common and cannibalism absent, with the result that survival of eggs and chicks is higher than in many other species of ground nesting gulls (Cullen 1957).

In the previous chapter it was suggested that the timing of breeding of the Kittiwakes nesting at North Shields was independent of food availability, and there is no evidence of any change in food abundance which could account for the seasonal variation in clutch size (Coulson *et al.* 1969). Perrins (1970) suggested that in evolutionary terms the annual decline in clutch size could be related to the poorer chances of raising late-hatching young; producing a smaller brood would enable more food to be given to each chick. The role of seasonal changes in day length as a proximate factor controlling date of laying has been discussed earlier. It seems likely that in Kittiwakes, like Herring Gulls (Parsons 1975a), the determination of clutch size may also be linked to proximate factors centred around time of breeding. This idea is strengthened by the finding that the decline in clutch size with date of laying is more rapid in northern colonies where the increase in day length is also more rapid.

Klomp (1970), reviewing the proximate factors associated with changes in clutch size, admits that little is known on the subject. All explanations given in papers on this topic centre around either food availability or time of breeding. It is difficult, therefore, to offer an explanation for the independent effects of age, nest site location and pair status observed in this study.

Kittiwakes, like many other species, show an increase in breeding success with age, which is independent of clutch size (Section 7.2.8). There may be a selective advantage, therefore, for younger birds to produce smaller broods, thereby increasing either the survival chances of those chicks in that particular year or the longerterm survival of the adult. There are not data to support this idea although Wooller and Coulson (1977) suggested that intermittent breeding (failure to breed being the ultimate reduction in clutch size) and variation in the effort involved in each breeding attempt enables a balance to be maintained between production of offspring and survival. A third explanation of changes with respect to breeding experience, which is almost impossible to quantify, is that the 'quality' of birds improved with age. Coulson (1968) suggested that there is a difference in 'quality' between birds nesting in the centre and on the edge of the colony. He found that males recruited to the centre of the colony were heavier (during year of recruitment) than those entering the edge. In addition, he found that the weight of both males and females which subsequently survived for more than five years was greater, in both parts of the colony, than birds which died within five years of first breeding. Body weight may, therefore, be an indirect measure of bird quality, which may explain differences between the sizes of clutches laid in each part of the colony, although no correlation could be found between clutch size and body weight of first breeders in this study.

To discover why differences exist between the number of eggs laid by birds in relation to age or nest site location, and why certain birds breed at a particular time in the season, it may be necessary to try and quantify differences between birds, either in terms of their ultimate survival or in terms of differences in body size or weight.

CHAPTER 6 : EGG SIZE AND SHAPE

6.1 Introduction

Because of their economic importance to the poultry industry the size and shape of eggs is one aspect of avian biology which has previously been investigated at length (see Romanoff and Romanoff 1949). In studies of wild bird populations various papers have discussed the effects of clutch size, breeding age, date of laying and pair status upon egg dimensions, for example: Herring Gull (Davis 1975, Parsons, 1972, 1976), Kittiwake (Coulson 1963a), Red-billed Gull (Mills 1973, 1979), Shag (Coulson *et al.* 1969) and Yellow-eyed Penguin (Richdale 1955). In recent years the interest in oological studies has focussed on the effect of egg size upon chick survival. It was thought for a long time that older birds breed more successfully as a direct result of the accumulation of experience, but it has now been shown that even in wild birds there is a strong correlation between egg size and breeding success (Parsons 1970, Nisbet 1973). Since egg size increases amongst older birds, controversy exists as to the relative importance of each factor. Further consideration of this problem will be made in the next chapter. However, before this can be done it is necessary to re-investigate the factors affecting egg dimensions in the Kittiwake. Since Coulson (1963a) published a paper which was entirely dedicated to this topic, attention will be focussed upon aspects of the subject which have not yet been fully investigated, such as the tendency for individual females to lay eggs with similar dimensions in different years. In addition, only egg volume will be considered in the initial review of within year variations since it is generally accepted that this measure is most important biologically, being an indication of the amount of energy put into the egg and also the reserves available to the hatching chick.

Egg volume and shape index were calculated from the formulae given by Coulson (1963a):

Egg volume = Length x Breadth x Breadth x 0.0004866

Shape Index = (Breadth/Length) x 100

Length and breadth were measured as outlined in the methods section of Chapter 1.

Throughout this chapter the first egg of the clutch is referred to as the 'a' egg, the second as the 'b' egg and the third as the 'c'. In some of the sections which follow, only eggs from clutches of two will be used in the analysis, thereby removing the effect of clutch size upon egg size. In addition, the mean size or shape of the two eggs will be used, where order of laying is unimportant, enabling the inclusion of data from nests in which laying sequence is unknown.

6.2 Within Year Variations in Egg Size

6.2.1 Clutch Size, Laying Sequence and Egg Volume

Data presented in Table 6.1 are the same as those produced by Coulson (1963a) and, although sample sizes have been greatly increased, the results broadly confirm his earlier findings. Egg size decreases with laying sequence and both 'a' eggs, and 'b' eggs from clutches of two and three become larger as clutch size increases. These two trends mean that not only is the last egg of the clutch characteristically smaller than those laid earlier but also, there is a similarity in volume between the last eggs laid in clutches of two and three, and the egg from the clutch of one. Similar trends have been reported in the Common Tern (Gemperle and Preston 1955), Herring Gull (Parsons 1970, 1972), Red-billed Gull (Mills 1979), Ring-billed Gull (Ryder 1975) and others.

TABLE 6.1 : Egg Volume in relation to Clutch Size and Laying Sequence

	Mean Egg Volume (ml)		
	'a' egg	'b' egg	'c' egg
C/1	41.63		
C/2	43.60	41.97	
C/3	43.85	43.42	41.23

	S.D. and Sample Sizes		
C/1	4.38 (122)		
C/2	3.32 (722)	3.35 (722)	
C/3	2.75 (128)	3.17 (128)	2.91 (128)

6.2.2 Female Breeding Age, Clutch Size and Egg Volume

On average, there is no difference between the size of eggs laid in clutches of two by females breeding for the first or second time (Figure 6.1), although these birds lay significantly smaller eggs than individuals with a breeding age of more than two (see Appendix 6.1). The overall pattern of change shows an increase in egg volume with breeding age, and although amongst older age groups results are very variable, there is no evidence of any consistent decline. In all age groups the first egg of the clutch is significantly larger than the second (Appendix 6.1) and the size of the difference between the two eggs does not change with increasing age.

There is no consistent or significant difference between the volume of eggs from clutches of one and three laid by females of differing ages, although sample sizes are small (Table 6.2). In many age groups the 'c' egg from the clutch of three (which is similar in size to the one egg clutch) is significantly smaller than that of the 'a' and 'b' eggs.

Differences in egg volume in relation to clutch size and laying sequence are, therefore, independent of female breeding age.

The increase in egg size with breeding age reported in Red-billed Gulls (Mills 1979), Shags (Coulson *et al.* 1969) and Yellow-eyed Penguins (Richdale 1955) was more marked than that found here, reflecting the increased variability of clutch size in the Kittiwake. Although Mills (1979) found a slight decline in size of eggs laid by Red-billed Gulls which were older than 9, and Richdale (1955) a significant reduction in egg size amongst birds older than 14, there was no evidence of this amongst the oldest birds in this population.

Figure 6.1 : The relationship between egg volume (ml) and female breeding age (years) for eggs from clutches of two

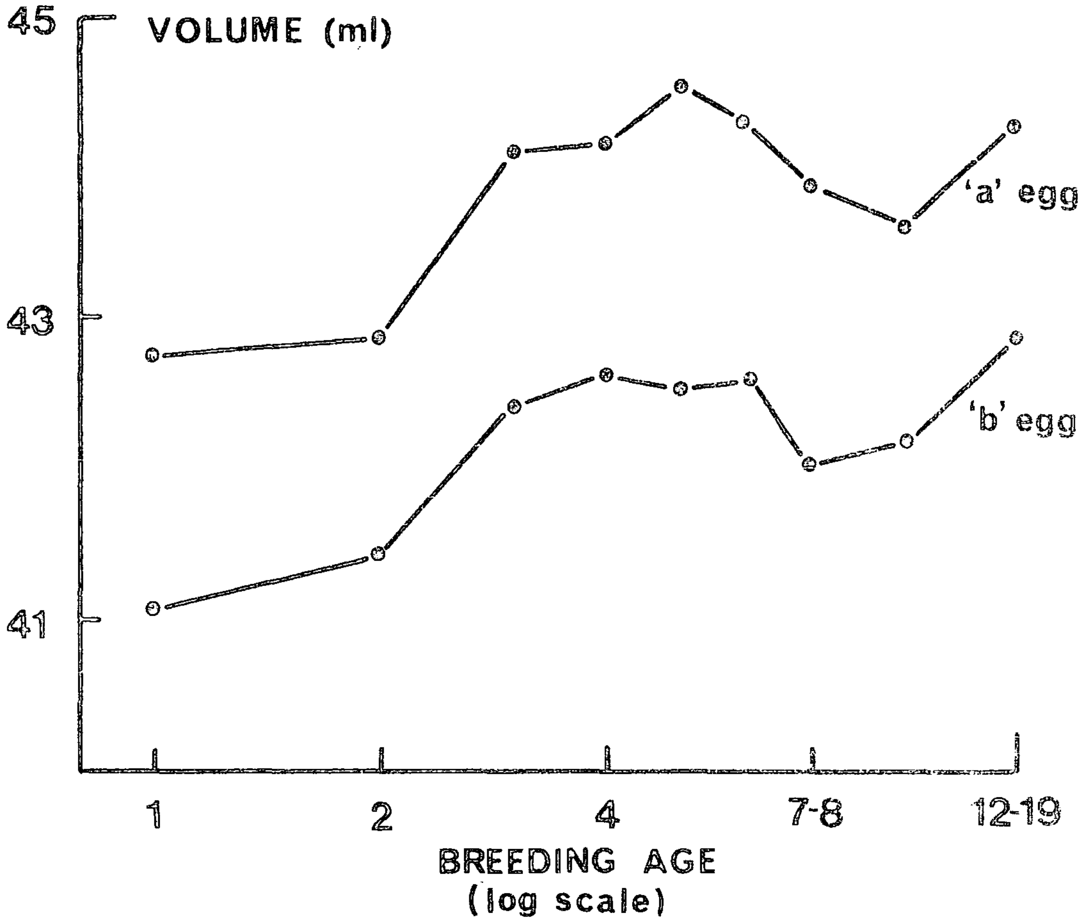


TABLE 6.2 : The Volume of Eggs from Clutches of One and Three laid by Females of Differing Ages

One Egg Clutch

Female Breeding Age (years)	Egg Volume (ml)	S.D.	Sample Size
1	41.52	4.62	48
2	40.41	4.53	18
3-4	41.55	4.80	17
5-7	43.22	3.81	20
8-19	41.47	3.41	14

Three Egg Clutch

Female Breeding Age (years)	Volume 'a' egg	Volume 'b' egg	Volume 'c' egg	Difference** 'a' and 'c'	Difference** 'b' and 'c'
1	44.45	43.04	41.20	n.s.	n.s.
2	43.66	43.89	42.31	n.s.	n.s.
3-4	43.83	43.61	41.21	t = 3.22	t = 2.98
5-7	44.04	43.42	40.85	t = 4.91	t = 3.65
8-19	43.58	43.23	41.21	t = 4.34	t = 3.12

	Standard Deviations			Sample Sizes
	'a' egg	'b' egg	'c' egg	
1	3.85	3.65	3.54	10
2	3.22	3.16	3.09	17
3-4	2.42	2.36	2.18	16
5-7	2.85	3.37	3.23	44
8-19	2.32	3.23	2.62	41

** Difference column shows results of Student's t test. Where t value is given, difference is significant at 1% level.

6.2.3 Pair Status and Egg Volume

On average, eggs laid in clutches of two by experienced females which retain the same mate are approximately 2% larger than those laid by birds which change mate, a difference which is significant (Table 6.3). This effect is independent of female breeding age, although amongst birds of the same age the difference between the two groups is not significant (Figure 6.2). In birds which change mate, egg size reaches a maximum amongst those with a breeding age of 3-4 years but in females which have retained the same mate, egg size continues to increase to a peak amongst birds breeding for the fifth, sixth or seventh time. The effect of pair status upon egg size therefore becomes more marked in older individuals. Retention of the same mate from the previous year was found to result in the production of larger eggs in Red-billed Gulls (Mills 1979) although the effect was not significant.

6.2.4 Male and Female Breeding Age and Egg Volume

In Table 6.4 data have been broken down to show the effects of the breeding ages of the two members of the pair upon egg volume (age groupings were chosen after reference to Figure 6.1). On average, pairs of first breeders laying clutches of two produce eggs which are 3-4% smaller than those produced by pairs containing at least one experienced bird, this difference being significant ($t = 5.40$, d.f. = 1031, $P < 0.001$). Amongst birds of a particular age there is no consistent change in egg size with increasing age of the partner although, on average, the largest eggs are produced by pairs of older birds. Ryder (1975) found similar differences in the size of eggs laid by Ring-billed Gulls, grouped according to whether the pair

TABLE 6.3 : The Volume of Eggs from Clutches of Two laid by Experienced Females which have retained the Same Mate as in the previous year or which have Changed Mate

		Change Mate	Same Mate	Difference t test
	Mean	43.44	44.22	t = 2.77
'a' Egg	S.D.	3.32	3.15	d.f. 532
	N	244	290	$P < 0.01$
	Mean	41.92	42.54	t = 2.16
'b' Egg	S.D.	3.36	3.24	d.f. 532
	N	244	290	$P < 0.05$

Figure 6.2 : The relationship between egg volume (ml) and female breeding age (years) for birds laying clutches of two which have retained the same mate as in the previous year (-----) and those which have changed (————)

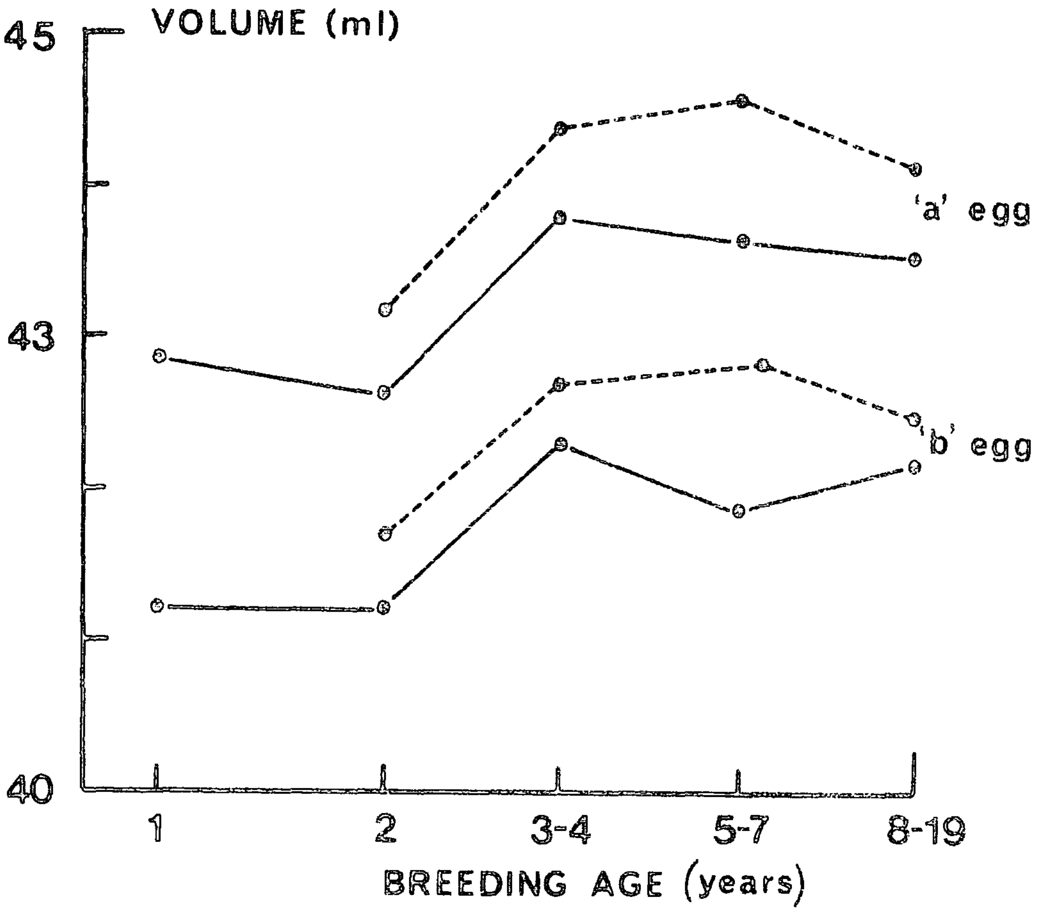


TABLE 6.4 : The Volume of Eggs from Clutches of Two, produced by Pairs grouped according to the Breeding Ages of both the Male and Female

		Male Breeding Age (years)		
		1	2	3-19
		Mean Volume of 'a' and 'b' eggs (ml)		
Female Breeding Age (years)	1	41.50	42.33	42.18
	2	42.82	42.26	42.03
	3-19	42.50	43.36	43.40
		S.D. and Sample Sizes		
Female Breeding Age (years)	1	3.07 137	3.40 36	2.78 58
	2	3.01 30	2.33 47	2.70 53
	3-19	2.71 94	2.77 76	3.17 502

	Mean	S.D.	N
Pairs containing one or more experienced birds	43.02	3.04	896

contained 0, 1 or 2 individuals with mature plumage (as opposed to immature plumage). Mills (1979) found a consistent increase in the size of eggs laid by particular aged females as the age of the male partner increased, an effect which was attributed to the date of laying of each of the groups.

6.2.5 Date of Laying and Egg Volume

Coulson (1963a) found that, on average, the volume of all eggs laid in the colony increased during the first half of the breeding season and then declined towards the end. If the third egg from the clutch of three was excluded from this analysis, however, an overall decline was found throughout. Figures 6.3 and 6.4 show the relationships between egg volume and date of laying for eggs from different-sized clutches. The 'a' egg from the clutch of one, the 'b' from the clutch of two and the 'c' from the three egg clutch all show a marked decline as the season progresses:

C/1 'a' egg : $r = 0.25$ Slope = 0.11 ± 0.04 $P < 0.01$ $N = 122$

C/2 'b' egg : $r = 0.15$ Slope = 0.06 ± 0.01 $P < 0.001$ $N = 1083$

C/3 'c' egg : $r = 0.09$ Slope = 0.05 ± 0.04 n.s. $N = 227$

There is no corresponding change in the size of the 'a' or 'b' egg from the clutch of three, and while there is a slight decline in the first egg from the clutch of two, this is not significant. The size of the difference between the last eggs of clutches of two and three and those laid earlier in sequence increases, therefore, as the season progresses. Parsons (1971) found that in Herring Gulls also the 'c' egg showed the greatest variation in clutches of three, although Barth (1967) had earlier found the opposite. Parsons explained this difference in results as being due to the fact that Barth included

Figure 6.3 : The relationship between egg volume (ml) and relative date of laying for eggs from clutches of one (▼) and three (●)

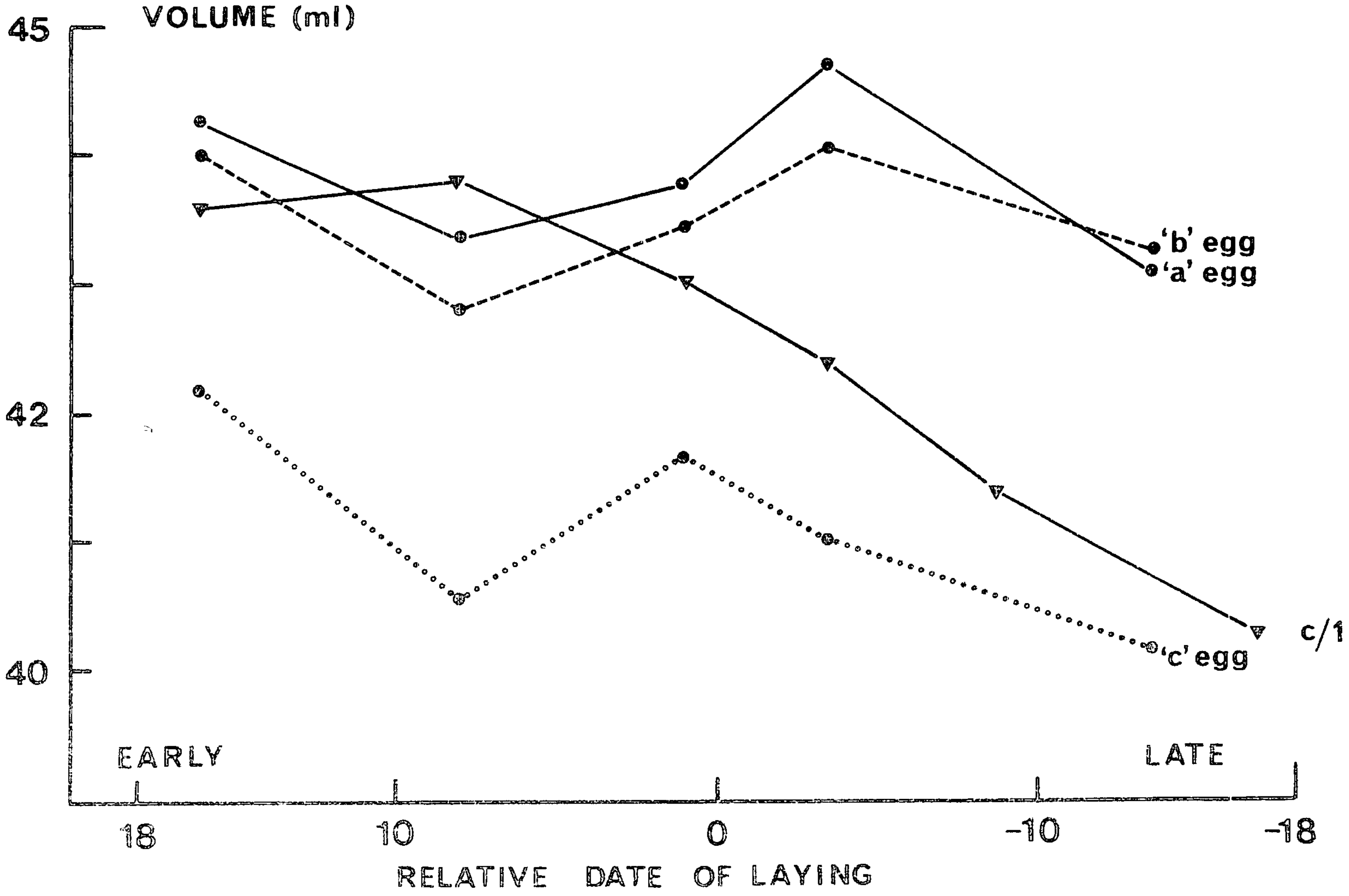
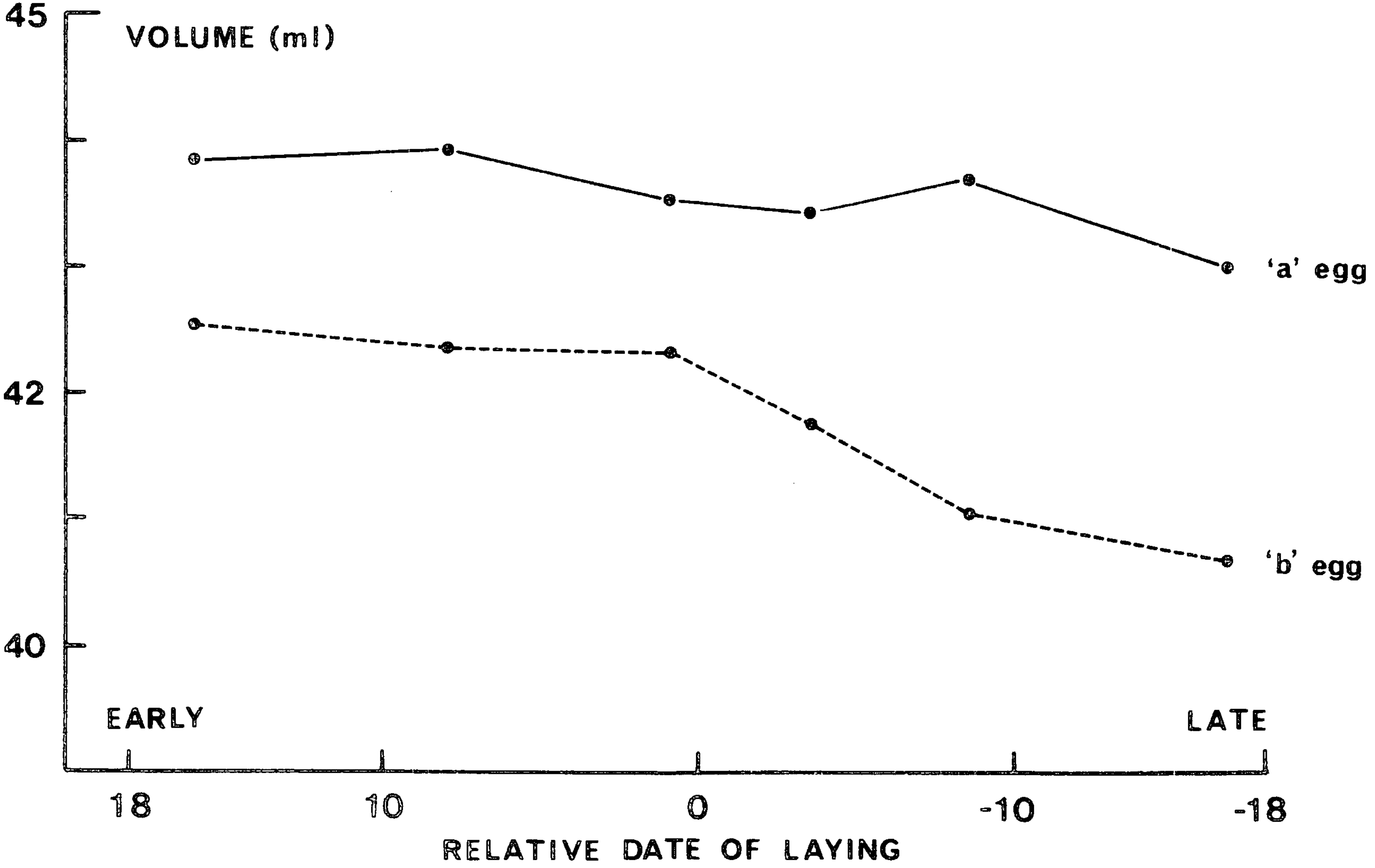


Figure 6.4 : The relationship between egg volume (ml) and relative date of laying for eggs from clutches of two



re-laid clutches in his analysis. (While these all tend to be laid in the latter part of the breeding season, the difference between the first two and the last egg is less marked in re-laid clutches than in those which may be termed 'normal' clutches.)

6.2.6 Multivariate Analysis of Factors associated with Variations in Egg Volume

Regression models describing the relationship between the volume of eggs from different-sized clutches, and all factors found to have a significant independent effect, are shown in Table 6.5.

Relative date of laying is the only factor found to have a significant independent effect upon the volume of eggs laid as clutches of one. On average, a delay in laying of 10 days results in a 2.6% reduction in egg size. (Pair status was not included in the analysis of clutches of one egg, permitting the inclusion of first breeders which make up 41% of the sample.)

The size of the 'a' egg from the clutch of two is influenced both by the breeding age of the female member of the pair (male breeding age has no significant independent effect) and the status of the pair, retention of the same mate and increase in breeding age resulting in the production of larger eggs. Both these factors independently affect the size of the 'b' egg and, in addition, a significant reduction in egg size is found to occur as the season progresses.

Pair status was the only factor included in the analysis which was found to affect the volume of 'b' and 'c' eggs from clutches of three, whilst none were found to have any significant effect upon the 'a' egg.

TABLE 6.5 : Multivariate Analysis - Factors associated with Variations in the Volume of Eggs from different sized Clutches

One Egg Clutch

Volume = 42.47 + 0.11 (Relative Date of Laying)

$R^2 = 9\%$ N = 115

Two Egg Clutch

'a' Egg Volume = 42.78 + 0.64 (Pair Status) + 1.11 ($\log_{10}$ Female Breeding Age)

$R^2 = 2\%$ N = 435

'b' Egg Volume = 41.05 + 1.24 ($\log_{10}$ Female Breeding Age) + 0.04 (Relative Date of Laying) + 0.55 (Pair Status)

$R^2 = 3\%$ N = 435

Three Egg Clutch

'a' Egg No significant factors

'b' Egg Volume = 42.58 + 1.25 (Pair Status)

$R^2 = 3\%$ N = 109

'c' Egg Volume = 40.30 + 1.18 (Pair Status)

$R^2 = 3\%$ N = 109

Factors included in the Analysis

Egg Volume

Relative Date of Laying

Log_{10} Female Breeding Age, Log_{10} Male Breeding Age

Nest Site Location : 0 = edge 1 = centre

Pair Status : 0 = change mate 1 = same mate

Pair status not included in analysis of one egg clutches since many are laid by first breeders.

6.3 Individual Variation in Egg Size and Shape

Little of the variation in egg size could be explained in terms of proximate factors such as date of laying, breeding age and pair status after the effects of clutch size and order of laying had been removed. Coulson (1963a) found that amongst six females breeding at North Shields there was a similarity in the size and shape of eggs laid by the same bird in different years, although too few data were available to test this idea statistically. The tendency for females to lay eggs with similar dimensions has been recorded in Herring Gulls (Davis 1975), Yellow-eyed Penguins (Richdale 1957) and various wader species (Vaisanen *et al.* 1972).

6.3.1 Characteristics of Eggs laid by the Same Female in Different Years

Appendix 6.2 is a simple visual representation of data showing that eggs from successive clutches of two laid by the same female have characteristic dimensions.

The results of an analysis of covariance (Table 6.6) show that after removing any effect of relative date of laying, female breeding age, nest site location and pair status, individual differences between females account for between 62% and 79% of the remaining variation in the mean size and shape of eggs from clutches of two.

The repeatability of these factors is very high, between 0.85 and 0.93, indicating a marked tendency for individuals to lay successive clutches of eggs which have very similar measurements.

6.3.2 Consistency of Egg Size and Shape within the Clutch

There is a highly significant positive correlation between the length, breadth, volume and shape index of the 'a' and 'b' eggs from clutches of two (Table 6.7). The slopes of the lines are all positive

TABLE 6.6 : Results of Analysis of Covariance : showing the amount of variation in the mean size and shape of eggs from clutches of two attributed to individual differences between females (after any effect of the factors listed below has been removed).

Egg Length

	Sum-Squares	d.f.	Variance
Between bird	2184.7481[a]	158	13.8275[x]
Within bird	569.9065	531	1.0733[y]
Total	2754.6546[b]	689	3.9981

$F(158,531) = 12.88 \quad P < 0.001$

r^2 Individual Differences between Females = a/b = 0.793

Repeatability = x/(x+y) = 0.928

Egg Breadth

	Sum-Squares	d.f.	Variance
Between bird	416.1057	158	2.6336
Within bird	192.5943	531	0.3627
Total	608.7000	689	0.8835

$F(158,531) = 7.26 \quad P < 0.001$

r^2 Individual Differences between Females = 0.684

Repeatability = 0.879

Factors included as covariates:

Female Breeding Age ($\log_{10}$)

Nest Site Location : 0 = edge nest 1 = centre nest

Pair Status: 0 = change mate 1 = same mate

Relative Date of Laying

/continued

TABLE 6.6 (contd.) : Results of Analysis of Covariance : showing the amount of variation in the mean size and shape of eggs from clutches of two attributed to individual differences between females (after any effect of the factors listed below has been removed).

Egg Volume

	Sum-Squares	d.f.	Variance
Between bird	4615.8792	158	29.2144
Within bird	1544.2498	531	2.9082
Total	6160.1290	689	8.9407

$F(158,531) = 10.05 \quad P < 0.001$

r^2 Individual Differences between Females = 0.749

Repeatability = 0.910

Shape Index

	Sum-Squares	d.f.	Variance
Between bird	1006.3772	158	6.3695
Within bird	612.8840	531	1.1542
Total	1619.2612	689	2.3502

$F(158,531) = 5.52 \quad P < 0.001$

r^2 Individual Differences between Females = 0.622

Repeatability = 0.847

Factors included as covariates:

Female Breeding Age ($\log_{10}$)

Nest Site Location : 0 = edge nest 1 = centre nest

Pair Status : 0 = change mate 1 = same mate

Relative date of laying

TABLE 6.7 : The Relationship between the Size or Shape of the 'a' and 'b' Eggs from Clutches of Two and the Consistency of this Relationship in Clutches laid by the Same Female in Consecutive Years

a. Relationship between 'a' and 'b' eggs from the same clutch

	r	Regression Coefficient	Standard Error	P
Length	0.70	0.683	0.026	<0.001
Breadth	0.68	0.724	0.029	<0.001
Volume	0.75	0.759	0.025	<0.001
Shape Index	0.60	0.596	0.030	<0.001

N = 709

x = size or shape of 'a' egg

y = size or shape of 'b' egg

b. Consistency of the above relationships in successive clutches laid by the same female

	r	N	P
Length	0.17	293	<0.002
Breadth	0.20	293	<0.001
Volume	0.12	293	<0.05
Shape Index	0.25	293	<0.001

$$x = \frac{\text{(size or shape of 'b' egg)}}{\text{(size or shape of 'a' egg)}} \quad \text{Last year}$$

$$y = \frac{\text{(size or shape of 'b' egg)}}{\text{(size or shape of 'a' egg)}} \quad \text{This year}$$

and indicate that, on average, the first egg is larger and has a higher shape index (is relatively broader) than the second. Further, there is a significant positive correlation between the ratio of the size or shape of the two eggs in clutches laid by the same female in consecutive years (Table 6.7, part b) despite year-to-year variations in time of breeding.

6.3.3 Pair Status and Variations in the Size and Shape of Eggs laid by the Same Female in Consecutive Years

As suggested earlier, there is a significant positive correlation between the size or shape of eggs from clutches of two laid by the same female in consecutive years (Table 6.8). In addition, this relationship remains irrespective of whether the female had changed mate or not over the corresponding period. In fact, correlations are higher amongst females which have changed mate than in those which have retained the same mate, the opposite of the trend found in Herring Gulls by Davis (1975). This suggests that females which retain the same mate lay different-sized eggs, usually larger, in the second year than in the first, whilst those which change mate produce similar-sized eggs in each. Coulson (1966) found that, on average, within the colony as a whole, experienced females which changed mate show little change in their date of laying, whilst those which retain the same mate lay progressively earlier as they get older. (In Chapter 3 it was shown that these relationships differed in the centre and edge of the colony although overall the trend for the colony as a whole was the same.) This suggests that there may be a relationship between the change in laying date of an individual female in consecutive years, and the corresponding change in the size and shape of eggs laid by the bird (see following section).

TABLE 6.8 : The Association between the Size or Shape of Eggs from Clutches of Two laid by the Same Female in consecutive years in relation to whether the Bird changed Mate or not over the corresponding period

		Females which change mate					Females which retain the same mate				
		r	b	S.E.	P	c	r	b	S.E.	P	c
Length	'a' egg	0.76	0.75	0.06	<0.001	13.98	0.69	0.69	0.05	<0.001	17.10
	'b' egg	0.68	0.67	0.07	<0.001	18.04	0.63	0.64	0.06	<0.001	19.82
Breadth	'a' egg	0.72	0.73	0.07	<0.001	10.93	0.57	0.51	0.06	<0.001	20.01
	'b' egg	0.53	0.49	0.07	<0.001	20.53	0.51	0.46	0.06	<0.001	21.46
Volume	'a' egg	0.77	0.82	0.06	<0.001	8.02	0.66	0.66	0.06	<0.001	15.57
	'b' egg	0.57	0.54	0.07	<0.001	19.70	0.62	0.59	0.06	<0.001	17.51
Shape Index	'a' egg	0.71	0.63	0.06	<0.001	27.19	0.61	0.56	0.05	<0.001	32.16
	'b' egg	0.67	0.66	0.07	<0.001	25.30	0.48	0.49	0.07	<0.001	37.58
		N = 115					N = 176				

Equations of the form : $y = bx + c$

where : y = size of shape of eggs laid this year
x = size or shape of eggs laid last year

The slopes of the regressions in Table 6.8 are all lower than unity and the intercepts pass through a value which is greater than zero. This indicates that while, on average, females tend to lay larger eggs in the present year than the last, the change in egg size over this period is more marked amongst birds which laid smaller eggs in the first year. Increase in egg size with female breeding age has been shown (Figure 6.1) to be greater amongst younger individuals; the same birds which tend to lay the smallest eggs in the colony. To remove the possibility that the results obtained in Table 6.8 are an age effect, data referring to egg volume have been split up into two groups according to the age of the female (Table 6.9). In both age groups the trends discussed above are seen to remain, although the slopes of the relationships are steeper for older females than for young, the intercepts lower and the correlations higher. This confirms the earlier finding that there is less change in egg size with increasing age amongst older birds, but still shows that the annual increase is more marked amongst birds which originally produced smaller eggs in the previous year.

6.3.4 Change in Date of Laying of Individual Females Breeding in Consecutive Years and the Corresponding Change in the Size and Shape of Eggs laid by those Birds

Females laying clutches of two, and which breed earlier in the present year than they did in the last, show a corresponding increase in the size of eggs produced (Table 6.10). This effect is more marked in the breadth of the eggs than the length, with the result that shape index tends to increase also. Correlations are higher and slopes greater in the relationships for the breadth, volume and shape index of the 'b' egg than the 'a', reflecting again the more marked decline in size of 'b' eggs laid at different times in the season, reported earlier.

TABLE 6.9 : The Association between the Volume of Eggs laid by the Same Female in consecutive years in relation to the age of the Bird and the Status of the Pair

	Young Females (2-5 years)					Old Females (6-19 years)				
	r	b	S.E.	P	c	r	b	S.E.	P	c
Females which change mate										
'a' egg	0.77	0.82	0.08	<0.001	8.20	0.75	0.85	0.12	<0.001	6.71
'b' egg	0.49	0.46	0.09	<0.001	22.90	0.67	0.66	0.12	<0.001	14.66
	N = 77					N = 38				
Females retaining same mate										
'a' egg	0.58	0.59	0.09	<0.001	18.92	0.73	0.71	0.07	<0.001	12.79
'b' egg	0.58	0.50	0.08	<0.001	21.32	0.66	0.67	0.08	<0.001	13.97
	N = 80					N = 96				

Equations of the form : $y = bx + c$
where : y = volume of eggs laid this year
x = volume of eggs laid last year

TABLE 6.10 : Change in the Relative Date of Laying of Individual Females in Consecutive Years and the corresponding Change in the Size and Shape of Eggs from Clutches of Two

Egg Size or Shape		r	Correlation Coefficient	Standard Error	P
Length	'a' egg	0.11	0.0004	0.0002	<0.05
	'b' egg	0.04	0.0001	0.0001	n.s.
Breadth	'a' egg	0.16	0.0004	0.0001	<0.001
	'b' egg	0.26	0.0008	0.0002	<0.001
Volume	'a' egg	0.18	0.0011	0.0004	<0.01
	'b' egg	0.22	0.0017	0.0004	<0.001
Shape Index	'a' egg	0.01	0.00002	0.0001	n.s.
	'b' egg	0.14	0.0006	0.0002	<0.01

N = 290

x = (relative date of laying this year - relative date of laying last year)

y = (egg size or shape this year/egg size or shape last year)

Multivariate analysis (Table 6.11) indicates that change in date of laying is the only factor to have a significant effect upon change in egg size, and that this is restricted to changes in the breadth and volume of the 'a' and 'b' eggs and to the shape index of the 'b' egg.

6.3.5 Body Size and Egg Size

Lack (1968) and Coulson and Thomas (1978) found a significant positive correlation between the average body weight of different species of birds and the mean clutch volume laid by each. Very little data exist on the relationship between body size and egg size in single species, other than the work carried out on the Domestic Hen (e.g. Graham 1932) although Coulson (1963a) noted that the size of eggs laid by Kittiwakes increases towards the north of their range, as does their mean body weights.

Limited data exist on the body size of females caught at North Shields in their year of first breeding, although only two measures of size (wing length and body weight) are available. The data presented in Table 6.12 show the mean size of eggs laid by 'large' and 'small' birds. On average, larger birds produce larger eggs, although only in the relationship between body weight and egg length or volume are these differences significant.

Many of the factors found to affect clutch size in the previous chapter were also shown to have similar effects upon egg size in this chapter. Despite this, no correlation was found between body size and clutch size.

TABLE 6.11 : Multivariate Analysis - Changes in the Size and Shape of Eggs from Clutches of Two laid by the Same Female in Consecutive Years

Regression Models (Sample Size 278)

Length 'a' Egg No significant factors

Length 'b' Egg No significant factors

Breadth 'a' Egg

Change = 1.0036 + 0.0004 (Change in Relative Laying Date)

$R^2 = 2\%$

Breadth 'b' Egg

Change = 1.0030 + 0.0008 (Change in Relative Laying Date)

$R^2 = 6\%$

Volume 'a' Egg

Change = 1.0107 + 0.0010 (Change in Relative Laying Date)

$R^2 = 3\%$

Volume 'b' Egg

Change = 1.0108 + 0.0017 (Change in Relative Laying Date)

$R^2 = 4\%$

Shape Index 'a' Egg No significant factors

Shape Index 'b' Egg

Change = 1.0002 + 0.0007 (Change in Relative Laying Date)

$R^2 = 2\%$

Factors included in the Analysis

Change in Size and Shape of Eggs laid in Each Year
Change in Relative Date of Laying
Change in Breeding Age of Male Partner
Pair Status : 0 = Change Mate 1 = Same Mate

TABLE 6.12 : The Relationship between Body Size and Egg Size amongst Females breeding for the first time which lay Clutches of Two

Body Weight	Length (mm)	Breadth (mm)	Volume (ml)	Body Weight (gms)	
Less than 345g	54.20(2.01)*	39.61(1.17)	41.44(3.18)**	323.3(15.8)	62
More than 344g	55.24(2.22)*	39.90(1.05)	42.83(2.99)**	369.0(26.1)	75

Wing Length	Length (mm)	Breadth (mm)	Volume (ml)	Wing Length (mm)	
Less than 302mm	54.45(2.00)	39.60(1.06)	41.61(2.89)	296.7(4.7)	73
More than 301mm	55.09(2.37)	39.77(1.15)	42.45(3.18)	306.8(3.7)	65

* difference significant : $t = 2.88$, $P < 0.01$

** difference significant : $t = 2.62$, $P < 0.01$

All means are shown ± 1 S.D.

6.4 Between Year Variations in Egg Size

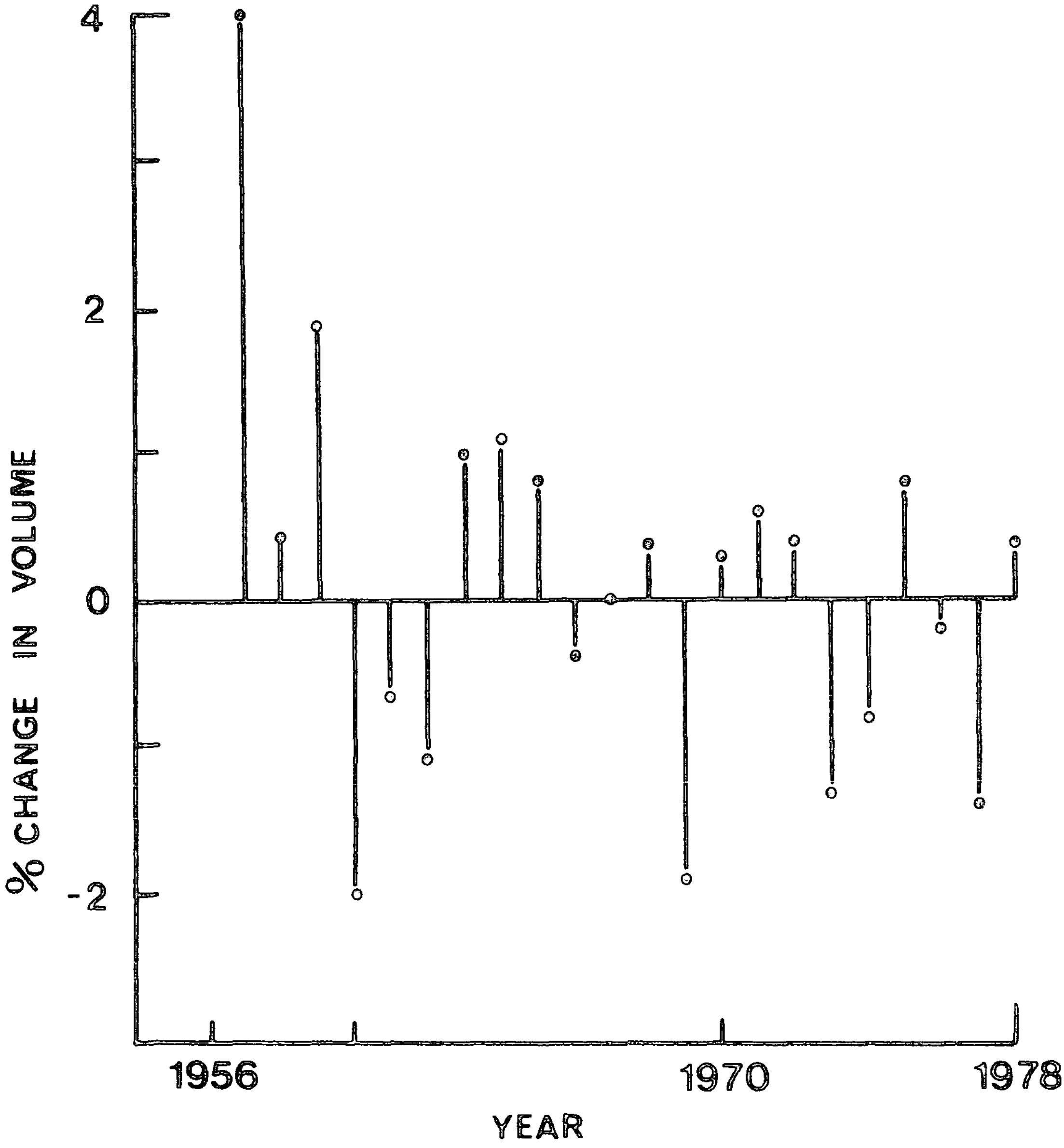
The mean volume of all eggs laid in clutches of two at North Shields since 1957 is 42.81ml (S.D. = 3.10, N = 1083). The annual deviation from this value (expressed as a percentage) is shown in Figure 6.5. Clearly, the size of eggs laid in the colony over the 22 years has remained remarkably consistent, varying on average by only 1% in any one year. Three of the eight years in which the annual deviation was more than 1% correspond to seasons early in the colony's development, in which fewer than 42 pairs laid clutches of two. The 'smaller' eggs laid in 1969, 1973 and 1977 coincide with three of the four years in which breeding was started'unusually late' (see Section 4.4, Chapter 4), although overall there is no correlation between the mean date of laying of the colony in each year and the mean volume of two egg clutches produced. In fact, no correlation was found between year-to-year changes in any of the variables discussed in earlier chapters and the annual variation in egg volume.

6.5 Discussion

Both clutch size and laying sequence affect the volume of eggs laid by Kittiwakes. Female breeding age and pair status have independent effects upon the volume of eggs laid in clutches of two, although neither factor was found to influence eggs from clutches of one and three. The effect of laying date upon egg size appears to be restricted to the last egg laid in the clutch (the 'a' egg in clutches of one).

Individual females have been shown to lay eggs which have characteristic dimensions, both within the clutch and from year to year. Only in part does this result from the tendency of the birds to breed at a similar time in different seasons and it seems likely that the 'size'

Figure 6.5 : Annual variations in the mean volume of all two egg clutches laid in the colony at North Shields



of the female is of equal or greater importance. In addition, of course, it is not possible to exclude the possibility that egg size is inherited, although data from North Shields are not plentiful enough to investigate this at present.

Mills (1979), Perrins (1970), Royama (1966) and others have discussed the importance of courtship feeding, changes in food availability through the season and the foraging ability of different age groups of birds upon the provision of additional nutrient for the female at the time of egg formation. In earlier chapters, however, it was suggested that date of laying and clutch size were independent of food availability for birds breeding in this colony and it seems unlikely that this factor would have any marked effect upon egg size.

Paludan (1951) and Parsons (1972) suggested that the reduction in the size of the last egg of the clutch is linked with physiological changes associated with the termination of laying, the follicle producing this egg being susceptible to the depressive influence of incubation. Accordingly, one would expect the depressive effect of incubation to be similar in 2 and 3 egg clutches after the 'a' egg is laid, when, in fact, this is not the case (Barrett 1978). Barrett therefore suggested that some other factor is also involved which determines the size of both the clutch and the last egg of the clutch.

The progressive reduction in the size of the last egg of the clutch through the season can only in part be explained in terms of the tendency for younger birds, which produce smaller eggs, to be late layers. Coulson *et al.* (1969) suggested that one reason for the smaller eggs laid by younger birds and late layers is that these individuals have insufficient time for the development and functioning of the reproductive system since they spend a shorter time at the colony before laying. In Chapter 4 it was shown that some of the earliest birds to lay in a particular year were first breeders or very young birds and these individuals spend very little time at the colony before laying. The independent effects of age and date of laying, however, indicate that early laying young birds produce larger eggs than those laying later in the season, which would suggest that this explanation may be too simple. It would explain why young birds breeding at a particular time lay smaller eggs than older individuals, although it would not explain the decline in the size of the last egg of the clutch through the season amongst birds of the same age. Parsons (1972) viewed the smaller size of the 'c' egg as a means of synchronising egg hatching although Barrett (1978) could find no correlation between egg size and incubation period in the Kittiwake. He did, however, find a seasonal shortening of the incubation period similar to that reported in the Herring Gull (MacRoberts and MacRoberts 1972, Parsons 1972) and this he attributed to changes in the behavioural responses of adults with respect to incubation. If, as Paludan (1951) and Parsons (1972) suggested, the reduction in the size of the last egg of the clutch is associated with the depressive influence of incubation upon the follicle producing it, this may explain the increase in the size of the difference between the last egg of the clutch and any laid earlier, as the season progresses. This effect would not, however, explain the seasonal decline in the size of the egg from the clutch of one, or the consistency in the size of the 'b' egg from the clutch of two.

It was suggested in the previous chapter that seasonal changes in clutch size may be linked to changes in some environmental factor such as day length. The progressive decline in the size of the last egg of the clutch may result from a similar controlling mechanism (egg size reduction may be regarded as an intermediate 'stage' in the reduction of clutch size).

There is, in general, a poor understanding of the mechanisms controlling the variation in egg size within the season. This is especially true of a colony such as North Shields where food availability cannot be considered a proximate factor. Since, in many studies of the breeding biology of birds, food has been found to be of major importance, it is likely that variations in egg size, with respect to such factors as laying date, may have evolved in response to food availability. As outlined earlier, Perrins (1970) suggested that the seasonal reduction in clutch size may have evolved in response to the poorer chance of raising late-hatched chicks. In the same way, an increase in the size difference between eggs from late-laid clutches may be a mechanism of enhancing the survival of chicks hatching early in sequence in years when food is short.

While several proximate factors have been shown to affect the size of eggs laid by different birds, the amount of variation explained by each is very small. Almost 75% of the variation in the volume of eggs from clutches of two could be explained in terms of differences between individual females. The tendency of some females to lay consistently larger eggs than others, even after the effects of breeding age, date of laying etc have been removed, may, as outlined above, reflect either differences in body size or any genetic differences between birds. The relationship between body size and egg size, which has been shown in a small group of first breeders, is likely to be linked both to the physical constraints put upon egg size by the anatomical structure of the individual and the 'physical condition' of the bird. Here again, it becomes apparent that there is a need to capture and measure breeding adults if more of the variation in egg size is to be explained.

CHAPTER 7 : Breeding Success

7.1 Introduction

In this chapter an attempt will be made to investigate the relationships between the various factors studied at North Shields which affect the breeding success of the birds and to separate the relative effects of each. This has been examined by the use of multivariate analysis and by a programme of egg exchange exercises similar to those carried out by Parsons (1970) and Nisbet (1978). In addition, by following in detail the fate of each egg and chick produced in the colony during the 1976, 1977 and 1978 breeding seasons it is hoped to provide additional data which will enable the breeding biology of this population to be compared with that of others.

Several measures of the annual breeding success will be used. In addition to the number of chicks hatched and fledged per pair, the following statistics have been employed in the analysis:

Hatching Success = (No. Chicks Hatched/No. Eggs Laid) x 100
Fledging Success = (No. Chicks Fledged/No. Chicks Hatched) x 100
Breeding Success = (No. Chicks Fledged/No. Eggs Laid) x 100
= (Hatching Success x Fledging Success)/100

As outlined above, during three years (1976, 1977, 1978), eggs were exchanged between different nests in the colony. As a result, analysis of within-year variation in success will only be made on data gathered before 1976. Much of the analysis will be restricted to clutches or broods of two, thereby removing any effect of clutch size upon hatching success, or brood size upon fledging success. Finally, data from the relatively few nests in which either eggs were damaged or stolen by human interference have been excluded from the analysis, with the result that the totals referring to clutch size do not agree with those reported earlier.

7.2.1 Summary of Breeding Success

An average of 61 out of every 100 eggs laid in the colony at North Shields give rise to fledged young (Table 7.1). Fledging success is higher than hatching success and in some years approaches 100% (Section 7.4). On average, each pair of breeding adults raises 1.3 chicks to fledging in each year. However, within as well as between years there is a high degree of variation in the number of chicks fledged by different pairs in the colony. Only 21% of birds failed to hatch any eggs, whilst 55% hatched all the eggs they laid. Only 4% of pairs which produced nestlings failed to fledge at least one, and 64% fledged all the chicks they hatched. In all, almost 43% of pairs were totally successful (i.e. they fledged chicks from all the eggs they laid) whilst 25% failed to fledge any chicks in a year ('Failed Breeders').

7.2.2 Causes of Egg and Chick Loss

The fate of all eggs laid in the colony during the 1976, 1977 and 1978 breeding seasons are recorded in Table 7.2 (excluding those taken by man).

In all, 95% of eggs laid at North Shields during these three years remained in the nest until the expected time of hatching. This is far higher than values obtained in other studies on Kittiwakes, 81% (Maunder and Threlfall 1972), 69-75% (Swartz 1966). Barrett (1978) found that, on average, 55% of eggs survived the incubation period but in 1975, at his study colony on Hekkingen, from a total of 92 eggs, only 4 remained 27 days after they had been laid. The main causes of

TABLE 7.1 : Summary Table - Breeding Success at North Shields

a. Overall Success

	Number per Pair				
	0	1	2	3	Mean
Clutch Size	-	132	1052	222	2.06
Chicks hatched/Pair	290	323	696	97	1.43
Chicks fledged/Pair	350	408	595	53	1.25

	Mean	S.E.	N
Hatching Success	69.4%	1.23	1406
Fledging Success	87.4%	0.99	1116
Breeding Success	60.7%	1.30	1406

b. Type of Success and Failure

	Frequency	% of Total (1406)
Total Hatching Failure	290	20.6
Total Hatching Success	773	55.0
Total Fledging Failure	60	4.3
Total Fledging Success	903	64.2
Total Breeding Success	601	42.8

TABLE 7.2 : Causes of Egg Loss during the Years 1976, 1977 and 1978

Category	Frequency	% of Total
1. Number of eggs laid	397	100
2. Number of chicks hatching	251	63
3. Undamaged, fully incubated eggs which fail to hatch	99	25
4. Eggs damaged during incubation	4	1
5. Eggs disappearing during incubation	17	4
6. Eggs laid outside the nest	1	-
7. Eggs deserted by breeding adults	16	4
8. Adults stop incubation to 'foster' neighbouring chick	6	2
9. Unknown	3	1

egg loss recorded by these workers includes predation by gulls and Ravens, nest collapse caused by high seas during storms and eggs being kicked from the nest by fighting adults. As outlined in earlier chapters, there is no evidence of any egg loss from non-human predators at North Shields. In addition, no nests were found to have collapsed. It seems likely, therefore, that the 17 eggs lost from the nest disappeared either as a result of 'clumsy' incubation by the adults or during fights (observed on only one occasion) or through the sudden disturbance of adults by people moving around inside the warehouse. It was noted that three of the nests from which eggs were lost had very shallow nest cups and, in one case, two eggs laid by a pair of inexperienced birds (on a nest from the previous year which had no new nesting material on it) rolled off soon after laying.

Only four eggs were found to have been damaged during incubation, but in two nests in which four eggs were laid (excluded from the analysis), in each case at least two of the eggs were either broken or pushed down into the nesting material at the bottom of the cup. This result confirms the view of Cullen (1957) that one of the factors influencing the evolution of clutch size in the Kittiwake is the constraint imposed upon the size of the nest cup by the cliff-nesting habit of the birds.

Three pairs of adults stopped incubating their own eggs to 'foster' chicks from neighbouring nests on the same window-ledge. In each case, the chicks were returned to their real parents on two occasions but were found back on their 'adopted' nest on the following visits. (Similar occurrences have been reported in a number of other years.) This result would seem to suggest that the stimulus offered by a begging chick is sufficient to cause an adult to stop incubating, although in a species which lays more than one egg this may be unexpected.

In each of the three cases the chicks involved were over ten days old. Since Kittiwake chicks normally hatch at two-day intervals, in a nest containing a chick of this age, any eggs remaining are unlikely to hatch. Having said this, Emlen and Miller (1969) showed in Ring-billed Gulls that the provision of a chick of any age (up to 6 days old), even to an adult which had only been incubating for less than two weeks, resulted in the birds adopting parental behaviour in preference to incubation. Similar results, although less conclusive, were also obtained by Beer (1966), Goethe (1953), Paludan (1951) and Weidmann (1956) in various other gull species.

Sixteen eggs failed to hatch as a result of abandonment by the adults. Coulson and White (1958a) noted several instances of first breeders deserting their eggs and suggested that the urge to incubate may not be fully developed in birds capable of breeding. Data from all years since 1954 confirm that the incidence of desertion is significantly higher amongst pairs containing at least one first breeder (Table 7.3).

Chick survival at North Shields is high. Amongst the 40 chicks which failed to fledge during the three years of this study it was not possible to differentiate between those which died in the nest and those which died as a result of falling from the nest. Excluding the possibility of predation, which was found to be a cause of chick mortality in the studies of Barrett (1978) and Maunder and Threlfall (1972) although not found to occur by Cullen (1957), the other main causes of chick loss reported for the Kittiwake are as follows: starvation, as a result of an inability of the adults to change rapidly enough from incubation to 'chick care'; thermal stress amongst very young chicks; inter-sibling aggression and simply falling from the nest (Barrett 1978, Coulson and White 1958b, Cullen 1957, Maunder and Threlfall 1972). In 1976 at North Shields, 8 chicks were found to have died during a four-

TABLE 7.3 : The Incidence of First Breeders amongst Pairs which desert their Eggs

	Pairs containing at least one First Breeder	Pairs containing no First Breeders
% Pairs which desert	6.98	1.84
Sample Size	559	869
Difference	$\chi^2_1 = 24.2$	$P < 0.001$

day period, all aged between 20 and 30 days. A post-mortem carried out on one* found no evidence of starvation and it was suggested that the bird may have died from some 'stress factor'. The nature of the post-mortem examination did not, however, exclude the possibility that a viral infection may have been responsible.

7.2.3 Time of Egg and Chick Loss

The age at which embryonic development ceased amongst eggs which failed to hatch, and the age at which chicks were found dead in the nest or disappeared from it, is shown in Table 7.4.

Of 80 eggs collected during the 1976, 1977 and 1978 breeding seasons, 45% showed no evidence of embryonic development. This group comprises both infertile or 'addled' eggs and those which contained embryos which failed to develop for more than two days. After this time the embryo and germinal disc is clearly visible (see Maunder and Threlfall 1972). 39% of eggs which showed some signs of development contained embryos which were less than 16 days old. There was no significant difference, however, between the proportions of eggs dying in each half of the incubation period. No correlation could be found between egg size and the age at which embryonic development ceased. Neither was there any relationship between this factor and clutch size or parental breeding experience. In such a small sample, however, it would be unlikely that any trends would emerge unless they were marked.

The proportion of chicks dying at a particular age for the years 1976, 1977 and 1978 show no clear pattern, although 36% of those

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* Post-mortem carried out by M.A.F.F. at Lasswade.

TABLE 7.4 : Age of Embryos and Chicks when Mortality occurred

1. Egg Stage (data from years 1976-1978)

Age of embryo (days)	Frequency
0-2	36
3-5	1
6-10	7
11-15	9
16-20	15
21-25	6
26-27	6

* (see below) Data on time of chick death are available for 200 (69.2%) of all chicks which died. The total number of available chicks is therefore taken as 1562 (69.2% of the total number of chicks hatched in the colony between 1954-1978)

2. Chick Stage

Age of chick (days)	Frequency (1976-1978)	Frequency (all years)	% of chicks available (all years)*
0 (Hatching)	1	27	1.7
1-5	13	49	3.2
6-10	6	42	2.8
11-15	5	22	1.5
16-20	1	14	1.0
21-25	10	16	1.1
26-30	3	10	0.7
31-35		5	0.4
36-40		5	0.4
41-45		6	0.4
46-50		3	0.2
51-55		1	0.1

which failed to fledge died either at hatching or within 5 days. Data for these three years are somewhat distorted by the group of older chicks which died during the 1976 breeding season. Similar data were obtained from daily worksheets used at North Shields in previous years. In some years this information was not available, whilst in others data only exist for part of the season. The sample is not, therefore, random neither is its accuracy certain. The results (Table 7.4) show that a total of 38% of chicks which failed to fledge died either at hatching or during the first five days thereafter, whilst almost 60% died up to 10 days after hatching. The decline in mortality with increasing age and, in particular, the tendency for most mortality to occur at or soon after hatching has been found in many larid species: California Gull, Common Tern, Glaucous-winged Gull, Herring Gull, Ring-billed Gull, Southern Black-backed Gull (Vermeer 1970, Morris *et al.* 1976, Harris 1964, Kadlec *et al.* 1969, Morris and Haymes 1977, Fordham 1964). Barrett (1978) found in his study of Kittiwakes that approximately half the chicks that died did so during the first ten days after hatching.

The major causes of chick mortality have been discussed in the previous section. Factors such as the change-over from incubation to parental behaviour and thermal stress will normally only influence the survival of very young chicks. Barrett (1978) reports that Kittiwake chicks become fully homeothermic when about 10 days old, but up to this time they are susceptible to adverse weather conditions.

7.2.4 Clutch Size, Brood Size and Success

There is no significant difference between the hatching success of eggs from clutches of two and three (Table 7.5). However, both have a significantly higher success than eggs from clutches of one (C/2 :

TABLE 7.5 : The Hatching Success of Eggs and Fledging Success of Chicks in relation to Clutch Size and Brood Size

a. Hatching Success

Clutch Size	No. Chicks hatched/Pair 0	1	2	3	Mean	Success Mean	(S.E.)	Number of Pairs
1	77	55			0.42	41.7	(4.29)	132
2	197	234	621		1.40	70.2	(1.41)	1052
3	16	34	75	97	2.14	71.3	(3.04)	222

b. Fledging Success

Brood Size	No. Chicks fledged/Pair 0	1	2	3	Mean	Success Mean	(S.E.)	Number of Pairs
1	31	292			0.90	90.4	(1.64)	323
2	29	109	558		1.76	88.0	(1.23)	696
3	0	7	37	53	2.47	82.5	(3.86)	97

c. Breeding Success

Clutch Size	No. Chicks fledged/Pair 0	1	2	3	Mean	Success Mean	(S.E.)	Number of Pairs
1	79	53			0.40	40.2	(4.27)	132
2	248	309	495		1.24	61.7	(1.50)	1052
3	23	46	100	53	1.82	60.8	(3.28)	222

$t = 6.31$, d.f. = 1182, $P < 0.001$; c/3 : $t = 5.63$, d.f. = 352, $P < 0.001$). Similar results have been reported in other studies on the Kittiwake by Barrett (1978), Coulson and White (1958b) and Cullen (1957), although Johansen (1977) quoted in Barrett (1978) found no significant effect of clutch size upon hatching success.

There is a consistent although not significant decline in fledging success as brood size increases although the actual number of chicks fledged per pair increases with brood size. These data also agree with the findings of Barrett (1978), Coulson and White (1958b) and Cullen (1957).

The net results of these two trends is that whilst the mean number of chicks fledged per pair increases with clutch size, breeding success of two egg clutches is greater than that of clutches of one and three.

7.2.5 Laying Sequence and Hatching Success

Amongst clutches of two in which only one egg hatches, and in clutches of three where one or two eggs hatch, there is a significant decline in hatching success with laying sequence (Table 7.6). Chardine (1976) found similar results in Ring-billed Gulls but Parsons (1971) could find no difference between the survival of 'a', 'b' and 'c' eggs from clutches of three in Herring Gulls.

Egg size declines with laying sequence in the Kittiwake (Section 6.2.1) and hatching success is correlated with egg size (Section 7.2.11). At least part of the variation observed here may therefore be explained in these terms. Another source of the variation may be linked to any differential fertility between eggs in relation to order of laying, although examination of unhatched eggs revealed no difference between the proportion of 'a' and 'b' eggs which showed no signs of embryonic development.

TABLE 7.6 : Hatching Success of Eggs in relation to Order of Laying (data from 1971-1978)

1. Two Egg Clutches in which only one egg hatches

	'a' egg	'b' egg	Sample Size
Hatching Success	75%	25%	73
Difference	$\chi^2_1 = 37.5, P < 0.001$		

2. Three Egg Clutches in which one or two eggs hatch

	'a' egg	'b' egg	'c' egg	Sample Size
Hatching Success	85%	75%	15%	20
Difference	$\chi^2_2 = 23.6, P < 0.001$			

3. Hatching Success of 'a' and 'b' eggs from clutches of two (in which only one egg hatches) laid during the first and second half of the season

		'a' egg	'b' egg	Sample Size
Hatching Success	Early* Started	71%	29%	41
	Late* Started	81%	19%	32

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* Early started clutches laid before the mean; late started laid after the mean.

A third and equally speculative explanation of the results may be connected with the change-over of adults from incubation to 'parental' behaviour after a chick appears in the nest. Any marked change in the behaviour of the adult after the first chick hatches could result in chilling or damage to those eggs which remain. Various workers have reported that hatching asynchrony increases through the breeding season (Courtney 1979, MacRoberts and MacRoberts 1972, Nisbet and Cohen 1975, Parsons 1972). Amongst clutches in which eggs hatch with greater synchrony there would be less time for any change in adult behaviour to occur before the eggs laid later in sequence hatch. The difference in hatching success between 'a', 'b' and 'c' eggs from early laid (more synchronous) clutches would accordingly be expected to be less marked than those laid later. Data from clutches of two used in this analysis support this idea although both differences between groups and sample sizes are small (Table 7.6).

7.2.6 Order of Hatching and Fledging Success

The last chick to hatch in broods of three in Herring Gulls has been shown to suffer a higher mortality than its siblings (Parsons 1970, 1971, Davis 1975) and a similar decline in the survival of chicks in relation to hatching sequence has been reported in Arctic Terns, Black-headed Gulls, Snow Geese and the South Polar Skua (Lemmetyinen 1972, Lundberg and Väisänen 1979, Syroechkovsky 1975, Procter 1975).

In this study, amongst broods of two in which only one chick fledges, it was found that the second chick to hatch has a significantly lower survival (as measured by the fledging success) than the first (Table 7.7). In addition, amongst the four broods of three chicks produced since 1975, in all cases the third chick to hatch died, whilst the first two survived to fledging. It appears, therefore, that in the

TABLE 7.7 : Fledging Success of Chicks in relation to Order of Hatching

(Data from 1976-1978)

1. Broods of Two in which one chick fledged

	'a' chick	'b' chick	'c' chick	N
Fledging Success	74%	26%		19
Difference	$\chi_1^2 = 8.5, P < 0.01$			

2. Broods of Three

	'a' chick	'b' chick	'c' chick	N
Fledging Success	100%	100%	0%	4

Kittiwake also, hatching sequence affects the subsequent survival of chicks, in this colony at least, since Barrett (1978) found no such relationship in his study.

Parsons (1975b) showed that both order of hatching and egg size affects the survival of the 'c' chick in Herring Gulls. This chick emerges from a smaller egg, has a smaller yolk reserve at hatching and faces greater competition from its older siblings during the first few days after hatching. Hatching sequence is invariably the same as laying sequence in the Kittiwake; therefore the last chick to hatch in a brood normally comes from a smaller egg. Kittiwakes exhibit asynchronous hatching and most mortality occurs soon after emerging from the egg. In these three respects the bird is very similar to the Herring Gull and it seems likely that the causes of differential mortality within the brood are the same as those reported by Parsons (1975b).

7.2.7 Nest Site Location, Pair Status and Breeding Success

Females which have bred on at least one occasion previously and which nest in the centre of the colony produce broods which are, on average, 10% larger than those of females nesting on the edge (Table 7.8) and this difference is significant ($\chi^2_3 = 9.26$, $P < 0.05$). In addition, they fledge on average 9% more chicks per pair than birds on the edge, although here the difference is not significant ($\chi^2_3 = 6.40$). Similarly, the mean number of chicks hatched and fledged per pair by birds retaining the same mate is, on average, 13% and 14% (respectively) greater than amongst those which change, both differences being significant ($\chi^2_3 = 16.75$, $P < 0.001$; $\chi^2_3 = 16.21$, $P < 0.01$). The two effects of nest site location and pair status are compounded such that the most productive individuals are those nesting in the centre of the

TABLE 7.8 : The Breeding Success of Experienced Females nesting in the centre or edge of the Colony which retain the Same Mate as in the Previous Year or which Change Mate

Nest Location and Pair Status	No. Chicks hatched/Pair					No. Chicks fledged/Pair					Hatching Success (from C/2)			Fledging Success (from B/2)		
	0	1	2	3	Mean	0	1	2	3	Mean	Mean	(S.E.)	N	Mean	(S.E.)	N
Edge	73	92	220	27	1.49	93	114	190	15	1.31	73.3	(2.47)	322	88.2	(2.18)	220
Centre	78	114	313	65	1.64	100	159	277	34	1.43	75.7	(2.13)	404	88.3	(1.82)	313
Change	77	100	232	24	1.47	98	128	197	10	1.28	72.3	(2.39)	350	87.7	(2.16)	232
Same	74	106	301	68	1.66	95	145	270	39	1.46	76.9	(2.18)	376	88.7	(1.82)	301
Edge Change	36	51	105	11	1.45	48	62	88	5	1.25	71.3	(3.53)	164	86.2	(3.37)	105
Edge Same	37	41	115	16	1.53	45	52	102	10	1.37	75.3	(3.43)	158	90.0	(2.80)	115
Centre Change	41	49	127	13	1.49	50	66	109	5	1.30	73.1	(3.25)	186	89.0	(2.78)	127
Centre Same	37	65	186	52	1.74	50	93	168	29	1.52	78.0	(2.81)	218	87.9	(2.39)	186

colony which retain the same mate, whilst birds on the edge which change mate are the least. The difference in brood size produced by these two groups is 20%, and for number of chicks fledged per pair, 22%.

Similar trends are found in the hatching success of eggs from clutches of two, although the differences are less marked (centre-edge = 2.4%, same mate - change mate = 4.6%) and not significant. In contrast, the fledging success of chicks from broods of two shows no consistent or significant variation with respect to either pair status or nest site location. The effects of these two factors upon breeding success of the Kittiwake result mainly, therefore, from differences in clutch size.

In several species of colonial nesting seabirds, centre-edge differences in breeding success have been found: Adélie Penguin (Spurr 1975, Tenaza 1971), Black-headed Gull (Patterson 1965), Ring-billed Gull (Dexheimer and Southern 1974) and Shag (Coulson 1971). Explanations for this effect include differences in the age structure of birds breeding in each part of the colony, differences in predation rate and, in the Adélie Penguin, disturbance to edge nesting birds caused by the movement of individuals to and from the centre of the colony. Retention of the same mate in Adélie Penguins has no direct effect upon breeding performance but does result in an increase in the proportions of pairs which actually lay eggs (Spurr 1975). In Red-billed Gulls, birds which retained the same mate fledged more chicks as a result of laying more eggs (Mills 1973). Pair status has no effect upon clutch size in Ring Doves but females which retained the same mate had a higher hatching success than those which changed (Erickson and Morris 1972).

7.2.8 Female Breeding Age and Success

The mean number of chicks hatched and fledged per pair increases with female breeding age, reaching a peak amongst birds which have previously bred for 4 years (Figure 7.1). In older individuals there is evidence of a decline. However, there is no significant difference between the mean number of chicks hatched and fledged by birds with a breeding age of 5 years and those with a breeding age of 12-19 years (number hatched per pair: $\chi^2_2 = 0.74$; number fledged per pair: $\chi^2_3 = 3.15$). Data used to produce Figure 7.1 are given in Appendix 7.1.

Haymes and Blokpoel (in press), Lloyd (1979), Perrins and Moss (1974) and Richdale (1957) all produced data which suggested that various aspects of breeding success may decline amongst the oldest members of the population.

Female breeding age has no significant effect upon the hatching success of eggs from clutches of one and three (Table 7.9) although there is a significant increase in the hatching success of two egg clutches amongst older birds. The regression equation describing the relationship amongst clutches of two suggests that, on average, birds with a breeding age of ten have a 16% higher hatching success than first breeders. There is no significant difference between the slopes of the three regressions. The value of the intercept for clutches of three is greater than that for clutches of two, which in turn is greater than that for one egg clutches, indicating that the relationship between clutch size and hatching success is independent of female age.

There is no significant relationship between female breeding age and the fledging success of chicks from broods of one and two (Table 7.9) although the success of chicks from broods of three increases

Figure 7.1 : The relationship between the number of chicks hatched and fledged per pair and female breeding age (years)

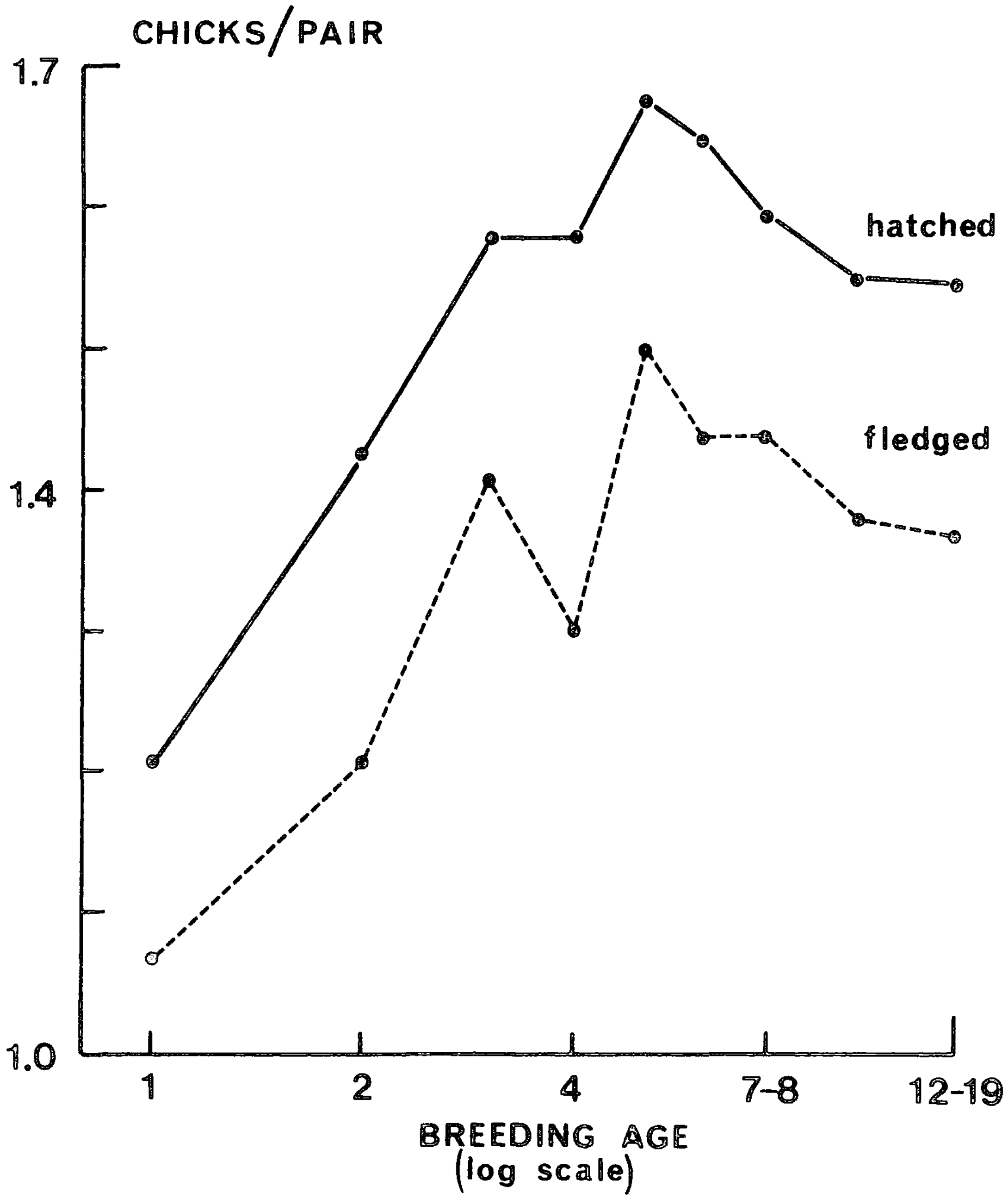


TABLE 7.9 : The Relationship between Female Breeding Age and the Hatching Success for Eggs from Different Sized Clutches and the Fledging Success of Chicks from Different Sized Broods

Hatching Success	r	P(r)	b	S.E.(b)	P(b)	c	N
One Egg Clutch	-0.06	n.s.	-8.17	13.20	n.s.	49.97	106
Two Egg Clutch	0.10	<0.001	10.71	3.39	<0.002	66.84	988
Three Egg Clutch	-0.04	n.s.	-3.95	6.65	n.s.	74.19	220
Fledging Success							
One Chick Brood	-0.03	n.s.	-2.89	5.52	n.s.	91.09	304
Two Chick Brood	0.03	n.s.	2.06	2.64	n.s.	86.91	676
Three Chick Brood	0.22	<0.016	16.29	7.33	<0.05	71.22	97

Equations of the form:

$$y = bx + c$$

where y = Hatching or Fledging Success

x = Female Breeding Age ($\log_{10}$)

significantly amongst older birds. Again, the values for the intercepts indicate that the relationship between fledging success and brood size is independent of female age.

Changes in success of Red-billed Gulls in relation to age result from an increase in the number of eggs laid by older birds (Mills 1973). In the Razorbill, the Ring Dove and the Shag (Lloyd 1979, Erickson and Morris 1972, Potts 1966) breeding success increases with age while clutch size remains constant. In Arctic Terns, Herring Gulls and Ring-billed Gulls (Coulson and Horobin 1976, Chabrzyk and Coulson 1976, Haymes and Blokpoel in press), like the Kittiwake, both clutch size and aspects of breeding success increase amongst older birds.

7.2.9 Breeding Ages of both Members of the Pair and Success

Amongst females of a particular age, increase in the breeding age of the male partner results in an increase in the mean number of chicks hatched and fledged by the pair (Table 7.10). The corresponding relationship for males of a particular age paired with females of differing ages is less consistent. Here, the most successful pairs are those containing young experienced females (breeding ages 2-5), reflecting the pattern of change in success with female breeding age discussed in the previous section. Overall, though, the most productive pairs are those containing two 'old' birds, whilst the least productive pairs contain two first breeders.

In part, the trends discussed above will reflect differences in the mean clutch size of each group although a similar overall pattern is found in the hatching success of eggs from clutches of two. There is no consistent pattern to changes in the fledging success of

TABLE 7.10 : The Breeding Success of Pairs grouped according to the Ages of Both the Male and Female

a. Number of Chicks Hatched per Pair

		Male Breeding Age (years)					
		1		2-5		6-19	
		$\bar{x}$	(N)	$\bar{x}$	(N)	$\bar{x}$	(N)
Female Breeding Age (years)	1	1.09	(156)	1.48	(79)	1.59	(17)
	2-5	1.52	(98)	1.60	(324)	1.68	(91)
	6-19	1.46	(33)	1.57	(158)	1.69	(202)

b. Number of Chicks Fledged per Pair

Female Breeding Age (years)	1	0.97	(156)	1.30	(79)	1.53	(17)
	2-5	1.35	(98)	1.39	(324)	1.42	(91)
	6-19	1.21	(33)	1.37	(158)	1.54	(202)

c. Hatching Success of Two Egg Clutch

Female Breeding Age (years)	1	62.50	(154)	72.50	(73)	63.34	(15)
	2-5	76.44	(87)	74.39	(285)	77.86	(70)
	6-19	75.85	(29)	71.31	(115)	79.85	(134)

d. Fledging Success of Chicks from Broods of Two

	Pairs of First Breeders	Pairs of 'old' birds (6-19 yrs)	Difference
Mean	88.46	90.71	t = 0.49
S.E.	3.62	2.73	n.s.
N	78	113	

chicks from broods of two with respect to male and female age, and the fledging success of pairs of first breeders is not significantly different even from that of pairs of 'old' birds (Table 7.10, part d).

The importance of the breeding experience of the male, as well as that of the female, for successful breeding has been shown in Common Terns, Red-billed Gulls and the Great Tit (Nisbet 1973, Mills 1973, Harvey *et al.* 1979) whilst Ryder (1975) found corresponding differences between pairs of Ring-billed Gulls grouped according to whether the individuals had mature or immature plumage.

7.2.10 Date of Laying and Success

The mean number of chicks hatched and fledged per pair increases at the beginning of the breeding season, reaching a peak amongst birds laying 5-10 days before the colony mean. Thereafter there is a gradual decline as the season progresses (Figure 7.2). A similar relationship exists between relative date of laying and hatching success of eggs from clutches of two (Figure 7.3) although there is no consistent change in the fledging success of broods of two produced at different times.

This pattern of the most productive birds breeding towards the middle of the season has been reported in the Adélie Penguin, Black-headed Gulls, Common Terns, Herring Gulls and the Razorbill (Spurr 1975, Patterson 1965, Lundberg and Väisänen 1979, Morris *et al.* 1976, Parsons 1975a, Brown 1967b, Lloyd 1979). In Ring-billed Gulls (Haymes and Blokpoel in press) a decline in nesting success throughout the season was found, while Harris (1969) found an increase in fledging success as the season progressed.

Figure 7.2 : The relationship between number of chicks hatched and fledged per pair and relative date of laying

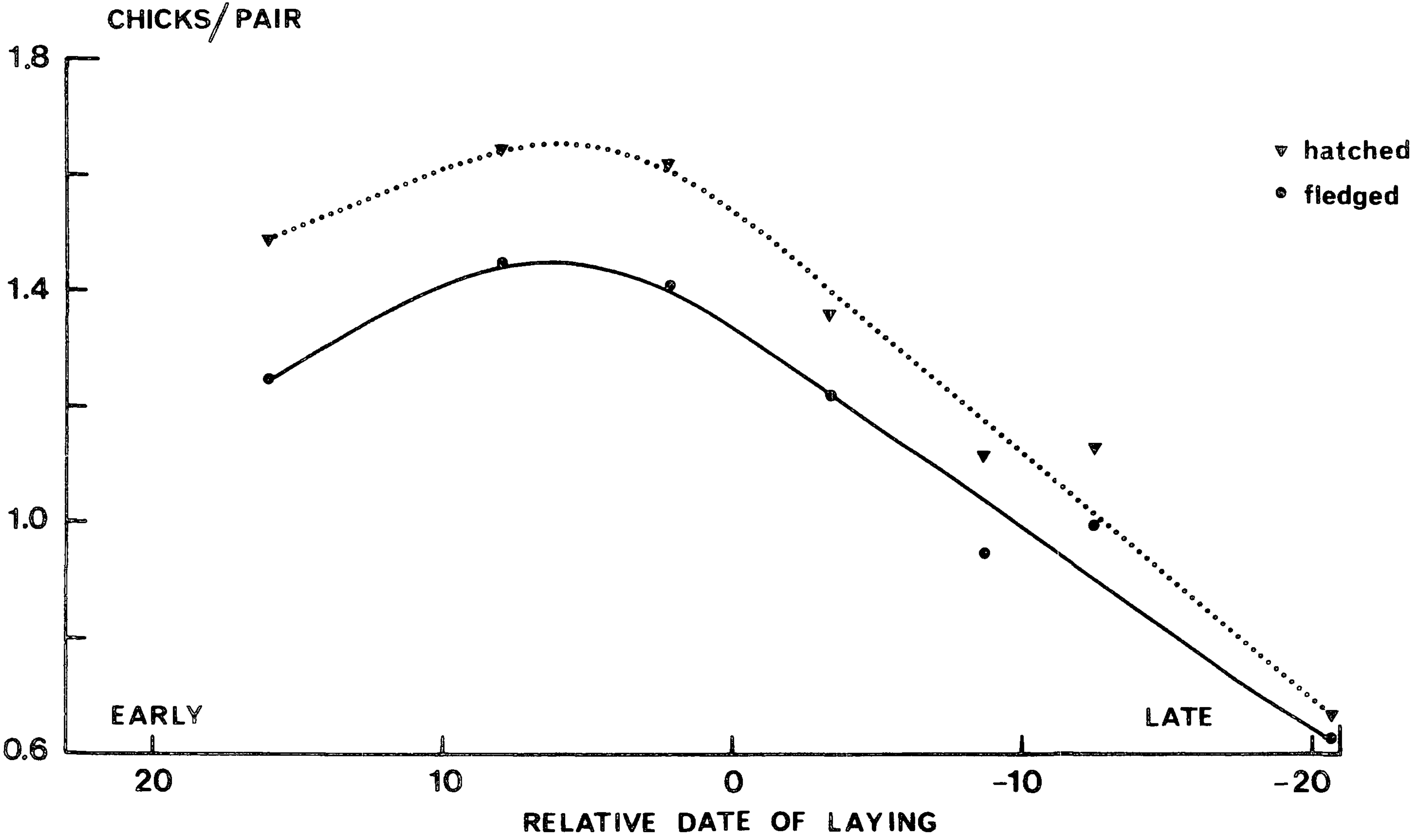
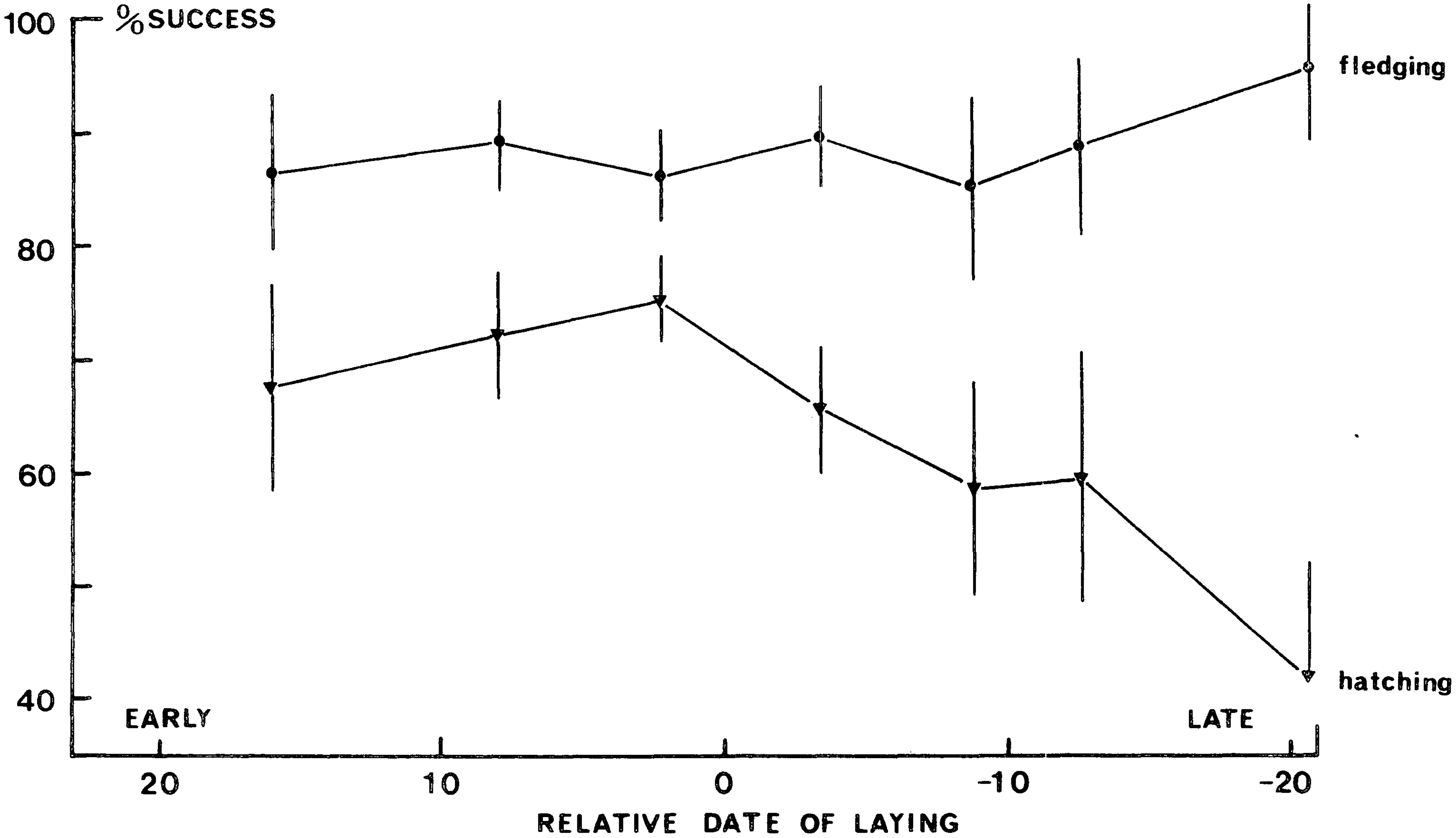

CHICKS/PAIR
1.8
1.4
1.0
0.6
▼ hatched
● fledged
EARLY
LATE
20
10
0
-10
-20
RELATIVE DATE OF LAYING

Figure 7.3 : The relationship between hatching or fledging success (± 2 S.E.) and relative date of laying


100
80
60
40
%SUCCESS
fledging
hatching
EARLY
LATE
20
10
0
-10
-20
RELATIVE DATE OF LAYING

7.2.11 Egg Size and Success

Owing to the way in which data have been gathered at North Shields it is not possible to follow the fate of individual eggs within the clutch in years prior to 1976. As a result, the mean volume of eggs from clutches of two and three will be used in the analysis which follows.

There is a significant positive correlation between egg volume and the hatching success, fledging success and number of chicks fledged from clutches of two (Table 7.11). Similar relationships exist in three egg clutches, although there are no corresponding results for eggs and chicks from clutches of one.

Data presented in Table 7.12 show the correlations and regression equations describing the relationship between hatching success and egg size for clutches of two, data being first grouped according to female breeding age. In all age groups the relationship is positive. However, it is only significant amongst birds which have previously bred for at least two years. In addition, there is a tendency for the size of the correlation to increase with increasing age.

Similar data referring to the fledging success of chicks from broods of two (hatching from clutches of two) is shown in the second half of Table 7.12. Here the increase in fledging success with egg size is only significant amongst first breeders.

Egg size (volume or weight) has been shown to affect hatching success and chick survival both in commercial poultry breeds (Skoglund *et al.* 1952, Tindell and Morris 1964) and in various species of wild birds (Barrett 1978, Davis 1975, Lloyd 1979, Lundberg and Väisänen 1979, Nisbet 1978, Parsons 1970, Schifferli 1973 and Syroechkovsky 1975).

TABLE 7.11 : The Relationship between Egg Volume and Success in different sized Clutches

One Egg Clutch	r	P(r)	b	S.E.(b)	P(b)	c	N
Number of Chicks Hatched	0.06	n.s.	0.007	0.012	n.s.	0.275	99
Number of Chicks Fledged	-0.04	n.s.	-0.004	0.010	n.s.	0.350	99
Fledging Success	too few data						
Two Egg Clutch							
Number of Chicks Hatched	0.13	<0.001	0.032	0.008	<0.001	0.127	862
Number of Chicks Fledged	0.16	<0.001	0.040	0.008	<0.001	-0.426	862
Fledging Success	0.08	<0.015	0.715	0.329	<0.05	57.40	731
Three Egg Clutch							
Numbr of Chicks Hatched	0.08	n.s.	0.028	0.024	n.s.	0.932	197
Number of Chicks Fledged	0.14	<0.05	0.050	0.025	<0.05	-0.304	197
Fledging Success	0.18	<0.01	1.692	0.684	<0.02	13.12	183

Equations of the form : $y = bx + c$

y = success

x = egg volume

TABLE 7.12 : The Relationship between Egg Volume and Success amongst Females of Differing Ages

a. Hatching Success (eggs from clutches of two)

Female Breeding Age (years)	r	P(r)	b	S.E.(b)	P(b)	c	N
1	0.06	n.s.	0.81	0.97	n.s.	33.8	195
2	0.03	n.s.	0.41	1.28	n.s.	53.5	114
3-4	0.15	<0.02	1.48	0.68	<0.05	14.5	209
5-7	0.13	<0.05	1.56	0.89	n.s.	7.2	179
8-19	0.20	<0.01	2.49	0.95	<0.01	-31.4	165

b. Fledging Success (chicks from broods of two, hatched from C/2)

Female Breeding Age (years)	r	P(r)	b	S.E.(b)	P(b)	c	N
1	0.20	<0.02	1.58	0.75	<0.05	23.4	108
2	0.16	n.s.	1.61	1.20	n.s.	15.7	69
3-4	0.07	n.s.	0.72	0.87	n.s.	55.5	138
5-7	0.16	<0.05	1.19	0.69	n.s.	37.7	115
8-19	0.11	n.s.	0.90	0.77	n.s.	49.3	112

Equations of the form : $y = bx + c$

where y = Hatching or Fledging Success

x = Egg Volume

Some workers (e.g. Parsons 1970) suggest that this arises as a direct result of the 'quality' of the egg whilst others, such as Davis (1975), argue that this is a side effect of the tendency of older birds to lay larger eggs and that the breeding experience of the adults is more important. The results of this study would suggest that while the relationship between egg size and success is independent of female breeding age, its effect upon hatching success is more marked in pairs containing older birds, whilst its effect upon fledging success is only apparent in pairs containing first breeding females.

7.2.12 Egg Exchange Exercise: to separate the Effects of Parental Experience and Egg Quality on Breeding Success

Introduction and Methods

As outlined in the previous section, controversy exists as to the relative importance of egg size and parental experience upon the survival of eggs and chicks (see Parsons 1970, Davis 1975) and the results of this study have suggested that while egg size has a direct effect upon both hatching and fledging success, its importance depends upon the breeding experience of the adults also.

Parsons (1970) used a series of egg exchanges between different nests to separate the effects of egg size and hatching sequence upon chick survival in the Herring Gull. These methods inspired the idea that it may be possible to separate the rôles of parental experience and egg quality in a similar manner, an idea which was also taken up by Nisbet (1978).

With a view to the constraints which would be imposed by the small size of the colony at North Shields it was necessary to define the categories of birds used in the exercise in broad terms. Pairs were grouped according to both parental experience and pair status since both have been found to influence breeding success. Although, in general, the group entitled 'Young Birds' consists mainly of first breeders, in some cases newly-formed pairs comprising birds which had previously bred for between 1 and 4 years were also included. In such situations, eggs would be exchanged with those produced by old birds which had bred together for a number of years. In this respect the two nests used in each exchange can be considered as being matched pairs. Complete clutches of two were exchanged between corresponding pairs of birds which had laid within 4 days of each other (thereby removing any effect caused by altering the length of the incubation period). No consideration of egg size was taken into account at this stage, although a separate analysis is shown for exchanges which involved moving large eggs from old pairs to young pairs, and vice-versa. Control data were obtained from the rest of the colony in the same manner.

Results

In the control group of nests the hatching success of old birds was, on average, 14% higher than that of young birds (Table 7.13). In the experimental group, however, the hatching success of old birds was actually 5% lower than that of young birds. Put in an alternative way, the hatching success of young birds with old birds' eggs was, on average, 9.8% higher than that of young birds with their own eggs, while old birds with young birds' eggs had an 8.6% lower hatching success than old birds with their own eggs. The net effect of the egg exchange exercise was, therefore, that the

TABLE 7.13 : Egg Exchange Exercise - to separate the effects of parental breeding experience and egg quality on hatching and fledging success

Hatching Success

a. All clutches exchanged

		Own eggs	Exchanged eggs	Difference (Exchanged - Own)
Young Birds	$\bar{x}$	60.4	70.2	+9.8
	S.E.	5.0	5.0	7.07
	N	96	84	180
Old Birds	$\bar{x}$	74.1	65.5	-8.6
	S.E.	6.0	5.2	7.94
	N	54	84	138

b. Exchanges involving moving large eggs from old birds to young and small eggs from young birds to old

		Own eggs	Exchanged eggs	Difference (Exchanged - Own)
Young Birds	$\bar{x}$	60.4	69.6	+9.2
	S.E.	5.0	6.8	8.44
	N	96	46	142
Old Birds	$\bar{x}$	74.1	60.9	-13.2
	S.E.	6.0	7.2	9.4
	N	54	46	100

/continued

TABLE 7.13 (contd) : Egg Exchange Exercise - to separate the effects of parental breeding experience and egg quality on hatching and fledging success

Fledging Success

a. All clutches exchanged

		Own eggs	Exchanged eggs	Difference (exchanged - own)
Young Birds	$\bar{x}$	84.5	83.1	-1.4
	S.E.	4.8	4.9	6.86
	N	58	59	117
Old Birds	$\bar{x}$	87.5	87.3	-0.2
	S.E.	5.2	4.5	6.88
	N	40	55	95

b. Exchanges involving moving large eggs from old birds to young and small eggs from young birds to old

		Own eggs	Exchanged eggs	Difference (Exchanged - Own)
Young Birds	$\bar{x}$	84.5	81.3	-3.2
	S.E.	4.8	6.9	8.41
	N	58	32	90
Old Birds	$\bar{x}$	87.5	89.3	+1.8
	S.E.	5.2	5.8	7.79
	N	40	28	68

hatching success of these groups of birds was altered by 18.4%. This effect is significant ($t = 1.73$, d.f. 316, $P < 0.05$) using a one-tailed test.*

The effect of the egg exchange was even more marked in the experimental groups where egg size was taken into account, resulting in a change in hatching success of 22.4% which is also significant ($t = 1.77$, d.f. = 210, $P < 0.05$).

In both the control and experimental groups pairs of old birds show a higher fledging success than young birds, even in the group where small eggs were given to older birds and large eggs to young birds. In this exercise, therefore, egg size or quality does not appear to be primarily responsible for the fledging success of chicks.

The two main points which emerge from this exercise are firstly that while egg size or 'quality' appears to influence hatching success of eggs from clutches of two, any effect upon fledging success is overshadowed by the effect of the experience of the adults. Secondly, the concept of egg size and egg quality may not be one and the same thing. This result may indicate variation in the fertility of eggs laid by different aged birds, although no data to support this idea was found when examining eggs which failed to hatch.

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* Use of a one-tailed test is acceptable in this situation since moving eggs from old birds to young can only be expected to have either no effect, or to increase the hatching success of those birds (the opposite being true for moving young birds' eggs to old birds).

7.2.13 Multivariate Analysis of Factors affecting the Success of Clutches and Broods of Two

The results of a multivariate analysis carried out on data from clutches of two produced by 'young' (breeding age 2-5) and 'old' (6-19) females are presented in Table 7.14. None of the factors included in the analysis were found to affect the hatching success of eggs laid by young birds but, in older individuals, increase in egg volume, retention of the same mate from the previous breeding season and time of laying all independently enhance hatching success.

The reverse is found for the fledging success of chicks from broods of two (hatched from clutches of two). Here, amongst young birds, increase in egg volume is found to result in increased fledging success. However, in older birds none of the factors included in the analysis were found to have any significant effect.

7.3 Individual Variation in Breeding Success

The breeding success of each of the long-lived females referred to in earlier chapters is presented in Table 7.15. Individual differences in the mean number of chicks hatched and fledged per year result mainly from differences in the mean clutch size laid by each bird, although despite small sample sizes, significant differences in both hatching success exist between certain pairs of individuals.

Within the colony as a whole an analysis of covariance (similar to that reported in various other chapters) upon data from experienced females which have bred in the colony at least twice reveals that a significant proportion of the variation in hatching success of eggs from clutches of two (28%) and in fledging success of chicks from broods of two (31%) can be explained in terms of individual

TABLE 7.14 : Multivariate Analysis - Factors associated with Variations in the Success of Eggs and Chicks from Clutches and Broods of Two produced by 'Young' and 'Old' Females

Regression Models

Young Females (2-5 years)

Hatching Success : No significant factors

Fledging Success = 1.18(Egg Volume) + 35.95

$N = 251$, $r^2 = 2\%$, S.E. slope = 0.58

Old Females (6-19 years)

Dependent Variable = Hatching Success

Variables in Equation	Correlation Coefficient	Standard Error	P
Egg Volume	2.05	0.73	<0.001
Pair Status	9.62	4.56	<0.05
Date^2	-0.053	0.025	<0.05
Date	4.77	2.45	n.s.

$C = -122.41$ $N = 270$ $r^2 = 8\%$

Fledging Success : No significant factors

Variables included in the Analysis

Hatching Success - of eggs from clutches of two
Fledging Success - of chicks from broods of two hatching from clutches of two
Egg Volume - mean volume of eggs in clutch
Nest Site Location - 0 = edge nest 1 = centre nest
Pair Status - 0 = change mate 1 = same mate
Female Breeding Age ($\log_{10}$)
Date - relative date of laying + 50

TABLE 7.15 : The Success of Long-Lived Individuals

B.T.O. Ring	Clutch Size				No. Eggs Hatched/Yr					No. Chicks Fledged/Yr					Hatching Success		Fledging Success		Breeding Success	
Number	1	2	3	$\bar{x}$	0	1	2	3	$\bar{x}$	0	1	2	3	$\bar{x}$	$\bar{x}$	(S.E.)	$\bar{x}$	(S.E.)	$\bar{x}$	(S.E.)
EC11330	0	9	6	2.40	1	3	8	3	1.87	2	2	10	1	1.67	77.9	(10.7)	89.3	(8.0)	69.6	(11.9)
EC11778	0	9	1	2.10	3	1	6	0	1.30	3	2	5	0	1.20	61.9	(15.4)	92.3	(8.4)	57.1	(15.7)
202.0006	1	11	2	2.07	4	1	9	0	1.36	4	1	9	0	1.36	65.5	(12.7)	100.0	(0.0)	65.5	(12.7)
202.8402	0	6	3	2.33	2	1	5	1	1.56	3	0	5	1	1.44	67.0	(15.7)	92.3	(8.9)	61.8	(16.2)
202.8794	0	13	1	2.07	2	1	11	0	1.64	2	2	10	0	1.57	79.2	(10.8)	95.7	(5.4)	75.8	(11.5)
204.4067	1	3	10	2.64	1	6	5	2	1.57	2	6	5	1	1.36	59.5	(13.1)	86.6	(9.1)	51.5	(13.4)
204.4075	0	7	4	2.36	1	2	6	2	1.82	1	4	5	1	1.55	77.1	(12.7)	85.2	(10.7)	65.7	(14.3)
204.4874	0	14	0	2.00	6	2	6	0	1.00	6	2	6	0	1.00	50.0	(13.4)	100.0	(0.0)	50.0	(13.4)
204.4875	0	1	13	2.93	0	3	7	4	2.07	0	5	9	0	1.64	70.7	(12.2)	79.3	(10.8)	56.0	(13.3)
204.4892	1	14	0	1.93	0	3	12	0	1.80	1	2	12	0	1.73	93.3	(6.5)	96.1	(5.0)	89.7	(7.8)
204.4917	1	13	0	1.93	1	1	12	0	1.79	1	2	11	0	1.71	92.8	(6.9)	95.5	(5.5)	88.6	(8.5)

differences between females, after data have been corrected for any effect of breeding age, nest location, egg size and relative date of laying (Table 7.16). In addition, the repeatability of these factors (0.55) indicates a marked tendency for individual females to be equally successful in different years.

7.3.1 Pair Status and Change in Success of Individual Females

The effect of pair status will not be considered in the following analysis since in Chapter 3 it was shown that breeding success in one year could affect the probability of a pair undergoing divorce before the next.

7.3.2 The Success of Individual Females in Consecutive Years

Almost 39% of females which breed in consecutive years produce the same number of chicks in each; a similar proportion (37%) fledge the same number in each. On average, though, the mean number of chicks hatched and fledged by the same female increases by 1.9% and 0.7% annually.

Table 7.17 shows the percentage of females hatching or fledging a particular number of chicks last year which produce 0, 1, 2 or 3 this year. The overall trend is for females which were more productive in the previous year to be more productive this year also. There is no significant difference between the mean number of chicks hatched and fledged by birds which produced 0, 1 or 2 last year (hatch: $\chi^2_6 = 8.08$; fledge: $\chi^2_6 = 7.60$), but the mean brood size of females which hatched 3 chicks in the previous year is 22% greater than that of the other three groups and this difference is significant ($\chi^2_3 = 29.6$, $P < 0.001$). Similarly, the difference between the mean number of chicks fledged per pair this year by birds which fledged 3 chicks and those which fledged 0, 1 or 2 last year is 21% although it is not significant ($\chi^2_2 = 3.26$).

TABLE 7.16 : Results of Analysis of Covariance - showing the degree of variation in hatching success (of two egg clutches) and fledging success (of two chick broods) which can be attributed to the tendency of some females to be consistently more or less successful than others in a number of years (after data have been first corrected for any effect of factors listed below)

Hatching Success

	Sum-Squares	d.f.	Variance
Between bird	238109.82[a]	157	1516.62[x]
Within bird	616167.19	500	1232.33[y]
Total	854277.01[b]	657	1300.27

$F(157,500) = 1.23 \quad P < 0.01$

r^2 Individual Differences between Females = a/b = 0.279

Repeatability = x/(x+y) = 0.55

Fledging Success

	Sum-Squares	d.f.	Variance
Between bird	93935.20	128	733.87
Within bird	208948.80	349	598.71
Total	302884.00	477	634.98

$F(128,349) = 1.23 \quad P < 0.01$

r^2 Individual Differences between Females = a/b = 0.310

Repeatability = x/(x+y) = 0.55

Factors included as covariates:

Female Breeding Age ($\log_{10}$)
Nest Location : 0 = edge 1 = centre
Egg volume (only in analysis of hatching success)
Relative Date of Laying

TABLE 7.17 : The Association between the Number of Chicks Hatched or Fledged in Consecutive Years by the Same Females[**]

a. Number of Chicks Hatched in Each Year

		No. chicks hatched this year					
		0	1	2	3	Mean	N
Number of chicks hatched last year	0	14.7	24.8	56.6	3.9	1.50	129
	1	14.3	23.3	55.5	6.9	1.55	189
	2	17.8	18.4	54.1	9.7	1.56	444
	3	11.0	16.4	45.2	27.4	1.89	73

b. Number of Chicks Fledged in Each Year

		No. chicks fledged this year					
		0	1	2	3	Mean	N
Number of chicks fledged last year	0	21.7	31.1	44.1	3.1	1.29	161
	1	18.8	30.8	45.8	4.6	1.36	240
	2	21.6	23.6	48.8	6.0	1.39	402
	3	12.5	18.8	53.1	15.6	1.72	32

[**] Data show the percentage of females hatching or fledging a particular number of chicks last year which hatch or fledge 0, 1, 2 or 3 this year.

7.3.3 Change in Relative Date of Laying of the Same Female in Consecutive Years and the Corresponding Change in Success

There is a significant positive correlation between the change in relative date of laying of individual females breeding in consecutive years and the corresponding change in the number of chicks hatched and fledged by the bird (Table 7.18). The slopes of the relationships indicate that the number of chicks hatched and fledged is greater in the present year if the bird breeds relatively earlier in the present season than it did in the last. The same relationships for hatching and fledging success of clutches and broods of two are not significant, indicating that this result arises from changes in the number of eggs laid.

If data are broken down in relation to the breeding age of the bird (Table 7.18, parts 2 and 3) it is seen that the effect of change in relative date of laying is only significant amongst younger individuals.

7.3.4 Change in the Size of Eggs from Clutches of Two laid by the Same Female in Consecutive Years and the corresponding Change in Success

There is a significant positive correlation between the change in size of eggs from clutches of two laid by the same female in consecutive years and the corresponding change in the hatching success of those eggs ($r = 0.15$, $N = 413$, $P < 0.001$). The slope of the relationship (1.31 ± 0.43) indicates that females laying larger eggs in the present year tend to have a higher hatching success also. There is no corresponding relationship with fledging success of broods of two.

TABLE 7.18 : The Relationship between Change in Relative Date of Laying of Individual Females in Consecutive Years and the corresponding Change in Success

1. All Birds

	r	P	Slope	S.E. (Slope)	P	N
Change in No. of chicks hatched	0.14	<0.001	0.018	0.004	<0.001	834
Change in No. of chicks fledged	0.12	<0.001	0.014	0.004	<0.001	834
Change in hatching success	0.04	n.s.	0.225	0.253	n.s.	493
Change in fledging success	0.09	n.s.	0.360	0.257	n.s.	240

2. 'Younger' Females - (Breeding Age 2-5 years)

	r	P	Slope	S.E. (Slope)	P	N
Change in No. of chicks hatched	0.18	<0.001	0.020	0.005	<0.001	487
Change in No. of chicks fledged	0.16	<0.001	0.017	0.005	<0.001	487

3. 'Older' Females - (Breeding Age 6-19 years)

	r	P	Slope	S.E. (Slope)	P	N
Change in No. of chicks hatched	0.07	n.s.	0.011	0.008	n.s.	347
Change in No. of chicks fledged	0.05	n.s.	0.007	0.008	n.s.	347

Change in Success (y) = (Success this year - Success last year)

Change in Laying Date (x) = (Relative Date of Laying this year - Relative Date of Laying last year)

To separate the effect of increase in age over the two years from any effect of egg size, data have been broken down in Table 7.19 to show the hatching and fledging success of clutches and broods of two (hatched from clutches of two) in relation to whether the eggs laid this year are larger than those produced last year, or the reverse. Females which produce larger eggs in the present year than the last show a corresponding increase of, on average, 5% in hatching success, a difference which is not significant. There is no appreciable change in hatching success, however, amongst birds laying smaller eggs in the present year than the last.

Increase in egg size does not affect fledging success and while, on average, there is a 4.5% reduction in fledging success associated with the production of smaller eggs in the present year, this difference is also not significant.

7.4 Between Year Variation in Breeding Success

The mean number of chicks hatched and fledged per pair in each year has declined significantly over the period of this study (Figure 7.4). In part, this can be correlated with the annual variations in clutch size discussed in Section 5.4, but none of the other factors included in a multivariate analysis were found to have any significant effect (Table 7.20).

A similar overall decline was recorded for the hatching and fledging success of clutches and broods of two in three different age groups of birds (Table 7.21), indicating that this trend is not a function of the changing age structure of the population. Coulson and Wooller (1976) found that the mortality rate of adults breeding at North Shields has increased over the years, and in Section 3.4.2 it was shown that in years of high mortality the divorce rate of surviving pairs was high also.

TABLE 7.19 : The Hatching and Fledging Success of Eggs and Chicks Produced by the Same Female in Consecutive Years in relation to whether the Bird laid Larger or Smaller Eggs in the Present Year than the Last

Hatching Success (± S.E.)

	Egg Size Greater This Year	Egg Size Greater Last Year
	(N = 215)	(N = 278)
Hatching success last year	71.8 (3.1)	73.2 (2.7)
Hatching success this year	77.0 (2.9)	72.5 (2.7)
Difference (this - last)	+5.2%	-0.7%
P	n.s.	n.s.

Fledging Success (± S.E.)

	Egg Size Greater This Year	Egg Size Greater Last Year
	(N = 97)	(N = 102)
Fledging success last year	89.2 (3.2)	91.2 (2.8)
Fledging success this year	88.1 (3.3)	86.8 (3.4)
Difference (this - last)	-1.1%	-4.4%
P	n.s.	n.s.

Figure 7.4 : Annual variations in the mean number of eggs laid, chicks hatched and chicks fledged per pair in the colony at North Shields

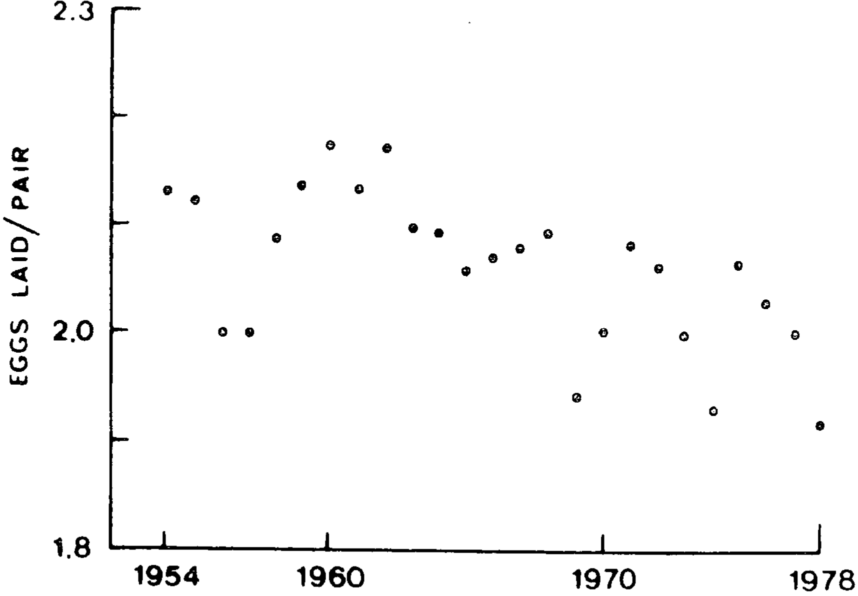
There has been a significant decline in the breeding success of the birds over the period of this study:

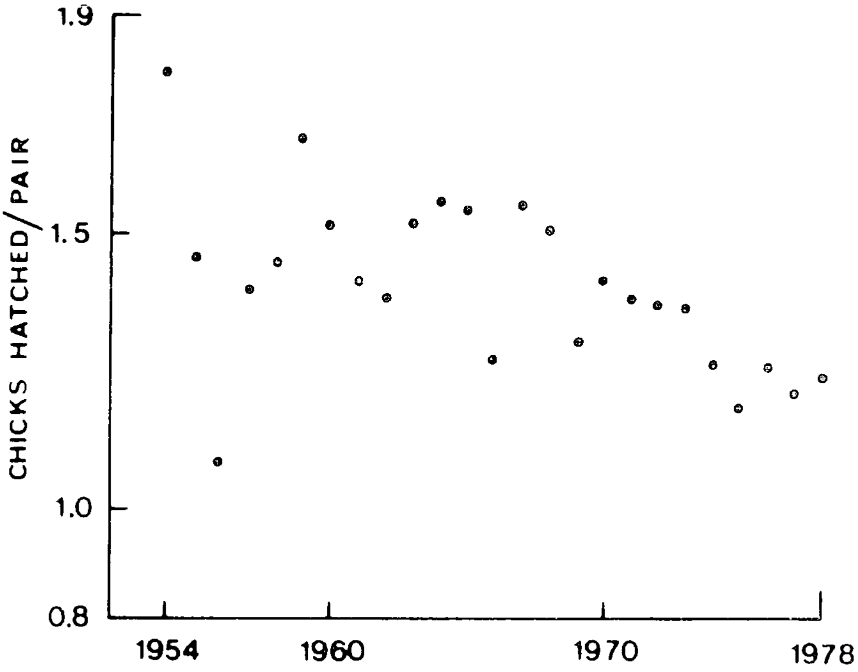
Clutch size Slope = -0.007 ± 0.002

No. Chicks hatched/pair Slope = -0.010 ± 0.004

No. Chicks fledged/pair Slope = -0.013 ± 0.004

N = 1607


2.3
2.0
1.8
EGGS LAID/PAIR
1954
1960
1970
1978


1.9
1.5
1.0
0.8
CHICKS HATCHED/PAIR
1954
1960
1970
1978

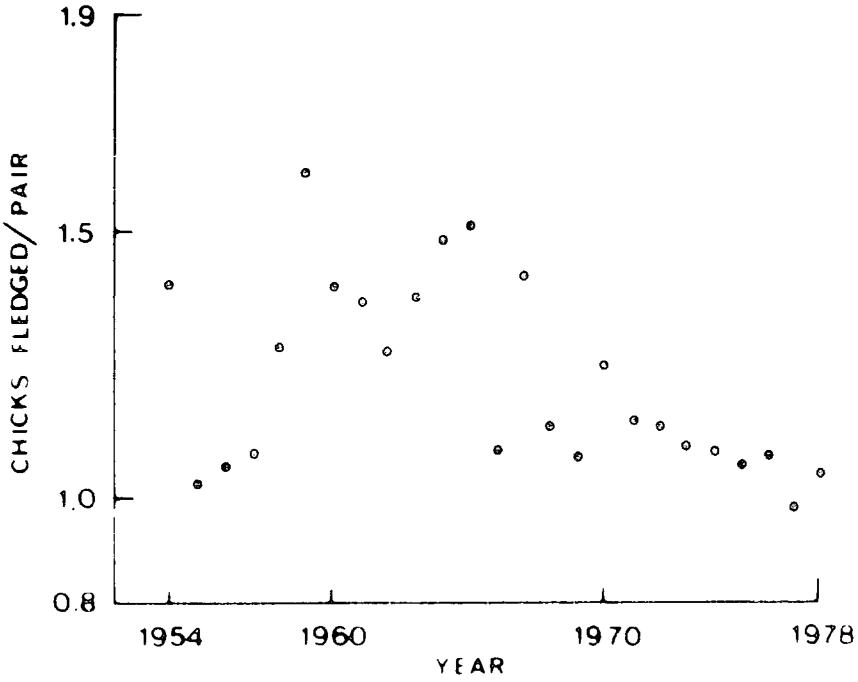

1.9
1.5
1.0
0.8
CHICKS FLEDGED/PAIR
1954
1960
1970
1978
YEAR

TABLE 7.20 : Multivariate Analysis - Factors associated with the Annual Variations in Breeding Success at North Shields

(Years prior to 1976)

Regression Models

Number of Chicks Hatched/Pair = -0.90 + 1.12 (Clutch Size)

$N = 20 \quad r^2 = 30\% \quad$ S.E. Slope = 0.41

Number of Chicks Fledged/Pair = -0.26 + 1.07 (Brood Size)

$N = 20 \quad r^2 = 69\% \quad$ S.E. Slope = 0.17

Factors included in the Analysis

Mean Number of Chicks Hatched/Pair in each year

Mean Number of Chicks Fledged/Pair in each year

Mean Clutch Size laid in each year

Mean Age of Birds in the Colony in each year

Mean Date of Laying in each year

TABLE 7.21 : Annual Decline in the Hatching and Fledging Success of Clutches of Two and Broods of Two and Three produced by Females of Different Ages

Hatching Success (Two Egg Clutch)

Female Breeding Age (years)	Year 1954-1964	1964-1969	1969-1975
1	67.24 (116)	69.38 (80)	62.50 (72)
2-5	73.10 (171)	78.37 (178)	70.63 (160)
6-19	80.33 (61)	76.61 (124)	73.05 (141)

Fledging Success (Two Chick Brood)

1	91.94 (62)	89.42 (52)	80.77 (39)
2-5	92.46 (126)	87.89 (128)	79.33 (104)
6-19	96.23 (53)	87.50 (96)	89.19 (97)

Fledging Success (Three Chick Brood)

2-5	78.16 (29)	84.85 (11)	70.83 (8)
6-19	80.39 (17)	89.39 (22)	88.10 (14)

Change of mate has been shown to affect the hatching success of eggs laid by females with a breeding age of 6-19 years. However, it was not found to affect fledging success. Reduced hatching success as a result of taking a new partner can be explained in terms of the time required for unfamiliar birds to develop a successful incubation rhythm. It is hard to explain how change of mate, or perhaps the lower overall physical condition of birds in years following winters of high mortality, could affect chick survival. If it could be explained in terms of the ability of birds to feed their chicks, one would expect a more marked decline in the fledging success of chicks from broods of three, and yet this is not the case (Table 7.21). This finding also rules out any changes in food availability over the years, which would be expected to have similar effects. Coulson and Wooller (1976) related the decline in adult survival to the increased competition for breeding sites in the colony, which was reflected in the progressively earlier return of birds. They ruled out any effects of toxic chemicals which might also have explained the reduction in success. It is difficult, therefore, to offer any explanation for the changes in fledging success.

Two future lines of research emerge from the findings of this section. Firstly, it is necessary to discover if the observed changes were restricted to the warehouse colony, or if they are found in other colonies of Kittiwakes in the area. Secondly, it would be useful to compare the causes of chick loss in different years, as well as any differences in chick growth rates which may follow the overall decline.

7.5 Between Colony Variation in Breeding Success

The hatching and fledging success of birds breeding at North Shields is the same as that found by Cullen (1957) for a colony of Kittiwakes breeding on the Farne Islands in Northumberland (Table 7.24). In addition, the hatching success does not differ significantly from that of birds nesting in Alaska in Newfoundland or in the colony at Runneskholmen in Norway, although the success of eggs produced on Hekkingen in Norway is significantly lower than that found in this study. The mean fledging success of chicks at North Shields is consistently higher than that found in any of the foreign colonies shown in Table 7.22. The mean number of chicks fledged per pair is also consistently higher than that reported in other colonies since, as outlined in Chapter 5, Section 5.5, the mean clutch size is greater at North Shields.

The absence of predation in this study colony and the apparent abundance of food in the area creates a situation in which the breeding biology of the Kittiwakes nesting on the warehouse is very different from that of birds in all the colonies discussed above, with the exception of the Farne Islands. Despite differences in predation and the incidence of egg loss from the nest (discussed earlier), hatching success in the Newfoundland colony and that in Alaska is higher, on average, than that found here. This suggests either that a difference exists in the fertility of eggs laid in each of the colonies or that predation and egg loss may not be random, being more likely to occur in nests of young birds, or more likely during the latter half of the breeding season. The comparative stability of environmental conditions at North Shields has resulted in only small year-to-year variations in breeding success, compared with the data obtained by Barrett (1978) for the colony at Hekkingen where in only three years of study, breeding success varied from less than 4% to 47% (Table 7.22).

TABLE 7.22 : Breeding Success in Different Kittiwake Colonies

(Values calculated from a variety of data given in different papers)

Colony	Years of Study	Clutch Size	Brood Size	No.chicks Fledged/ Pair	Hatching Success	Fledging Success	Breeding Success	Source of Reference
North Shields England	1954-1975	2.06	1.43	1.25	69%	87%	61%	This Study
Farne Islands England	1953-1955	1.94	1.34	1.18	69%	88%	61%	Cullen (1957)
Cape Thompson Alaska	1960-1961	1.84	1.34	1.05	73%	78%	57%	Swartz (1966)
Gull Island Newfoundland	1969-1970	1.85	1.35	1.03	73%	76%	56%	Maunder and Threlfall (1972)
Runneskholmen Norway	1974	1.98	1.33	0.89	67%	67%	45%	Barrett (1978)
Hekkingen Norway	1974	1.89	1.08	0.89	57%	82%	47%	Barrett (1978)
Hekkingen Norway	1975	1.52	0.06	-	4%	-	-	Barrett (1978)
Hekkingen Norway	1976	1.81	1.03	0.26	57%	25%	14%	Barrett (1978)

7.6 Discussion

The single major factor which influences the breeding success of Kittiwakes at North Shields is the number of eggs laid in the clutch, not only through its direct effect upon the number of chicks hatching and hence fledging per pair, but also since clutch size affects hatching success and brood size, fledging success. Increase in hatching success with clutch size was thought to be related to the increased stimulus for incubation offered by a larger number of eggs (Beer 1961, Brown 1967b). Parsons (1975a) found, though, that birds laying clutches of three followed by a smaller repeat clutch had a higher hatching success than those which originally laid clutches of two. This, he suggested, showed a lower reproductive or incubation drive amongst birds which normally lay small clutches. Coulson and White (1958a) attributed the poor hatching success of one egg clutches to the large proportion which are laid by first breeders, although the results of this study have shown that this relationship is independent of female breeding age.

The decline in chick survival with increasing brood size is thought, in many species, to be linked to the increased competition for food amongst siblings. The increase in chick survival from broods of three with female breeding age suggests that this may also be the case at North Shields. This does not necessarily imply any food shortage in the area, but rather an age-dependent relationship with the ability or the drive to make the necessary number of feeding trips to ensure the survival of all the chicks in the brood. A second explanation for changes in chick survival with increasing brood size may be the fact that a significant proportion of chick loss in the Kittiwake is thought to result from young falling from the nest. An obvious relationship may be expected to exist between brood size and the incidence of chick loss through falling.

Most chick mortality was found to occur at or soon after hatching and reasons for this have been discussed earlier. It would appear that this period of development is crucial to the survival of the embryo also and that this results in differences between the success of eggs in relation to laying or hatching sequence.

The effect of pair status and nest site location upon breeding success has been found to be primarily related to clutch size differences, although corresponding changes in hatching success were also found.

The relationship between female breeding age and success is somewhat complex. On average, the number of chicks hatched and fledged per pair increases to a maximum amongst birds which have previously bred for 4 years. In older birds there is evidence of a decline, although this is not significant. Since annual breeding success at North Shields has declined progressively over the period of study (in all age groups) and the proportion of old birds in the population has gradually increased, it seems likely that the decline in success of old birds is attributable to this change and is not a reflection of 'senility'. On average, individual females breeding in consecutive years tend to fledge more chicks in the present year than they did in the last, although approximately one-third of birds are equally successful in both years. There is a tendency for birds which hatched or fledged more chicks in the previous year to hatch or fledge more this year also. This results primarily from the number of eggs laid by the female in each, although analysis has shown that the hatching success of clutches of two and fledging success of broods of two is consistently higher in some individuals than others in successive years. Amongst females breeding in consecutive years those which lay earlier in the present year than the last show a corresponding increase in the number of chicks they hatch and fledge. In older birds, however, there is no such relationship.

Egg size is correlated with hatching success in two and three egg clutches. In clutches of two, however, this relationship is only significant amongst older birds. (This may explain why no correlation could be found between the volume of the one egg clutch and hatching success since most are produced by first breeders or young birds.) Fledging success increases significantly with egg volume in first breeders although the relationship is not significant in older birds. The results of an egg exchange exercise have shown, however, that egg size and egg 'quality' may not be one and the same thing. Eggs (irrespective of their size) exchanged between nests of old experienced pairs and young experienced pairs resulted in a relative improvement in the hatching success of the young birds and a lowering of the hatching success of the old birds. Fledging success of the resultant chicks was, however, unaffected by the swop and was related to the breeding experience of the adults.

Changes in success with increasing breeding age of adults, which are not related to clutch size, may be explained in a number of different ways. Increased hatching success may result from age-related differences in the fertility of eggs produced, although the small number of addled eggs found in the colony showed no tendency to come from a particular age group. Alternatively, these differences may be related to the quality of incubation given by different pairs of birds. Beer (1961) in a study of Black-headed Gulls and Wooller (1973) in an earlier study at North Shields have both shown that quality of incubation improves with experience, quality being measured both in terms of the frequency of occurrence of certain patterns of behaviour associated with incubation and also in the consistency and compatability of incubation rhythms shown by each member of the pair. If, in younger birds, the quality of incubation is very varied, this may mask any effects of egg size on hatching success. In pairs of older birds, however, the importance of variability of egg quality would become apparent. Nisbet (1978) found that the principal differences between eggs of Common Terns occurred in their dry albumen content, this constituent containing about two-thirds of the protein available to the developing embryo. Egg quality, as opposed to size, can be related to the relative proportions of the contents of the egg amongst eggs of the same size (Nisbet 1978).

Changes in the survival of chicks may be related either to the ability of the parents to obtain enough food or the time taken for the adults to change from incubation to chick care. In this second category, in particular, the importance of egg size becomes apparent. Parsons (1970) suggested that the relationship between egg size and chick survival (in Herring Gulls) was linked to differences in lipid content, its importance being associated with the yolk reserves which remain at the time of hatching. This could be vital to the chick's survival during the time taken for the parent-chick relationship to develop. The relationship between chick survival and egg size in this study was only found to be significant amongst first breeders, suggesting that these inexperienced birds may take longer to make the transition from incubation.

On average, birds breeding at North Shields are more successful than those found in foreign colonies, partly because of the time at which they breed and its effect upon clutch size, but also because of high chick survival. In addition, year-to-year variations have been found to be less marked than in some colonies, reflecting the apparent stability of environmental conditions.

A short-term study of the birds would reveal a colony in which predation and food availability (two factors which play a major role in the control of breeding success in the Kittiwake, Barrett 1978, Belopol'skii 1961, Maunder and Threlfall 1972) are not considered to be important; a colony in which breeding success is comparatively high and annual variations small. It would not, however, reveal the rather disconcerting progressive decline in success which has been found to occur over the past 20-25 years. This finding illustrates the need for more long-term studies of single populations, involving the collection of sufficient data to enable the effects of different variables to be removed from relationships being investigated.

CHAPTER 8 : FINAL DISCUSSION

While it is obviously impossible to enumerate all the factors associated with reproduction which can be regarded as contributing to the 'costs of breeding', it is possible to characterize some elements of the breeding cycle which can be correlated with, or are thought to result in increased adult mortality. Broadly, these may be grouped as follows:

i. The acquisition and retention of a mate and nesting site.

ii. The production and incubation of eggs and, in the case of birds, mammals and sub-social insects, the protection and provision of food for the young.

A number of writers (Gadgil and Bossert 1970, Wiley 1974, Williams 1966) have calculated theoretical 'energy' budgets in consideration of the optimal distribution of reproductive effort in a life history strategy. It is generally accepted that such reproductive strategies will have evolved as a balance between annual reproductive output and the resultant costs in terms of reduced survival. Breeding strategies associated with long-lived species such as the Kittiwake are characterized by delayed maturity and the production of only a small number of offspring in each year.

Immature animals are subjected to the normal processes of mortality and yet do not themselves contribute to the replacement of such losses. Wooller and Coulson (1977) pointed out that the production of even a small number of offspring by these individuals should be advantageous unless, in doing so, the life expectancy, and hence their lifetime reproductive output, is reduced. Since amongst birds, as well as other animals, the number of offspring produced by younger individuals tends to be lower than that of older members of the population (Lack 1954), the resultant costs which can be incurred by breeding at an earlier age (if the overall lifetime reproductive output is to be maintained) must be correspondingly lower also. For this reason, the intensity of competition for mates and breeding sites will influence the age at which individuals in the population start to breed. In Herring Gulls, first breeding has been shown to occur at an earlier age in colonies where nesting density is lower (see Chabrzyk and Coulson 1976, Harris 1970), and in the Brown Pelican, Williams and Joanen (1974) have found that individuals are recruited at an earlier age into newly formed colonies than into mature colonies. The stresses associated with the acquisition of a nest site and mate can be gauged from the results presented by Coulson and Wooller (1976): in the Kittiwake, it is normally the male which retains the nest site, but once the pair is formed, the female will aid in its defence. Coulson and Wooller found that while the mortality rate amongst males is normally higher than that amongst females, this difference between the sexes is most marked during the period January - March, the time of year when the male is actively defending its site and looking for a mate.

Coulson (1968) has shown that differential competition for nest sites between the centre and edge of the colony at North Shields has resulted in a segregation of birds in their year of recruitment according to what he considered to be the 'quality' of the individuals. He found that males entering the centre of the colony (the area where competition for nest sites is greater) were, on average, heavier than those recruited into the edge. In addition, he found that these differences in quality were reflected in the future survival of the birds. More recently, Wooller and Coulson (1977) have shown that amongst males nesting in the centre, individuals which were recruited at an earlier age were, on average, heavier and lived longer. However, they found no significant difference between the mean age of recruitment into the centre and the edge of the colony. These results were interpreted as showing that differences in age of first breeding amongst male Kittiwakes are related to individual differences in the ability of the birds to compete for sites and mates.

Increased population density has been shown to influence age of first breeding in mammals. In part this can be linked to competition for food, with a resultant effect upon growth and development rates (Sadleir 1969), but social dominance factors and competition for females results in many young but physiologically mature males failing to breed. Yearling male Mule Deer show interest in females at the beginning of the breeding season but are driven away from them by older males (Robinette and Gashwiler 1950). Some are, however, able to obtain matings with the few females which come into heat late in the breeding season when older males show less interest in does. In general, breeding late in the season results in lower reproductive output (see below), although competition associated with obtaining a mate is lower also.

In a wide variety of organisms there is a tendency for individuals to become more productive as they get older, although some decline may be found amongst the oldest members of the population associated with 'senility'. Tinkle (1967) recorded an increase in clutch size with age in lizards, and Fitch (1963, 1965), a decline in the proportion of non-reproductive Garter Snakes and Racers, amongst older individuals. In mammals, a common pattern is for the oldest and youngest members of the population to be the least fecund (Mitchell *et al*. 1977, Sadleir 1969), a similar situation to that found in fish (Nikolsky 1963). Age-related changes in the reproductive output of birds, discussed in earlier chapters, result from changes in clutch size, changes in breeding success and from changes in the proportions of breeding females in each age group. Wooller and Coulson (1977) suggested that increased fecundity in older Kittiwakes could be achieved either by more efficient breeding, or by putting more effort into each successive breeding attempt. In non-avian species, age-related changes in reproductive output are often associated with increase in body size, and it has often been impossible to separate the relative effects of each; for example, clutch size increases with carapace length in the Green Sea Turtle, but carapace length is known to increase progressively with age (Simon and Parkes 1976). In reptiles, variations in clutch size with body size can be directly related to the amount of material available for egg formation (Hahn and Tinkle 1965). In mammals, it is known that uterus size can influence pre-natal litter mortality (Millar 1973); however, infertility, delayed oestrus and reduced litter size can also be related to the 'overall physical condition' of the individual (Sadleir 1969).

Age-related changes in the mortality rate of Kittiwakes which follow a similar pattern to that of changes in breeding success were suggested as reflecting either the effect of increased reproductive effort amongst older birds, or the cumulative effects of successive breeding attempts (Wooller and Coulson 1977). These workers proposed that within the breeding lifetime of an individual, the balance between reproductive output and survival could be adjusted on a year-to-year basis, by annual variations in clutch size (and hence brood size) or by failing to breed altogether. Intermittent breeding in the Kittiwake is most frequent in the year following first breeding (Wooller and Coulson 1977), from which it can be inferred that breeding makes greater demands upon these inexperienced individuals. In high density populations of rabbits, and in cattle feeding on pastures which are low in calcium, failure to breed is also more common after the first pregnancy (Myers and Poole 1962, McClure 1961). While the causes of this phenomenon differ between birds and mammals, the comparison is made to illustrate that in both groups it is inexperienced individuals which are less able to withstand or redress the 'costs' associated with breeding.

It is generally accepted that animals breed at the time of year when environmental conditions are optimal for the production of young. It has been known for a long time that a wide variety of organisms use change in day-length as a proximate factor which acts as a cue for the onset of breeding (Marshall 1942, Bullough 1951) and yet there is often a large variation in the period over which breeding occurs, both within a single population and between neighbouring populations of the same species. The results of this study would appear to indicate that in the North Shields colony, where food availability is not thought to act as a proximate factor, the speed with which an individual female is brought into breeding condition is linked both to environmental cues such as day length, courtship by the mate, social stimulation from the rest of the colony and the speed with which the bird responds to these factors. In many other avian species, however, the time taken for the female to obtain enough food for egg formation is thought to be a major factor which influences date of laying (Perrins 1970). The sexual cycle in Red Deer hinds is believed to be primarily determined by photoperiod but modified by the 'condition' of the individual, poor condition resulting in a delay in oestrus (Mitchell *et al.* 1977). In most other mammalian studies, factors correlated with timing of breeding have centred around day length and food availability or quality (Sadleir 1969).

Time of breeding is significant to individuals within the population since it has been shown to influence their reproductive output. In birds (*loc. cit.*), mammals (Sadleir 1969) and reptiles (Tinkle 1967, Hoddenbach and Turner 1968), later breeding results in a reduction in clutch or litter size and breeding success. In this study the decline in clutch size and hatching success through the season was found to occur in different age groups of birds, although Sadleir points out that some of the results obtained in mammalian studies may reflect the tendency for young (less successful) individuals to come into oestrus later than older members of the population. In addition, it has been found that the mean body weight of females breeding at different times in the season tends to decline also (Hewson 1968). Perrins (1970), discussing the timing of breeding in birds, argued that the actual date of laying of a female is a balance between the evolutionary advantages of earlier breeding (in that more surviving young are produced) and the physiological state of the bird. Here it has been suggested that individual differences in time of breeding may reflect differences in the speed of response to environmental cues, differences in the time required to obtain enough food for egg formation, variations in the 'overall physical condition' of members of the population and, in the case of males, the effects of social factors associated with the competition for mates. If later breeding results in reduced clutch or litter size, the resultant costs of breeding are reduced also. There may in fact be a selective advantage in breeding later in the season if this enhances the survival and hence the future reproductive potential of an individual. Annual variations in time of breeding may be regarded as a method of varying the costs of breeding as envisaged by Wooller and Coulson (1977).

Lack (1948) extended his original thesis on the evolution of clutch size in birds (Lack 1947, 1948a) and showed that it could be applied to variations in litter size in mammals. Many of the factors associated with breeding success in Kittiwakes and other birds are seen to have a similar influence in groups as diverse as reptiles, fish and mammals. This may reflect some of the common physiological and hormonal relationships found throughout the animal kingdom and the way in which reproductive strategies have evolved. In making a brief review of ecological studies of non-avian species, it becomes apparent that the inter-relationships between factors affecting the breeding biology of different populations have never been fully investigated. Long-term studies of single populations of mammals do exist, notably the work carried out on the Rabbit in Australia and New Zealand (e.g. Dunsmore 1974, Gibb *et al*. 1978, Mykytowycz and Fullagar 1973). However, such studies were approached from the behavioural rather than the ecological viewpoint.

Despite the fact that a wealth of data now exists on the Kittiwakes at North Shields, many of the relationships between different factors remain unexplained and it is only possible to speculate as to the causes of each. Paramount in this respect is the consistency in time of breeding of individual females in different years. The future of ecological studies must lie in a more inter-disciplinary approach. For example, many workers have investigated the hormonal control of breeding in birds (reviewed in Murton and Westwood 1977) although most of these studies have been made on captive individuals in the laboratory. By carrying out this type of work in the field it should be possible to incorporate the results into a more eco-physiological study. Further, pair-formation and pre-copulatiory behaviours have been catalogued for a number of species. However, with few exceptions (for example, Nisbet 1973), fieldwork ceased when eggs were laid and no attempt was made to relate the behaviour of the birds to their subsequent reproductive performance. A third line of research which is now more frequently pursued involves the use of manipulative studies. (A small scale exchange of eggs was made in this study to investigate the relative effects of parental experience and egg quality upon success.) It should be possible to investigate a number of ecological relationships in the same manner, for example, the effect of chick production upon the maintenance of the pair bond or, perhaps even more interesting, the effects of raising a large number of chicks in successive years, upon adult survival.

It has become apparent on a number of occasions during this research that a single breeding season cannot be strictly considered in isolation and that the breeding success of a pair in one year can influence the breeding of those birds in the future (and of other pairs in the colony, if the birds change mate). If ecological studies are to develop into a more comprehensive approach involving interference with breeding adults, then it is necessary to assess the effect of this disturbance when analysing data. There is still an important place for studies such as that carried out at North Shields, based upon the principle of non-interference, in order that a standard be obtained against which experimental results can be set.

SUMMARY

Introduction

1. The breeding biology of a colony of Kittiwakes nesting on a warehouse at North Shields, Tyne and Wear, has been studied continuously since the colony's formation in 1949. Adults have been individually colour-marked during their year of first breeding and, since 1954, details of each breeding attempt made in the colony have been recorded annually (including date of return, pair formation, time of breeding, clutch and egg size and breeding success). A large body of data has now been built up which permits long-term changes in the breeding of the colony to be related to changes in the population itself. In addition, using computer-based statistical tools such as multivariate analysis, it is possible to investigate the inter-relationships between these different factors.
2. The warehouse was first colonised in 1949 by 4 pairs of birds. The population then increased to a maximum of over 103 pairs in 1967 since when there has been a gradual decline to 73 pairs in 1978.
3. The mean breeding age of adults in the colony increased to a maximum in 1967 since when, while there has been little change amongst females, there has been a slight decline in males.

Date of Return to the Colony

4. Date of return to the colony advances progressively with increasing breeding age. On average, birds with a breeding age of ten years return 43 days earlier than first breeders. The relationship, which is logarithmic, is similar for both sexes, although amongst birds of the same age, males return, on average, 3.7 days earlier than females.
5. The annual mean date of return of the entire colony has advanced since the mid-1950s. In part, this can be correlated with changes in the age structure of the breeding population.
6. Birds of both sexes which breed in the centre of the colony arrive back, on average, 5 days earlier than those which breed on the edge. This tendency is maintained in all age groups of birds.
7. Amongst breeding pairs which have survived since the previous year the mean difference in date of return between the two birds is 12.6 days in pairs which remain together and breed again, but is 23.9 days amongst pairs which divorce.
8. 17% of pairs which divorce arrive back at the colony within 4 days of each other, showing that not all cases of divorce can be accounted for

in terms of asynchrony of return. Amongst divorcing pairs, however, there is a tendency for one of the two birds to disappear for a period of time soon after its return. This may be another factor which contributes to the break-up of the pair bond.

9. The relative breeding ages of the members of the pair affect the difference in date of return of the two birds only if the pair is newly formed in the present year.

The Pair Bond

10. One pair of birds has remained together for a total of 14 consecutive breeding seasons. However, on average, 50% of pairs remain together for only one.
11. There is a strong tendency for birds to mate with a partner of a similar breeding age. On average, 30% of pairs contain birds of exactly the same breeding age, while 51% contain birds whose ages differ by a maximum of only one year. As birds get older, amongst those which change mate the difference in age between themselves and their new partner increases, the effect being more marked amongst females.
12. The divorce rate amongst pairs surviving from one year to the next declines progressively with increasing female breeding age from 39% amongst birds breeding for the second time, to 13% for birds with a breeding age of ten years. The survival of adults has also been shown to decline with increasing breeding age, with the result that the major cause of the break-up of the pair bond changes from divorce, amongst younger birds, to bereavement amongst older birds.
13. The prior association of the two members of a pair has been shown to affect the probability of that pair undergoing divorce before the next year. This relationship becomes more marked amongst older birds. After removing the effect of female breeding age, the probability of divorce of pairs formed in the present year is 0.33; of pairs formed in the previous year is 0.20; and of pairs formed two or more years ago is 0.11.
14. 40% of birds which changed mate took new partners from pairs which had divorced. Amongst birds whose mates had died since the previous breeding season this value was 31-35%. There is a significant positive correlation between the annual mortality rate of adults and the annual divorce rate, indicating that in years when mortality causes more change of mate, increased divorce reinforces this effect, even though in years of higher mortality fewer pairs survive to undergo divorce.

15. The probability of divorce amongst pairs which failed to fledge any chicks in the previous year (0.32) is significantly greater than that of pairs which fledged at least one (0.25). The effect of breeding failure upon divorce is less marked amongst older birds.

16. Only 10% of pairs which remain together from one year to the next change site. On average, 30% of males which change mate move site at the same time, while amongst females this effect is even more marked (63%). 46% of females whose mates die move site, whilst 75% of those which divorce move. In males, too, change of site is more likely following divorce than bereavement, although the difference is not significant. In both sexes the proportion of birds which change site declines with increasing age, the effect being more marked amongst females. On average, 44% of birds from pairs which returned to the colony, but moved to a new site, retained the same partner as in the previous year.

Date of Laying

17. The pattern of laying of birds at North Shields approximates to a normal distribution. During the 25 years in which laying dates have been recorded, 1725 clutches were all produced within a 63-day period, mean 18.7 May (S.D. 9.4 days).

18. Birds nesting in the centre of the colony breed, on average, 3.6 days earlier than those on the edge. Despite differences in the total number of pairs breeding in each part, the spread of laying in each is the same.

19. The mean relative date of laying* of first breeding females (-2.11±0.56) is significantly later than that of experienced birds (+1.06±0.23), although amongst females which have previously bred on at least one occasion there is no difference between the relative date of laying of birds of differing ages. The spread of laying declines amongst older birds (from 9.19 days in females with a breeding age of 2, to 7.45 days in females with a breeding age of 16-19 years).

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*Relative date of laying of a bird is the deviation (in days) of the laying date of that individual from the mean date of laying of the whole colony in that year.

20. There is a tendency for both males and females nesting on the edge of the colony to breed progressively earlier as they get older, whilst this trend is reversed amongst experienced birds in the centre.
21. In both the centre and edge, females which change mate tend to lay later than those which retain the same mate. The difference between the mean date of laying of females which retain the same mate and those which change mate as a result of the death of last year's partner is, on average, 0.6 days, whilst amongst females which divorced their old mates the difference is more marked (1.7 days). Change of mate has no significant or consistent effect upon time of breeding of males.
22. If data are broken down according to both nest site location and pair status the relationship between time of breeding and age is seen to differ markedly between the sexes. In all groups, however, the difference in time of breeding of birds which retain the same mate and those which change is seen to increase amongst older birds.
23. In both the centre and on the edge of the colony increase in male age results in progressively earlier laying by the female, whilst increase in female age results in progressively later laying. There is no consistent or significant difference between the mean date of laying of corresponding groups of pairs which have retained the same mate, or changed mate since last year, indicating that differences in time of breeding of birds in relation to pair status result from differences in the relative ages of the two members of the pair.
24. The mean date of return to the colony of the members of the pair only affects the subsequent date of laying of the female if the pair was newly formed in the present year. In addition, amongst newly formed pairs, delay of laying associated with later return is only apparent in birds which arrive back at the colony, on average, after 13 February.
25. Individual females show a marked tendency to lay at the same time in different breeding seasons. Analysis has shown that over 39% of the total variation in relative date of laying in the colony can be attributed to differences between females (after the effect of nest site location, pair status and the breeding ages of the female and her mate have been removed).
26. There is a significant positive correlation between the relative date of laying of the same female in consecutive breeding seasons irrespective of whether the bird has changed mate or not over the corresponding period.

27. Amongst females which change mate, differences in the relative date of laying of the bird in consecutive years can be related to the difference between the breeding age of the new partner and the old. The slope of the relationship between change in relative date of laying (y) and change in breeding age of the male partner (x), 0.57±0.15, indicates that if the female takes a new partner which is older than the last, the bird will tend to lay earlier in the present season than it did in the previous one.

28. Between-year variations in the mean date of laying of the whole colony are small, with only one year (1969) significantly later than the rest. The onset of breeding has advanced since 1954 although there has been no corresponding change in the termination of laying in each year. In years when laying started early, the pattern of laying of the colony approached that of a normal distribution. However, when laying started later, the pattern of laying was negatively skewed. The onset of breeding was unusually late in the four years of this study. It was not possible to correlate this with any changes in the population itself, although two of the seasons followed winters in which adult mortality was higher than that recorded in any other year.

Clutch Size

29. The mean clutch size recorded at North Shields is 2.05 eggs, clutches of one and three comprising 9.8% and 14.6% of the total.

30. Amongst experienced females, birds nesting in the centre of the colony produce clutches which are, on average, 6% larger than those laid by birds on the edge, whilst females which have retained the same mate lay clutches which are, on average, 7% larger than those which have changed mate. The two effects of nest site location and pair status are compounded such that the largest clutches are produced by birds nesting in the centre of the colony which have retained the same mate as in the previous year.

31. Clutch size increases with female breeding age, reaching a peak amongst birds which have previously bred for between 8 and 10 years. In older birds there is evidence of a decline, although this is not significant. The change is most marked between birds breeding for the first and second time but, on average, females with a breeding age of 10 years produce clutches which are 16% larger than those produced by first breeders.

32. The mean clutch size produced by different pairs increases with the breeding ages of both partners, such that pairs of 'old' birds (breeding age 6-19 years) produce clutches which are, on average, 23% larger than those of first breeders.

33. Clutch size increases during the first quarter of the breeding season, reaching a peak amongst birds laying 7-10 days before the mean date of laying of the colony. Thereafter there is a gradual decline as the season progresses. The overall decline is more marked than in other seabirds, reflecting the fact that Kittiwakes show less variation in egg size.

34. Two egg clutches are laid throughout the breeding season, clutches of three being produced mainly during the first half, and clutches of one during the latter half.

35. Clutch size is primarily correlated with date of laying although female breeding age, nest site location and pair status all have significant, independent effects.

36. There is a consistency in the number of eggs laid by the same female in different years. Changes in clutch size associated with change of mate result primarily from an increase in the proportion of two egg clutches produced and a decline in the proportion of clutches of three.

37. Individual females which breed later in the present year than they did in the last show a corresponding decline in the number of eggs they lay. On average, a delay in laying of 10 days results in a corresponding decline in clutch size of 7%.

38. Between year variations in the mean clutch size laid in the colony are small, although an overall decline has been recorded over the last 20-25 years which can in part be correlated with annual variations in mean date of laying.

39. Geographical variations in clutch size of Kittiwakes in 5 different colonies can be correlated with timing of breeding in each ($r = -0.85$). Amongst birds breeding in North Norway and Arctic Russia, the decline in clutch size in relation to date of laying is twice as rapid as that found at North Shields, reflecting, perhaps, the more rapid change in day-length which is found at higher latitudes.

Egg Size and Shape

40. Egg volume declines with laying sequence and both 'a' eggs and 'b' eggs from clutches of two and three become larger as clutch size increases. There is a similarity in volume between the last eggs from clutches of two and three and the one egg clutch.

41. The volume of eggs from clutches of two increases with female breeding age, although the change is only marked between birds breeding for the second and third time, where the difference is, on average, 2.7%. Female breeding age was found to have no consistent or significant effect

upon the volume of eggs from clutches of one and three. Differences in egg volume in relation to clutch size and laying sequence remain, after data have been broken down by female breeding age.

42. On average, eggs laid in clutches of two by experienced females which had retained the same mate as in the previous breeding season are approximately 2% larger than those produced by birds which had changed mate, a difference which is significant. The effect of pair status upon egg size is independent of female breeding age, although amongst birds of the same age, differences between the two groups are not significant.
43. Pairs of first breeders laying clutches of two produce eggs which are, on average, 3-4% smaller than those produced by pairs containing at least one experienced bird, a difference which is significant. Amongst birds of a particular age there is no consistent change in egg size with increasing age of the partner although the largest eggs are produced, on average, by pairs of older birds (breeding age 3-19 years).
44. The last eggs from clutches of two and three, and the egg from the clutch of one, all show a progressive decrease in size through the breeding season. There is no such change in the volume of the 'a' and 'b' eggs from the three egg clutch, and the decline is less marked in the 'a' egg from the clutch of two.
45. The only factor found to have a significant independent effect upon the volume of eggs laid as clutches of one is date of laying. On average, a delay in laying of 10 days results in a 2.6% reduction in egg size. The size of the 'a' egg from the two egg clutch is influenced both by the breeding age of the female member of the pair and pair status. Both these factors independently affect the size of the 'b' egg and, in addition, a significant reduction in egg size is found to occur as the season progresses. Pair status was the only factor found to affect the volume of 'b' and 'c' eggs from clutches of three, whilst none of the factors included in the analysis were found to influence the size of the 'a' egg.
46. Less than 10% of the variation in egg volume could be explained in terms of the factors discussed above, but between 62% and 79% of the variation in the size and shape of eggs from clutches of two can be attributed to differences between females (after the effect of date of laying, breeding age and pair status have been removed).

47. There is a highly significant positive correlation between the various measures of size or shape of the 'a' and 'b' eggs from clutches of two. In addition, there is a significant correlation between the ratio of these values in successive clutches laid by the same bird, and between the absolute size or shape of eggs from successive clutches of two.
48. The correlation between the size or shape of eggs laid by the same female in consecutive clutches of two is higher amongst birds which change mate than amongst those which retain the same mate over the corresponding period.
49. Changes in the size or shape of eggs laid by the same female in consecutive years can be linked to corresponding changes in time of laying.
50. Amongst female first breeders there is a positive relationship between body size (wing length or body weight) and the size of eggs from clutches of two laid by those birds.
51. Annual variations in the mean volume of eggs from all clutches of two laid in the colony are small, being on average only 1%.

Breeding Success

52. An average of 61 out of every 100 eggs laid in the colony give rise to fledged young. 43% of pairs are totally successful (fledge chicks from all the eggs they produce) while 25% fail to fledge any chicks in a year. On average, each pair of breeding adults raises 1.3 chicks to fledging.
53. During the three seasons 1976, 1977 and 1978 only 5% of eggs were lost from the nest during the incubation period. Causes of hatching failure include damage to eggs during incubation (1% of all eggs laid), adults stopping incubating their own eggs to 'foster' chicks from neighbouring nests (2%) and desertion (4%). The incidence of desertion by breeding adults is significantly higher amongst pairs containing at least one first breeder (7%) than amongst pairs containing two experienced birds (2%).
54. Of 80 eggs which failed to hatch during the 1976, 1977 and 1978 breeding seasons, 45% showed no evidence of embryonic development. 39% of eggs which showed signs of development contained embryos which were less than 16 days old.
55. 38% of chicks which failed to fledge died either at hatching or during the first five days thereafter, whilst almost 60% died up to 10 days after hatching. The mortality rate of chicks was found to decline progressively with increasing age.

56. Hatching success increases with clutch size, but fledging success declines with increasing brood size. On average, the mean number of chicks fledged from clutches of three (2.47) is greater than that of two and one egg clutches (1.76, 0.90). However, the breeding success of two egg clutches (62%) is higher than that of both one and three egg clutches (40%, 61%).
57. In both clutches of two and three, hatching success declines with laying sequence, and in broods of two and three, fledging success declines with hatching sequence.
58. Differences in the number of chicks hatched and fledged per pair, with respect to nest site location and pair status, result primarily from differences in the number of eggs laid (outlined earlier). The hatching success of eggs from clutches of two laid by experienced females nesting in the centre of the colony is, on average, 2.4% higher than that of eggs produced by birds on the edge, and the hatching success of two egg clutches produced by birds which have retained the same mate as in the previous year is, on average, 4.6% higher than that of eggs laid by birds which have changed mate. The two effects of nest site location and pair status are compounded such that the hatching success of the two egg clutch produced by females nesting in the centre of the colony which have retained the same mate as in the previous breeding season is, on average, 6.7% greater than that of eggs from birds nesting on the edge which have changed mate. Fledging success of two chick broods is unaffected by both nest site location and pair status.
59. The mean number of chicks hatched and fledged per pair increases with female breeding age, reaching a peak amongst birds which have previously bred for 5 years. In older individuals there is evidence of a decline although this is not thought to reflect 'senility'.
60. The hatching success of two egg clutches increases with female breeding age. On average, the hatching success of eggs produced by birds with a breeding age of ten is 16% higher than that of eggs produced by first breeders. There is no relationship between female breeding age and the hatching success of eggs from clutches of one and three.
61. The fledging success of chicks from broods of one and two is unaffected by the breeding age of the female parent although there is a significant increase in the fledging success of chicks from broods of three, with increasing female breeding age.
62. Differences in the number of chicks hatched and fledged by pairs grouped according to the breeding ages of both the male and the female result primarily from differences in clutch size. Increase in male age results

in a progressive increase in the hatching success of eggs from clutches of two. Trends associated with increasing female age are less consistent, although the hatching success of eggs produced by pairs of old birds is the highest of all groups, being 17.4% greater than that of pairs of first breeders. Fledging success of chicks from broods of two is unaffected by the breeding ages of the adults.

62. The mean number of chicks hatched and fledged per pair increases at the beginning of the breeding season, reaching a peak amongst birds laying 5-10 days before the mean date of laying of the colony. Thereafter there is a gradual decline as the season progresses. In the main, such changes result from differences in the mean number of eggs laid per pair at different times in the season, although a similar pattern of change is found for the hatching success of eggs from clutches of two. Fledging success of chicks from broods of two is unaffected by date of laying.

63. The hatching and fledging success of clutches of two increases significantly with egg size. A similar relationship exists for eggs and chicks from clutches of three.

64. The relationship between egg size and the hatching success of two egg clutches is positive in all age groups of females, although it is more marked and only significant amongst older birds. The fledging success of chicks from broods of two (hatched from clutches of two) increases with egg volume in different age groups, although this relationship is only significant amongst first breeders.

65. To separate the effects of egg quality and parental experience, complete clutches of two were exchanged between nests occupied by pairs of old experienced birds and pairs of young birds breeding together for the first time. The effect of the exchange was to improve the hatching success of young birds by 10% and to reduce the hatching success of old birds by 9%, relative to the controls. It did not, however, influence the fledging success of the chicks which subsequently hatched. In both the control and experimental groups the fledging success of chicks in nests occupied by older experienced birds was, on average, 3.5% greater than that of young pairs.

66. None of the factors studied are correlated with variations in the hatching success of eggs produced by young experienced females (breeding age 2-5 years), although egg volume has a significant effect amongst eggs produced by birds with a breeding age of 6-19 years. The reverse of this was found in the fledging success of chicks from broods of two; egg volume being correlated with the survival of chicks produced by younger birds, whilst none of the factors were found to have any effect upon the survival of chicks produced by older birds.

67. A consistency in the number of chicks hatched and fledged by the same female in different years reflects the consistency in clutch size discussed earlier. Analysis has shown, however, that a significant proportion of the hatching success of two egg clutches (28%) and the fledging success of two chick broods (31%) can be attributed to individual differences between females, and a marked tendency for individuals to be equally successful in different years (after the effect of egg size, nest site location, breeding age and date of laying have been removed).

68. Females which breed later in the present year than they did in the last show a corresponding reduction in the number of chicks they hatch and fledge. This results from changes in clutch size discussed above.

69. Changes in the hatching success of eggs from clutches of two, which result from changes in the size of eggs laid by the same bird in consecutive years, have been recorded. It has not been possible, however, to separate this relationship from the increase in female breeding age over the same period.

70. An overall decline in the mean number of chicks hatched and fledged per pair in each year has been found over the period of this study. In part, this can be related to changes in clutch size, although a corresponding decline in hatching and fledging success is also reported. Possible reasons for this change have been discussed.

71. The breeding biology of the birds at North Shields differs from that of other colonies of Kittiwakes in that food availability and predation are not thought to affect the success of the birds. The mean number of chicks fledged per pair is greater than that reported in most other colonies, partly because of differences in time of breeding and hence clutch size, but also because, on average, fledging success is higher. However, the hatching success of eggs does not differ markedly from that reported elsewhere.

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Appendix 1 Scientific Names of Species referred to in Text

Albatross, Laysan	*Diomedea immutabilis* Rothschild
Blackbird, Redwinged	*Agelaius phoeniceus* (Linnaeus)
Tricoloured	*Agelaius tricolor* (Audubon)
Budgerigar	*Melopsittacus undulatus* (Shaw)
Cormorant	*Phalacrocorax carbo* (Linnaeus)
Cormorant, Double-crested	*Phalacrocorax auritus* (Lesson)
Domestic Hen (Domestic Fowl)	*Gallus domesticus* Linnaeus
Dove, Ring	*Streptopelia risoria* Linnaeus
Ringed Turtle	*Streptopelia risoria* Linnaeus
Flycatcher, Pied	*Ficedula hypoleuca* (Pallas)
Fulmar	*Fulmarus glacialis* (Linnaeus)
Gannet	*Sula bassana* (Linnaeus)
Goose, Snow	*Anser caerulescens* (Linnaeus)
Guillemot	*Uria aalge* (Pontoppidan)
Guillemot, Pigeon	*Cepphus columba* Pallas
Gull, Black-headed	*Larus ridibundus* Linnaeus
California	*Larus californicus* Lawrence
Glaucous-winged	*Larus glaucescens* Naumann
Herring	*Larus argentatus* Pontoppidan
Lesser Black-backed	*Larus fuscus* Linnaeus
Red-billed	*Larus novaehollandiae scopulinus* Forster
Ring-billed	*Larus delawarensis* Ord
Southern Black-backed	*Larus dominicanus* Lichtenstein
Swallow-tailed	*Creagrus furcatus* Néboux
Kestrel	*Falco tinnunculus* Linnaeus
Kittiwake, Black-legged	*Rissa tridactyla* (Linnaeus)
Pelican, Brown	*Pelecanus occidentalis* Linnaeus

Penguin, Adélie	*Pygoscelis adéliae* (Hombron & Jacquinot)
Fiordland Crested	*Eudyptes pachyrhynchus* G. R. Gray
Royal	*Eudyptes schlegeli* Finsch
Yellow-eyed	*Megadyptes antipodes* (Hombron & Jacquinot)
Pigeon, Wood	*Columba palumbus* Linnaeus
Quail, Bob-white	*Colinus virginianus* (Linnaeus)
Razorbill	*Alca torda* Linnaeus
Robin	*Erithacus rubecula* (Linnaeus)
Scoter, Velvet	*Melanitta fusca* (Linnaeus)
Shag	*Phalacrocorax aristotelis* (Linnaeus)
Shearwater, Manx	*Puffinus puffinus* (Brünnich)
Slender-billed	*Puffinus tenuirostris* (Temminck)
Skua, South Polar	*Catharacta maccormicki* (Saunders)
Skylark	*Alauda arvensis* Linnaeus
Sparrow, Song	*Melospiza melodia* (Wilson)
Starling	*Sturnus vulgaris* Linnaeus
Stork, White	*Ciconia ciconia* (Linnaeus)
Tern, Arctic	*Sterna paradisaea* Pontoppidan
Common	*Sterna hirundo* Linnaeus
Thrush, Mistle	*Turdus viscivorus* Linnaeus
Song	*Turdus ericetorum* Turton
Tit, Great	*Parus major* Linnaeus
Deer, Mule	*Odocoileus hemionus* (Rafinesque)
Red	*Cervus elaphus* (Linnaeus)
Domestic Cattle	*Bos taurus* (Linnaeus)
Rabbit	*Oryctolagus cuniculus* Linnaeus
Snake, Garter	*Thamnophis sirtalis*
Racer	*Coluber constrictor*
Turtle, Green sea	*Chelonia mydas* (Linnaeus)

Appendix 1.1 The number of Breeding Pairs, the mean Breeding Age of Males and Females, and the Percentage of First Breeders in the Colony in each Year

Year	Colony size	% First Breeders		Breeding Age of Females			Breeding Age of Males		
		%	(N)	$\bar{x}$	(S.D.)	N	$\bar{x}$	(S.D.)	N
1949	4 ?								
1950	11								
1951	12								
1952	13								
1953	16								
1954	20	83	(29)	1.36	(0.50)	14	1.00	(0.00)	15
1955	34	53	(59)	1.60	(0.72)	30	1.48	(0.50)	29
1956	34	27	(59)	2.30	(0.92)	30	2.03	(0.87)	29
1957	35	18	(63)	3.07	(1.18)	31	2.53	(1.11)	32
1958	38	38	(73)	2.97	(1.79)	37	2.69	(1.58)	36
1959	44	45	(84)	3.23	(2.20)	43	2.59	(1.92)	41
1960	52	30	(100)	3.38	(2.48)	52	2.85	(1.99)	48
1961	61	27	(118)	3.76	(2.64)	59	3.15	(2.27)	61
1962	70	33	(138)	3.77	(2.92)	69	3.23	(2.47)	69
1963	83	26	(155)	4.06	(3.12)	78	3.60	(2.62)	77
1964	88	26	(168)	4.45	(3.30)	84	3.52	(2.55)	84
1965	104	24	(197)	4.65	(3.42)	98	3.69	(2.69)	99
1966	97	24	(186)	4.69	(3.64)	91	3.96	(2.92)	95
1967	103+	29	(202)	4.86	(3.98)	101	3.81	(2.98)	103
1968	96	14	(178)	5.32	(3.89)	87	4.67	(3.04)	91
1969	90	18	(143)	5.53	(3.95)	72	5.14	(3.36)	71
1970	98	22	(144)	5.51	(4.18)	72	4.92	(3.55)	72
1971	84	30	(155)	4.72	(3.92)	79	4.84	(3.73)	76
1972	86	18	(148)	5.18	(3.88)	74	5.00	(3.89)	74
1973	79	16	(145)	4.92	(3.57)	73	4.58	(3.48)	72
1974	72	24	(127)	5.56	(4.18)	63	4.14	(3.55)	64
1975	72	18	(136)	5.73	(4.23)	70	4.53	(3.39)	66
1976	69	26	(136)	5.43	(4.38)	68	4.26	(3.37)	68
1977	67	22	(127)	5.23	(3.92)	65	4.44	(3.56)	64
1978	73	22	(142)	5.59	(4.14)	71	4.69	(3.94)	73

APPENDIX 1.2 : Subprogrammes from the Statistical Package for the Social Sciences, used in Data Manipulation and Analysis

BREAKDOWN

'Breakdown' calculates and prints the sums, means, standard deviations and variances of a dependent variable among subgroups of the cases in the file, e.g.

```
BREAKDOWN      TABLES = AGE BY YEAR
```

would give an output showing the mean age of birds in each year of the colony's history, in addition to the other statistics outlined above.

FREQUENCIES

The subprogramme 'Frequencies' computes and presents one-way frequency distribution tables for discrete variables. In addition, an option includes the output of a range of descriptive statistics, e.g.

```
FREQUENCIES     GENERAL = AGE
```

would produce an output showing the number and frequency of birds of each age group in the population.

REGRESSION

The multiple regression analysis programme 'Regression' can be used as a method of analysing the linear relationship between a dependent variable and a set of independent variables. Very briefly, the method of operation selected was as follows: Relationships between different factors are calculated by the method of least squares regression analysis. Independent variables are entered into the regression equation in an order determined by the contribution of each to the explained variance. At each 'step', the residual sums of squares is partitioned amongst the remaining variables and their 'F' values adjusted.

SCATTERGRAM

The 'Scattergram' procedure card causes a two-dimensional scatterplot of data points to be produced, where the co-ordinates of the points are the values of the two variables being considered. In addition, this subprogramme prints out a number of statistics describing the relationship, including Pearson's correlation coefficient 'r', and the regression equation of the line of best fit.

For further details of these and other programmes, reference should be made to Nie *et al.* (1970).

APPENDIX 3.1 : Duration of the Pair Bond

Age of Pair (Years)	Number of Pairs	Frequency (% of total)	Proportion of ** Pairs Surviving
1	585	51.7	0.40
2	231	20.4	0.54
3	124	11.0	0.56
4	69	6.1	0.64
5	44	3.9	0.64
6	28	2.5	0.64
7	18	1.6	0.61
8	11	1.0	0.73
9	8	0.7	0.75
10	6	0.5	0.50
11	3	0.3	0.67
12	2	0.2	1.00
13	2	0.2	0.50
14	1	0.1	-
Total	1132		

** Proportion of Pairs Surviving : proportion of pairs of each age which remain together until the next year.

APPENDIX 4.1 : The Relative Date of Laying of Females of Differing Ages Nesting in the Centre and on the Edge of the Colony

Female Breeding Age	Edge	Centre	Difference (C-E)		
	Mean		$\bar{x}$	't'*	P
1	-2.45	-1.74	0.71	0.6	n.s.
2	-1.66	3.45	5.11	4.3	<0.001
3	-1.00	3.02	4.02	3.4	<0.001
4	-1.01	3.11	4.12	3.3	<0.002
5	-0.16	2.54	2.70	1.9	n.s.
6	-1.20	4.30	5.50	3.6	<0.001
7-8	-1.82	2.29	4.11	3.5	<0.001
9-11	-1.67	2.87	4.54	3.6	<0.001
12-19	0.97	0.11	-0.86	0.5	n.s.

	S.D. and Sample Size	
1	10.15(198)	11.59(182)
2	8.61(112)	9.08(111)
3	8.75 (82)	7.25(106)
4	8.22 (70)	7.25 (85)
5	8.25 (63)	8.13 (72)
6	8.21 (41)	7.12 (67)
7-8	7.90 (73)	7.25 (98)
9-11	7.76 (66)	7.55 (82)
12-19	7.17 (34)	8.06 (65)

* 't' = t test

APPENDIX 4.2 : The Relationship between Date of Return and Subsequent Date of Laying amongst Pairs grouped according to Nest Site Location and Pair Status

	Same Mate		Change Mate		Difference (C-E)	
	Edge	Centre	Edge	Centre	Same Mate	Change Mate
	Mean Relative Date of Laying					
Before 15 Feb	-1.24	2.61	0.10	3.19	3.85*	3.09
15 Feb- 7 March	0.20	2.70	1.38	3.80	2.50	2.42
8 - 30 March	-0.18	3.24	0.06	1.02	3.42**	0.96
After 30 March	-1.21	2.41	-4.63	-0.40	3.61	4.23

S.D. and Sample Sizes

	Same Mate Edge	Same Mate Centre	Change Mate Edge	Change Mate Centre
Before 15 Feb	7.72 98	6.84 139	8.25 48	9.65 68
15 Feb - 7 March	9.06 35	7.07 64	7.95 34	9.15 44
8 - 30 March	7.82 51	8.05 79	7.91 55	7.96 58
After 30 March	6.73 24	5.65 22	10.62 35	8.93 20

* Difference significant : $t = 4.0$, d.f. = 235, $P < 0.001$

** Difference significant : $t = 2.4$, d.f. = 128, $P < 0.02$

APPENDIX 5.1 : The Relationship between Female Breeding Age and Clutch Size - data used in preparation of Figure 5.1

Female Breeding Age (years)	Number of Eggs in Clutch			
	1	2	3	**Mean**
1	65	301	17	1.88
2	18	173	32	2.06
3	13	153	22	2.05
4	5	127	23	2.12
5	8	99	29	2.15
6	7	76	25	2.17
7	7	65	22	2.16
8	4	56	17	2.17
9-11	6	99	42	2.25
12-19	4	76	19	2.15

APPENDIX 5.2 : The Clutch Size Distribution of Pairs grouped according to the Breeding Ages of the Two Birds and the Status of the Pair

Numbers of one, two and three egg clutches laid by groups of birds shown in Table 5.3

			Male Breeding Age								
			1			2-5			6-19		
			C/1	C/2	C/3	C/1	C/2	C/3	C/1	C/2	C/3
Change Mate	Female Breeding Age	1	41	160	5	9	90	7	1	15	4
		2-5	12	101	11	9	130	16	3	45	7
		6-19	2	34	4	6	71	14	2	36	8
Same Mate	Female Breeding Age	2-5				15	212	55	2	37	15
		6-19				7	76	28	9	146	70

APPENDIX 5.3 : Relationship between Time of Breeding and Clutch Size in different Kittiwake Colonies

Colony	Years	Clutch Size	Laying Date**	Source of Reference
North Shields England	1954-78	2.05	18.7	This Study
Gull Island Newfoundland	1969-70	1.85	31.3	Maunder and Threlfall (1972)
Runneskholmen Norway	1974-76	1.83	33.8	Barrett (1978)
Hekkingen Norway	1974-76	1.78	29.6	Barrett (1978)
Karlov Islands East Murman	1937-40	1.96	17	Belopol'skii (1961)

** Mean Date of Laying = Days after 30 April.

APPENDIX 6.1 : The Volume of Eggs from Clutches of Two laid by Females of Differing Ages

a. Difference in size of eggs laid by young and old females

	Female age (years)	2-5	6-19	
		Egg Volume (ml)		Difference t test
'a' egg	Mean	42.79	44.09	t = 5.04
	S.D.	3.26	3.28	d.f. 696
	N	249	449	P < 0.001
'b' egg	Mean	41.21	42.43	t = 4.74
	S.D.	3.22	3.33	d.f. 696
	N	249	449	P < 0.001

b. Difference between size of 'a' and 'b' eggs laid by different age groups

Female Breeding Age	'a' egg Mean (S.D.)	'b' egg Mean (S.D.)	N	Difference t	P
1	42.76 (3.41)	41.07 (3.33)	160	4.49	<0.001
2	42.85 (2.98)	41.44 (3.02)	89	3.14	<0.002
3	44.11 (3.54)	42.43 (3.30)	88	3.25	<0.002
4	44.12 (3.59)	42.61 (3.55)	65	2.41	<0.05
5	44.55 (3.23)	42.55 (3.10)	62	3.52	<0.001
6	44.27 (2.91)	42.61 (2.97)	49	2.80	<0.01
7-8	43.86 (3.29)	42.03 (3.57)	76	3.29	<0.01
9-11	43.60 (3.24)	42.17 (3.57)	64	2.37	<0.02
12-19	44.30 (2.84)	42.90 (3.11)	45	2.23	<0.05

APPENDIX 6.2 : Length of Eggs laid in Clutches of Two by Individual Females in Different Years

Female Ring Number	202·8402	204·4874	202·8794	204·4075	204·4892	202·0006	EC11778	204.4917	EC11330
a. Length of 'a' Egg (mm)									
	51.4	51.3	55.8	55.2	55.5	57.3	57.8	58.9	57.1
	51.1	51.7	50.8	54.6	56.1	54.6	56.5	56.0	54.7
	51.9	51.7	53.2	54.6	56.6	56.6	57.4	58.0	62.1
	53.4	52.7	54.6	57.3	55.8	54.3	57.9	57.4	58.1
	50.4	52.7	53.7	53.7	56.5	55.9	56.1	58.5	56.5
	53.0	53.2	52.6	53.0	54.5	54.9	56.7	56.7	60.0
		50.9	55.1	54.0	54.3	55.9	57.7	57.5	58.4
		52.3	54.7		53.9	55.3	58.8	56.8	57.9
		52.8	53.8		57.4	55.6	57.9	59.0	57.4
		53.4	53.5		51.4	57.7	56.2	57.2	
b. Length of 'b' Egg (mm)									
	51.9	53.0	54.6	54.5	55.5	56.7	57.0	60.2	56.8
	52.4	50.5	50.9	54.8	53.8	54.2	56.4	56.1	55.8
	50.7	52.3	54.8	55.5	54.3	56.4	58.5	57.5	56.6
	51.9	51.2	53.7	56.5	53.6	58.6	56.7	57.2	56.1
	51.9	52.7	54.7	56.5	54.1	56.5	56.5	58.4	53.4
	53.2	51.9	52.4	54.2	55.3	55.4	56.1	58.8	57.2
		51.3	53.0	52.8	56.6	56.1	56.4	57.0	54.3
		49.9	53.3		53.7	55.5	56.0	55.8	55.2
		53.2	54.4		56.2	56.9	56.3	57.4	53.9
		51.8	55.0		55.3	55.8	58.2	58.4	

/continued

APPENDIX 6.2 : Breadth of Eggs laid in Clutches of Two by Individual Females in Different Years
(cont.)

Female Ring Number	204.4075	202.3402	EC11330	202.8794	204.4874	202.0006	EC11778	204.4917	204.4892
a. Breadth of 'a' Egg (mm)									
	40.2	39.9	38.8	408.	40.0	39.9	40.0	40.9	43.2
	40.4	39.5	41.4	40.3	41.3	40.2	40.4	41.2	42.8
	30.6	39.9	40.3	40.1	40.9	41.1	41.2	41.6	43.2
	39.3	39.5	41.2	40.7	41.3	40.4	41.2	41.7	43.0
	39.9	39.7	39.7	41.7	40.6	40.9	39.8	41.4	42.8
	38.6	40.1	40.8	40.5	40.5	41.6	41.6	41.5	42.8
	38.9		40.1	40.7	39.9	40.4	41.1	40.7	43.3
			40.1	40.5	40.5	41.2	41.3	41.6	43.2
			40.0	39.8	39.9	40.3	41.4	41.9	42.8
				40.2	41.6	40.2	41.2	41.1	43.0
b. Breadth of 'b' Egg (mm)									
	40.2	39.4	38.8	41.0	41.6	40.5	39.9	40.9	43.4
	40.7	39.5	39.1	39.9	41.1	40.3	39.6	41.2	43.3
	40.4	38.0	39.6	41.4	39.0	40.0	41.6	41.1	42.5
	39.5	39.0	40.2	39.5	40.1	39.5	40.8	40.8	43.0
	39.9	39.3	38.7	40.5	41.9	39.8	41.3	41.5	43.9
	38.8	40.5	39.8	40.1	40.3	40.1	42.0	40.8	43.0
	37.6		39.8	41.0	40.6	41.0	40.7	41.2	43.1
			39.9	40.5	39.0	40.5	40.8	40.5	42.1
			38.4	40.5	40.1	34.4	40.0	41.5	43.3
				40.8	40.1	39.9	40.6	40.8	43.3

APPENDIX 7.1 : The Number of Chicks Hatched and Fledged per Pair by Females of Differing Ages

Female Breeding Age (years)	Number hatched/pair					Number fledged/pair					
	0	1	2	3	mean	0	1	2	3	mean	N
1	80	93	137	5	1.21	95	107	109	4	1.07	315
2	39	38	96	11	1.43	44	59	79	2	1.21	184
3	18	43	92	10	1.58	28	46	84	5	1.41	163
4	15	34	74	9	1.58	26	44	59	3	1.30	132
5	16	17	63	14	1.68	19	26	56	9	1.50	110
6	12	21	46	13	1.65	15	28	43	6	1.44	92
7-8	18	32	65	15	1.59	23	38	58	11	1.44	130
9-11	25	16	55	16	1.55	29	22	50	11	1.38	112
12-19	14	10	48	4	1.55	17	16	41	2	1.37	76

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